

STUDIES ON AMPHISBAENIDS
(AMPHISBAENIA, REPTILIA)

1. A TAXONOMIC REVISION OF THE
TROGONOPHINAE, AND A FUNC-
TIONAL INTERPRETATION
OF THE AMPHISBAENID
ADAPTIVE PATTERN

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INTRODUCTION

THE ACRODONT AMPHISBAENIDS, or Trogonophinae, form a small group of highly modified species apparently adapted for a subterranean existence in arid regions. Four genera presently occupy discrete ranges in the region between northern Africa and Persia. The "ecology of collectors" has made most of the species excessively rare in museums.

In 1954 the Carnegie Museum received a series of five specimens of *Diplometopon zarudnyi* Nikolski, 1907, a form that had been omitted from the last revision of the Amphisbaenia (Vanzolini, 1951, MS). Detailed examination of this form focused my interest on the group. A check of specimens available in a number of museum collections showed that a revision of the Trogonophinae and a comparative description of some aspects of their anatomy were both possible and desirable. These have been attempted in the first part of the present studies.

Beyond the need for taxonomic analysis, it proved to be of interest to take a closer look at some of the fundamental adaptive requirements and their functional solutions by these species. It was hoped that analysis might lead to a better understanding of the specific modifications of the several lines. Because it has thus far proved impossible to obtain any live trogonophines, the second half of the present paper had to be based in large part on the pleurodont Floridian species *Rhineura floridana* (Baird), and the results extrapolated. The analysis presented in the second section thus forms more of a *Fragestellung* than a solution of the various problems encountered by burrowing animals.

The analysis was started because of the conviction that a thorough understanding of the characters and adaptive patterns on the specific and generic level is essential for a natural classification of suprageneric categories of reptiles in general and squamates in particular. Beyond this it appears to be most useful to gain an understanding of the most highly specialized members of a group. Such understanding may permit recognition of the initial modification of the most "primitive" or least specialized members.

Thanks are due to Mr. Charles M. Bogert, Dr. Richard G. Zweifel, and Mrs. Theresa McKnight of the American Museum of

Natural History (A.M.N.H.), the late Dr. Joseph R. Slevin and Mr. Alan E. Leviton of the California Academy of Sciences (C.A.S.), Mr. Neil D. Richmond of the Carnegie Museum (C.M.), Dr. Robert F. Inger and Mr. Hymen Marx of the Chicago Natural History Museum (C.N.H.M.), Mr. Arthur Loveridge and Dr. E. E. Williams of the Museum of Comparative Zoölogy (M.C.Z.), Dr. Lothar Forcart, Naturhistorisches Museum, Basel (N.M.B.), Drs. Robert Mertens and Konrad Klemmer of the Senckenbergischen Naturforschender Gesellschaft (S.M.F.), and Dr. Doris M. Cochran of the United States National Museum (U.S.N.M.) for the loan of, and permission to dissect or information on, specimens in their care. The specimens are referred to by the abbreviations listed in parentheses.

A number of friends have placed me in their debt by reading and commenting on portions of the manuscript. Among these are Dr. Ernest E. Williams of the Museum of Comparative Zoölogy, Mr. Walter Bock and Dr. Thomas Parsons of Harvard University, Mr. Charles M. Bogert and Dr. Samuel B. McDowell, Jr., of the American Museum of Natural History, Mr. D. Dwight Davis of the Chicago Natural History Museum, Dr. Kenneth W. Cooper and Dr. and Mrs. Coleman J. Goin of the University of Florida, Dr. Wilfred T. Neill of Ross Allen's Reptile Institute, and Dr. Angus d'A. Bellairs of St. Bartholomew's Medical College (London). I am especially indebted to the artists who prepared the illustrations. Their names have been indicated in the legends. Thanks are also due to various individuals who donated live specimens of *Rhineura floridana* for study, and to Mr. Howard Campbell for technical assistance.

The initial part of the descriptive work was performed at Harvard University while I was on a terminal Predoctoral Fellowship of the National Science Foundation. The functional study was completed while I was on a Postdoctoral Research Fellowship of the University of Florida at their Department of Biology, and the manuscript was prepared at the University of Buffalo. I am most grateful both to the granting institutions and to the departments that furnished facilities for this study.

A TAXONOMIC REVISION OF THE TROGONOPHINAE

THE TROGONOPHINAE have been considered a distinct category of the amphisbaenids by most authors since and even before the publication of Boulenger's "Catalogue of the lizards" (1885). The separation was based primarily, if not exclusively, on the acrodont dentition which had first been reported by Kaup in his diagnosis of *Trogonophis wiegmanni* (1830).

Loveridge revised the African species of amphisbaenids in 1941 and listed three acrodont genera with a total of six species (including mention of one restricted to Arabia). Vanzolini, in his revision of the Amphisbaenidae (1951, MS), followed Loveridge's arrangement but placed the acrodont forms in a separate subfamily, the Trogonophinae. He omitted any mention of the Irano-Arabian species *Diplometopon zarudnyi* Nikolski, 1907, a form that had received but cursory mention in the literature since its description. Later and in parallel with the first phase of the present study Haas (1957, p. 71) resurrected *Diplometopon* on the basis of 29 specimens, but without any discussion.

The acrodont forms recognized at the time of Haas's study were the following:

Trogonophis wiegmanni Kaup, 1830. Range: Northwest Africa, from the Moroccos and Tangiers to Algeria and Tunisia.

Pachycalamus brevis Günther, 1881. Range: Socotra Island.

Agamodon anguliceps Peters, 1882. Range: Somalia.

Agamodon compressus Mocquard, 1888. Range: Somalia.

Agamodon arabicus Anderson, 1901. Range: Abian County, Yemen.

Diplometopon zarudnyi Nikolski, 1907. Range: Northern Saudi Arabia, southern Iraq, extreme western Iran.

The races *Trogonophis wiegmanni marocana* Werner, 1931, from Chella, Rabat, Morocco, and *Agamodon anguliceps immaculatus* Calabresi, 1927, from Afghedud,

Somalia, had been placed in the synonymy of *T. wiegmanni* and *A. compressus* by Loveridge (1941).

Maps giving the distribution of the species and all localities referred to in the text are given in figures 1 and 2.

The present study was designed to determine whether *Diplometopon zarudnyi* is a valid species with acrodont dentition, whether the other described forms are valid, and finally what the relation is of these species to one another and to the other amphisbaenids. For this purpose I examined and here describe the integument (containing the more conventional taxonomic characters), the skull and anterior vertebral column, the hyoid, and the shoulder girdle of one representative of each genus. As the literature contained an indication of peculiarities in the arrangement of lungs and dermal innervation within the Trogonophinae, these items were also examined and are briefly commented on as bearing upon the last aspect of the problem.

In the descriptive section the sequence of comparison has always been *Trogonophis wiegmanni*, *Pachycalamus brevis*, *Diplometopon zarudnyi*, *Agamodon anguliceps*. This order was selected entirely for the sake of convenience, as it is in approximate relation to the degree of modification of the several species and hence simplifies the description. It does not imply any phylogenetic or other sequence, and divergences have been emphasized where necessary.

An exception to the sequence has been made in the discussion of the integument, in which the description of that of *Diplometopon* is presented first. This species has not been adequately discussed since Nikolski's remarks, which were based on a single specimen. The need for an adequate redescription has also prompted me to present a more detailed discussion of the other aspects of this species.

MATERIAL

The specimens examined for this study are here listed by museum numbers alone, as

locality data can be extracted from the Summary List of Species.

TROGONOPHIS WIEGMANNI

Two specimens (M.C.Z. Nos. 7430 and 27373) were dissected, and two previously prepared skulls (M.C.Z. No. 6001 and U.S.N.M. No. 12318) were used for the checking of the dissection. Upon completion of the study, Dr. A. d'A. Bellairs arranged for the gift of another specimen (A.M.N.H. No. 81892; for data, see Bellairs and Shute, 1954, p. 225) which was used for the checking of the presence of an epipterygoid and the internal structure of the semicircular canals. A.M.N.H. Nos. 1102 and 1103 were checked for external characters.

PACHYCALAMUS BREVIS

Two specimens (A.M.N.H. No. 73424 and U.S.N.M. No. 60653) were dissected, and external characters were checked on A.M.N.H. No. 73423.

AGAMODON ANGULICEPS

This is the only species of the genus represented in North American collections. Only two specimens of it were available. One (M.C.Z. No. 10784) was entirely dissected, while one side of the second (M.C.Z. No. 38697) was dissected to check a number of characters.

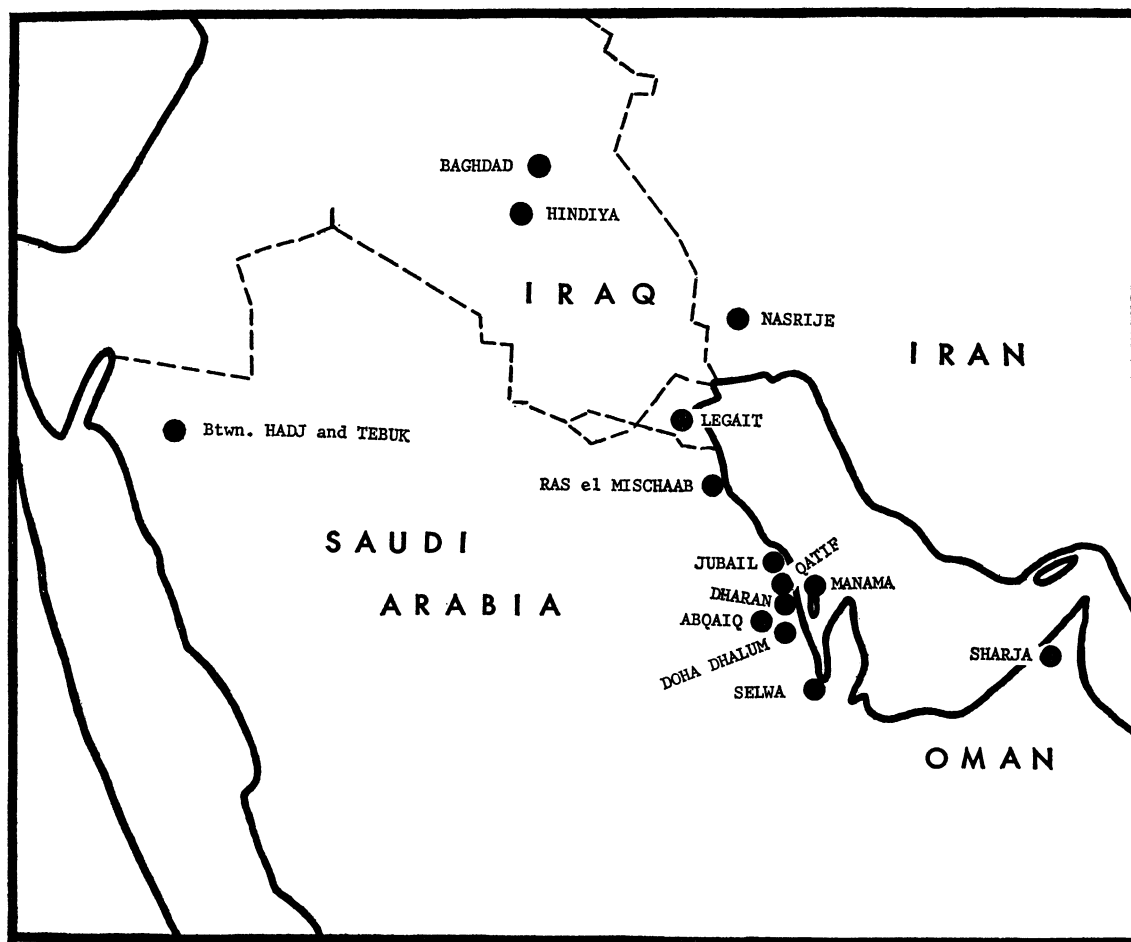


FIG. 1. Map showing localities from which specimens of *Diplometopon zarudnyi* have been examined or have been recorded in the literature.

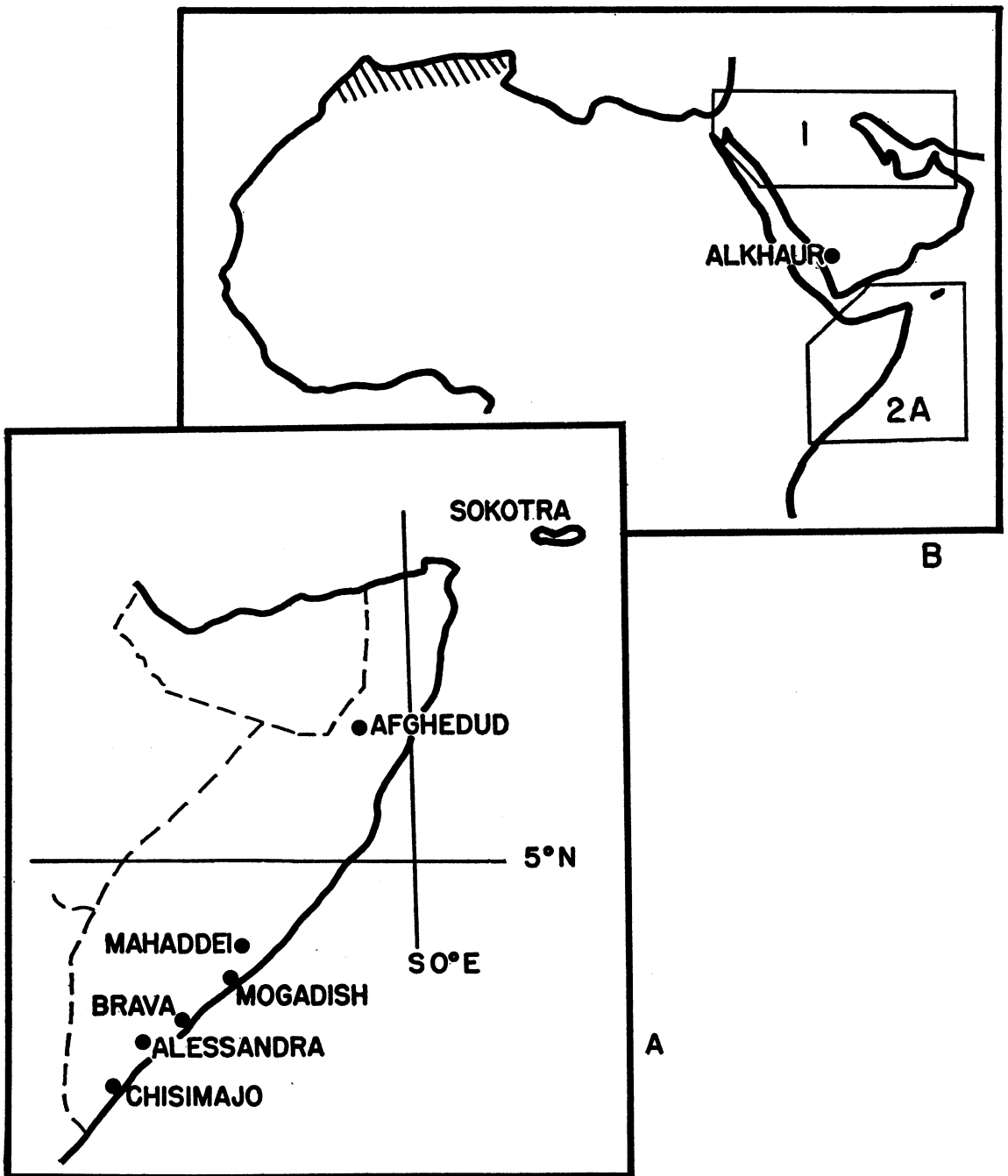


FIG. 2. A. Map showing localities for the three species of *Agamodon*. B. Map of northern Africa and southwest Asia, showing the ranges of the four genera (*Trogonophis*, hatched lines) and the areas given in detail in figures 1 and 2A.

DIPLOMETOPON ZARUDNYI

Five specimens (C.A.S. No. 34588, C.M. Nos. 33503 and 33504, C.N.H.M. No. 74007, and M.C.Z. No. 57176) were dissected. The first of these was a juvenile, while the second and the last were very poorly preserved adults. Thirty specimens (C.A.S. Nos. 84274, 84343–

84347, 84349–84354, 84373, 84405, 84406, 84426, 84454, 84501, 84529, 84534, 84539, and 84559, C.M. Nos. 33505, 33506, and 33522, C.N.H.M. Nos. 41955 and 74008, U.S.N.M. Nos. 121594, 127998, and 132401) were available for the checking of external characters.

DISCUSSION OF CHARACTERS

SHAPE AND SCUTELLATION
OF HEAD

DIPLOMETOPON

The proportions and relations of the cephalic scales of this species are shown in the three views of figure 3. Only minor differences exist between these views and the line drawings published by Nikolski and Haas. Such differences as there are concern the proportions of some of the minor scales. (It might be noted that the angle of view is different in Haas's drawings.)

The series of specimens shows only minor variation of the scutellation. Besides the occasional fusion of the last two lower labials (C.M. No. 33522), there is some variation in the length of the groove dividing the "post-frontal"¹ scale. This groove generally bisects the posterior one-third to one-half of the scale, though in one specimen (C.M. No. 33522) it extends only for one-third, and in another (C.A.S. No. 84345; cf. Haas), the scale is completely bisected. The variation seems to be individual, as indicated by a specimen (C.M. No. 33506) that has a portion along the length of the groove closed by fusion.

A remark should be made about the presence of a small semicircular scale, here referred to as the interlabial. This forms the edge of the upper lip and lies in the posi-

tion of the "true" rostral according to the customary definition. Its presence points to the pitfalls encountered in the placing of too much reliance upon "homologies" of amphisbaenid scales.

The eye is clearly visible and lies deep to the dorsal half of the ocular scale. It looks out through a transparent window, which lies just dorsal to a partial fold crossing the ocular. There seems to be some slippage of the skin over the internal tissues, as the eye is often more or less displaced from the window. In at least one specimen (C.A.S. No. 84588) the anterior edge of the eye is visible through the pre-ocular scale.

The drawings make further description of scutellation unnecessary. However, it may be useful to stress the characteristic head shape of this species.

The head of *Diplometopon* shows a smooth transition from the horizontally spatulate rostrum to the cylindrical trunk. All sections along planes passing at right angles to the longitudinal axis of the body will thus show a continuous increase in cross-sectional area. Two geometric changes describe the size reduction from trunk to rostrum: (1) The ventral and lateral surfaces show a gradual and radially symmetrical conic reduction. (2) The rostral shield may be represented by a unilaterally warped plane truncating this cone.

The rostral edge is actually formed almost entirely by the intersection of the dorsal and ventral aspects of the head, so that the lateral surfaces do not meet each other. The rostral shield covers the entire anterior part of the head, ascending at an angle of 60 degrees. (Here and throughout this paper angles are measured between a surface and the longi-

¹ The terminology of Loveridge, Vanzolini, and others is followed here even though, as already recognized and mentioned by previous authors, many of the scales referred to are probably not homologous to those to which these terms are applied in various lizards. Beyond this there is considerable doubt regarding their homologies even within the Amphisbaenidae (cf. Loveridge, 1941, p. 355).

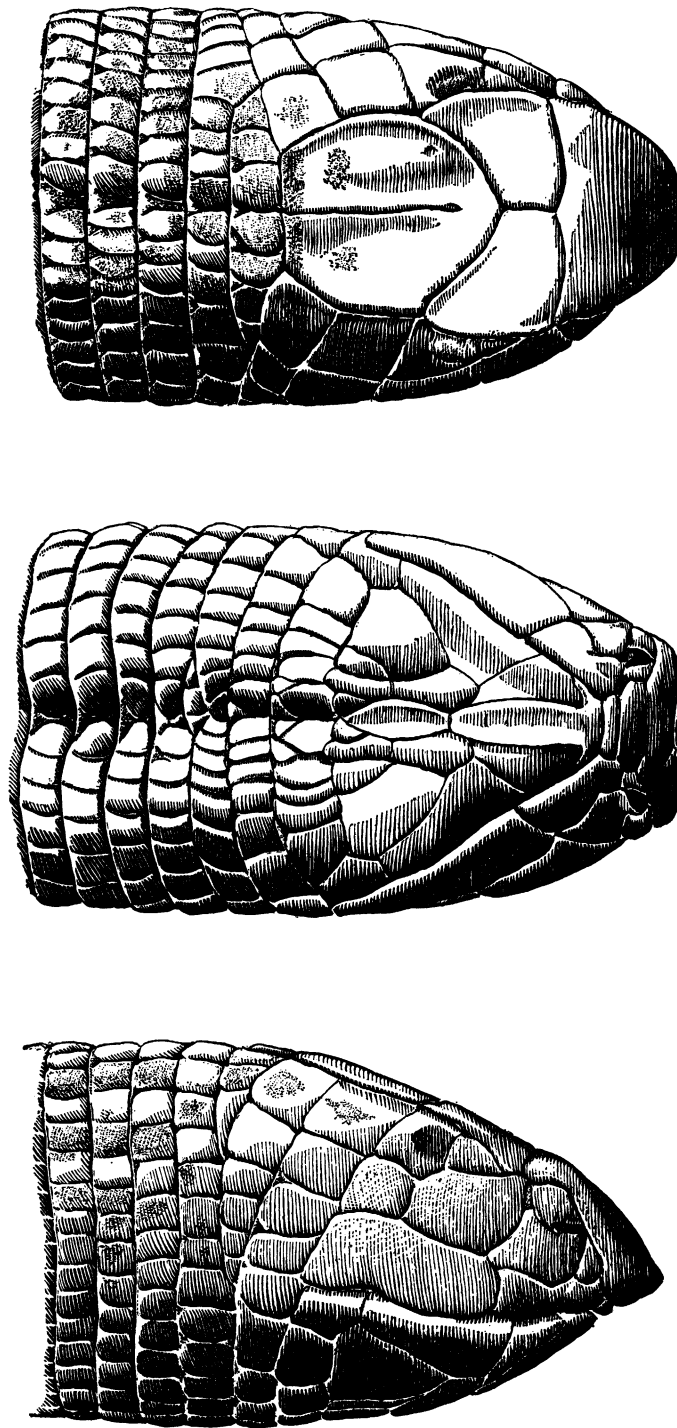


FIG. 3. Dorsal, ventral, and lateral views of the anterior integument of *Diplometopon zarudnyi* (C.M. No. 33505). Drawn by S. B. McDowell.

tudinal axis of the trunk.) The rostral angulation flattens out gradually so that the shield has an angle of 30 to 45 degrees at its raphe with the prefrontals. The curvature continues onto the large frontal scale, which at its posterior raphe lies almost parallel with the longitudinal axis.

The ventral aspect of the head sweeps back sharply from the rostral edge, which is held but slightly above the ventral surface of the animal. The lower jaw fits into a recess behind the upper labials. The largest and structurally most important scale of the lower jaw is the T-shaped symphyseal, which has an elongate and roughly oval central portion that forms much of the chin.

The dorsal edge of the lateral surface is formed by the clearly marked canthus rostralis. Along its anterior edge the side of the face slopes mediad ventrally. Behind the anterior part of the frontal the face falls vertically.

OTHER ACRODONT FORMS

Line drawings of the anterior scutellation of the three other species are given in figure 4. It can immediately be seen that *Trogonophis* is least specialized in general appearance, with the degree of modification of head shape and scutellation increasing towards *Pachycalamus* and *Agamodon*.¹ *Diplometopon* appears to be slightly less specialized than *Agamodon*, though closest to this form in a number of characters.

A comparison of the scales by number and presence as single or paired units is given in table 1. The superficial resemblance between the characters given for *Diplometopon* and those for *Pachycalamus* was probably what prompted Boulenger to consider the two species congeneric.

Certain trends are apparent when *Trogonophis*, *Pachycalamus*, *Diplometopon*, and *Agamodon* are compared in that order. Most striking is the decrease in the number of cephalic shields and the corresponding increase in the size of the anterior ones. Then there is an increase in the facial angle and, correlated with this, a reduction in the length of the head, a change from a rounded snout to a strongly marked horizontal "shovel-

edge" on the rostral, and a lowering of the level of the rostral tip from the midbody elevation to the ventral surface.

The head of *Trogonophis* is completely rounded and slightly compressed dorsoventrally, so that there is an oval cross section at the level of the eye. In *Pachycalamus* there has been some shortening, and the rostral-prefrontal-frontal surface inclines at an angle of 30 degrees at its rostral end and rises in a smooth curve to the dorsal junction. The rostrum presents a well-defined spatula anteriorly, but the rostral edge protrudes far beyond the tip of the lower jaw. There is no canthus rostralis, so that a cross section at the level of the eye would also be elliptical.

Diplometopon shows further curvature of the rostrofrontal surface, a rostral tip but slightly anterior to the mouth, and a marked canthus rostralis, which would give a cup-shaped cross section at the level of the eye. The species is also remarkable in possessing an interlabial scale. *Agamodon* continues all these trends, but there is no interlabial.² The canthus rostralis is very strongly marked and reaches its fullest development in *A. compressus*, in which the edges are strongly produced and extend dorsolaterally from the concave frontal surface.

POSTERIOR INTEGUMENT

DIPLOMETOPON

The body segments are rectangular, from one to two times as long as wide, and are arranged in regular annuli around the body. There is occasional alignment of segments along the long axis of the body, although this is normally not true. The large majority of annuli are as wide dorsally as ventrally; only a few of the nuchal ones are wider dorsally.

The annuli show a slight overlap, with the anterior edge of each annulus bent below the trailing edge of the next craniad annulus. The degree of protrusion varies and may be dependent upon relative contraction of the dermal muscles during killing and fixation. However, it is almost always possible to distinguish craniad and caudad edges.

² Mocquard's not very satisfactory illustration of *A. compressus* does show a line crossing the rostral in his ventral view of the head. However, his detailed discussion does not mention any such suture.

¹ Here and throughout the descriptive section reference is to *Agamodon anguliceps*, unless stated otherwise.

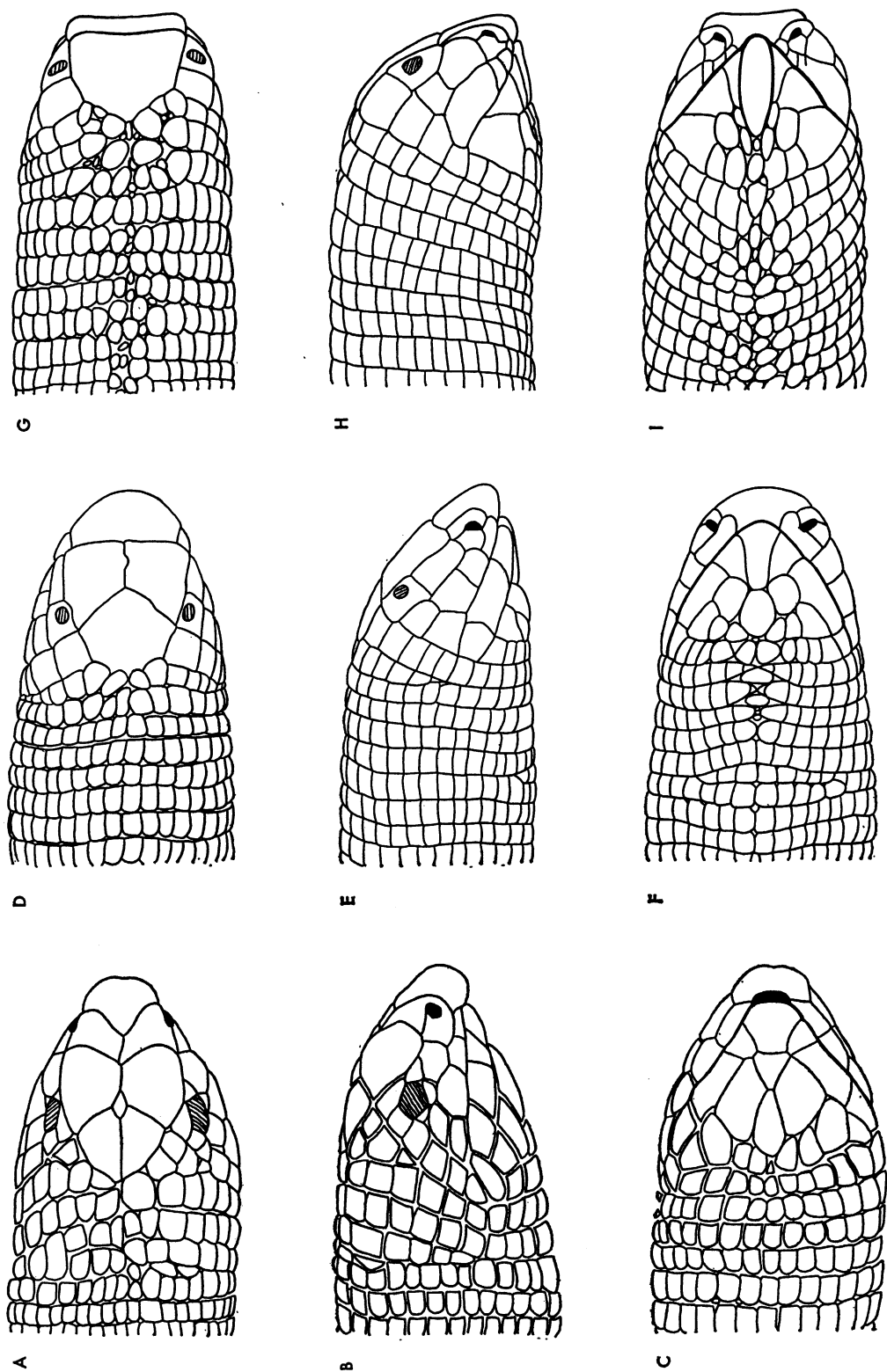


FIG. 4. Dorsal, lateral, and ventral views of anterior integument. A-C. *Trogonophis wiegmanni* (A.M.N.H. No. 81892). D-F. *Pachycalamus brevis* (M.C.Z. No. 10785). G-I. *Agamodon anguliceps* (M.C.Z. No. 10784). The azygous scale between frontals and post-frontals of *Trogonophis* often shows incomplete borders and other variation. Drawn by M. Franson.

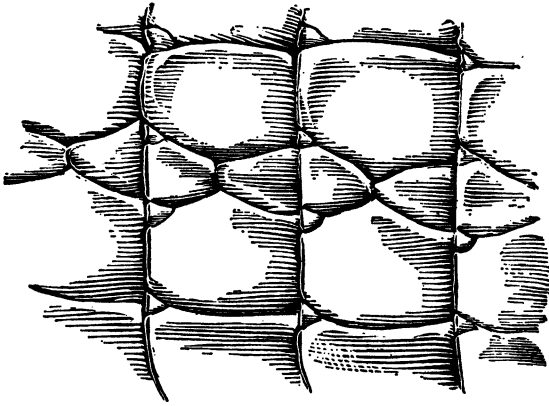


FIG. 5. View of dorsal groove of *Diplometopon zarudnyi* (C.M. No. 33505), to show rounding of bordering scales and insertion of small triangular scales. Drawn by S. B. McDowell.

There is a faint dorsal, as well as a strong ventral, groove. These grooves (see fig. 5) are marked by a slight widening of the segments bordering them on each side. The segments have their facing sides rounded or pointed, with the apices of opposite segments in contact across the groove. A pair of small triangular segments fills the gaps.

Along the ventral groove the annuli intersect at an obtuse, backward-pointing angle. Each annulus thus does not lie in a single plane normal to the long axis of the trunk, but has two halves in different planes, with their line of intersection lying in the sagittal plane.

The left and right half-annuli are generally aligned, though such is not always the case. There are also a number of instances in which there is an additional dorsal or ventral half annulus.

The patch of modified segments surrounding the anal region (fig. 6) is of an elongate oval shape. The ventral portions of some of the annuli bend around the anal region, so that only two to three of these actually drop out ventrally. Part of the compensation takes place by a reduction in size or a total disappearance of the ventral segments of the second and third pre-anal annuli. The four central segments of the semicircular first pre-anal annulus bear pre-anal pores in both sexes (two males have five and six pre-anal pores, respectively). These segments are

followed by the roughly circular anal patch, composed of six to eight elongate scales in fan-shaped symmetry around the midventral line. The elongate elements are often "broken," and, when they are counted, it is necessary to reconstruct the "fragments" lying in a line. Posteriorly these scales are met by a

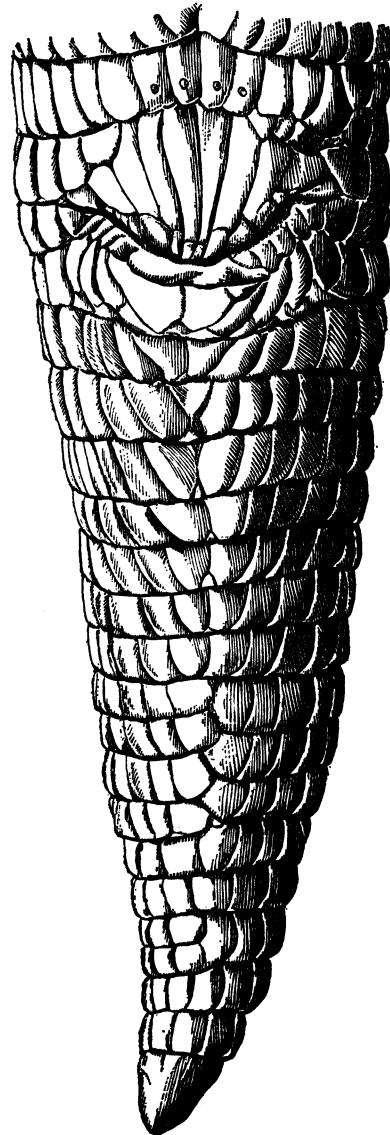


FIG. 6. Ventral view of cloaca and caudal region of *Diplometopon zarudnyi* (C.M. No. 33505). Note the small scales bordering the cloacal slit; several rows of these (not visible here) line the cloacal sphincter. Drawn by S. B. McDowell.

varying number of pentagonal to triangular scales which interdigitate slightly between them and form the true anals.

The cloacal slit is lined by two complete rings of small scales (not shown in the drawing) that lie within it and are invisible when it is closed. They seem to be readily prolapsed by the injection of fluid attendant upon preservation. Caudad the slit is followed by two rows of small modified segments, after which the regular annuli continue. The last two annuli of the caudal segments are more or less fused, giving the impression of a blunt conical spine. Both dorsal and ventral grooves are extremely faint on the tail, and the ventral groove in particular is marked only by a double row of slightly enlarged segments.

Certain meristic data regarding the body integument are listed in table 1. The data represent composites, including values from the literature.

OTHER ACRODONT FORMS

It is again possible to establish a sequence from *Trogonophis* to *Pachycalamus* to *Agamodon*, yet *Diplometopon* is unique in some characters, such as the presence of pre-anal pores in both sexes. The general trends of the sequence are those of the loss of lateral and the acquisition of ventral grooves, the acquisition of pre-anal pores in the males, the loss of specially modified neck annuli, and the shortening of the body relative to the tail (fig. 7).

The presence of lateral grooves in *Trogon-*

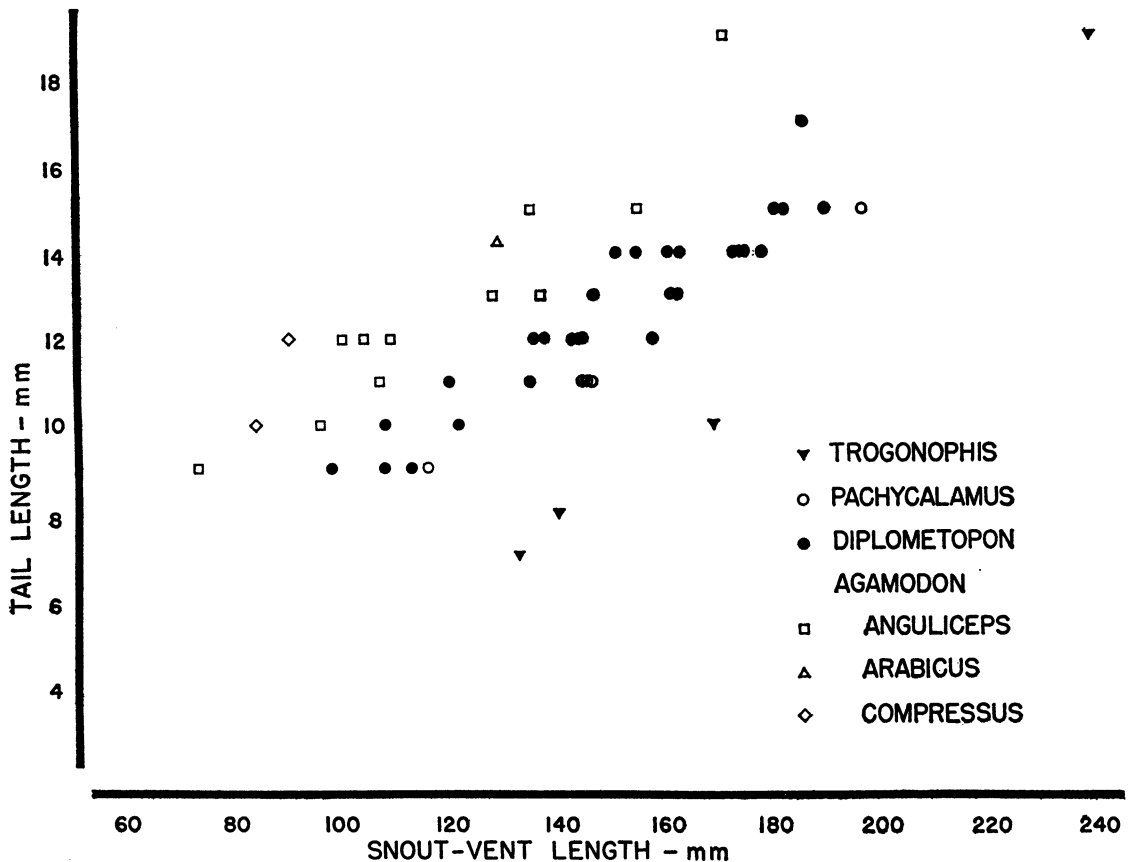


FIG. 7. Graph of the snout to vent length versus tail length for available specimens of the Trogonophinae. Data cited in the literature for these genera have also been added (*Trogonophis*, Loveridge, 1942. *Pachycalamus*, Boulenger, 1885. *Diplometopon*, Nikolski, 1907. *Agamodon*, Peters, 1882; Mocquard, 1888; Anderson, 1901; Calabresi, 1915, 1927; Scortecci, 1929, 1931.) All measurements were rounded off to the nearest millimeter.

TABLE 1
SCUTELLATION OF THE TROGONOPHINAE

	<i>Trogonophis wiegmanni</i>	<i>Pachycalamus brevis</i>	<i>Diplo-metopon zarudnyi</i>	<i>Agamodon anguliceps</i>	<i>Agamodon arabicus</i>	<i>Agamodon compressus</i>
Head region						
Number of rostrals	1	1	1	1	1	1
Number of frontals	2 ^a	2 ^a	2	1	1	1
Number of post-frontals	2	1 ^b	1 (split)	0	0	0
Interlabial	Absent	Absent	Present	Absent	Absent	Absent?
Do nasals touch?	Yes	No	No	No	No	No
Canthus rostralis	Absent	Faint	Marked	Marked	Marked	Marked
Position of rostral tip	Raised > $\frac{1}{2}$	Raised > $\frac{1}{2}$	On ventral line	On ventral line	On ventral line	On ventral line
Body region						
Cross section of trunk	Round	Round	Round	Round	Compressed laterally	Compressed laterally
Length of neck annuli compared to trunk annuli	Smaller	Equal	Equal	Equal	Equal	Equal
Position of grooves	Faint dorsal +lateral	Ventral	Dorsal +ventral	Dorsal +ventral	Dorsal +ventral	Dorsal +ventral
Number of ventral annuli to anals	135-156	165-173	172-180	123-137 (143)	161	144-160
Number of post-anal annuli	12-15	16-20	16-20	12-19	18	22-23
Segments per mid-body annulus	48-64	48-53	48-54	(46) 50-51	55	—
Number of preanal pores						
Male	0	2+2	4 (6)	2-6	0 (Sex?)	2 (Sex?)
Female	0	0	4	0	—	—
Number of anals	6-10	6-8	6-10	6-10	?	?

^a Prefrontal of Loveridge (1941).

^b Frontal of Loveridge (1941).

ophis alone would seem to be a primitive character in the acrodont group, as such grooves are found in all pleurodont amphisbaenids (Vanzolini, MS, p. 85).¹ Only traces

¹ A check of this statement by an examination of all the species in the collection of the Museum of Comparative Zoölogy confirms it for 49 species representing 17 genera. However, in *Cadea blanoides* there was no real fold and but a weak one in *C. palirostrata*. In both of these species there is a modified zone along the lateral midline where a number of half-annuli run out. The fold or division skips back and forth between non-aligned segments, which are slightly reduced along the midline.

of a dorsal sulcus can be noted in *Trogonophis*. A groove-like continuation of the suture dividing the paired cephalic shields fades out beyond the neck and reappears at intervals along the trunk. The modification of the segments adjoining the groove is very irregular. All grooves stop at the base of the tail.

In *Trogonophis* there are no pre-anal pores in either sex. The anal patch is simple and composed of a single row of large squarish anals. The slit is lined with segments.

In the anterior region of *Trogonophis*, the segments of the first five to seven annuli following upon the row in contact with the last lower labials are reduced in size and differentiated from the more regular segments of the posterior rows. The dorsal segments of the annuli do not show the reduction so clearly.

Pachycalamus has only a weakly marked ventral groove and neither lateral nor dorsal grooves. The ventral groove stops before the anal region. There are two pre-anal pores in males, but the segments bearing them are separated by two plain segments. The anterior annuli are not modified.

Diplometopon has both dorsal and ventral grooves, which continue faintly onto the tail. It also has a somewhat more complicated segmental arrangement around the cloaca. Both males and females have four (to six) pre-anal pores in a continuous series.

The genus *Agamodon* shows dorsal and ventral grooves with a segmental arrangement that appears at first glance to be unique in the amphisbaenids. Thus Loveridge (1941, p. 366) states that the "dorsal and ventral rows are strongly differentiated from the lateral segments." However, Peters' excellent figures of the type of *A. anguliceps* show that the apparent differentiation is superficial. The lateral half-annuli intersect at an angle as in *Diplometopon*. Instead of stopping at a "groove" their influence appears to continue for some distance beyond the intersection, and the resulting pattern is actually formed by the superposition of two segmental grids. This explanation holds for both dorsal and ventral patterns. A simple version of the phenomenon is shown in the nuchal region of *Diplometopon* (fig. 3). In all cases there is a rounding or hexangulation of the rectangular segments, coupled with the presence of an increased number of small to tiny intermediate scales, formed from, and in the place of, the "cut-off" corners.

The two specimens of *A. anguliceps* seen by me have about five dorsal and seven ventral rows of modified scales, but the figures are approximate, as it is difficult to tell where the count should be started. The grooves disappear at the base of the tail. Anderson refers to only three dorsal rows in *A. arabicus*, but his diagrammatic figure

(1901, pl. 14, fig. 2) shows that the situation is similar to the one described here. Mocquard's illustrations (1888, pl. 11, fig. 2; also Loveridge, 1941, fig. 4) are less clear regarding the pattern in *A. compressus*, which may be owing to the decidedly poorer draftsmanship of his artist, or to a more advanced and confusing pattern.

The cloacal region of *Agamodon* is closely similar to that of *Diplometopon*. As far as is known, there are pre-anal pores in males only. The pores are always in a continuous series.

COLOR PATTERN

Plate 45 shows the dorsal and ventral color pattern of preserved specimens of the four species available for comparison. *Trogonophis* again appears distinct, because most specimens of this species are not countershaded. Loveridge (1941, p. 362) mentions a color variant which is "uniform fuliginous grey, a little lighter below" (cf. Hediger, 1935, 1937). All other species of acrodont amphisbaenids are clearly countershaded, though such patterns in no case affect the head, which is unicolored in all four genera. No trends can be noted among the four genera.

Trogonophis shows speckled markings produced by the dark pigmentation of from one to six segments along an annulus. There is no coordination of pattern between adjacent annuli. (See Hediger, 1935, fig. 2, for photographs of living specimens.)

Pachycalamus is uniformly brown dorsally, except for the head which is yellowish white, as is the ventral surface.

Diplometopon has a unicolored brown head and a slightly lighter body color. The dorsal and lateral surfaces are marked with irregular speckles of varying size and arrangement. On most specimens the speckles occupy only single segments. The ventral surface is immaculate. (See Schmidt and Inger, 1957, and Mertens, 1959, for photographs of living specimens.)

Agamodon anguliceps (*sensu* Loveridge) also has a mottled pattern. The species is yellowish white dorsally, with darker brown markings that may "coalesce to form an interrupted longitudinal line" (Loveridge, 1941, p. 367). Most of the spots cover more



Color patterns of the four species of the Trogonophinae. 1. *Trogonophis wiegmanni* (A.M.N.H. No. 81892). The skin of the midbody region has been spread to demonstrate the continuity of pattern around the body and the lack of countershading. 2. *Pachycalamus brevis* (M.C.Z. No. 10785). 3. *Diplometopon zarudnyi* (C.M. No. 33506). 4. *Agamodon anguliceps* (Carl Gans collection, from the Révoil collection, Museum National d'Histoire Naturelle, Paris). Approximately four-fifths natural size.

than 10 segments. The ventral surface is immaculate.

Agamodon arabicus has the "majority of the segments. . . generally partially or wholly marked by a dark brown spot, absent, however, from the lower half of the sides and ventral aspect" (Anderson, 1901, p. 141). The head plates are yellowish.

Agamodon compressus and *A. anguliceps immaculatus* are described as uniformly dark dorsally and lighter ventrally.

SKULL

GENERAL COMPARISON

There are several orders of similarity and difference to be discussed in an analysis of this type. The first concerns differences in shape and structure of the individual elements. Another level of comparison, and one on which major emphasis is here placed, involves differences in the shape and arrangement of the skull as a whole.

A number of characters indicate the primitive position of the skull of *Trogonophis* among the forms examined. This species is unique in amphisbaenids in the possession of an epipterygoid and has retained the prefrontals, which are found in all pleurodont but in no other acrodont amphisbaenids. The head shape of *Trogonophis* also reminds one most strongly of that of such relatively unmodified pleurodont amphisbaenines as *Blanus*¹ and *Amphisbaena* (cf. Vanzolini, MS). The skull of *Trogonophis* has therefore been used as the basis for a comparison of the acrodont skulls by the method of deformed coordinates. In examining figure 8, one must bear in mind that this type of diagram suffers from two major defects. The first of these stems from the fact that a three-dimensional structure is compared on the basis of a two-dimensional surface and that (lateral) deformations in the third dimension cannot be taken into account. It might also be argued that this type of diagram has little meaning

when applied to a composite structure rather than to a single bone. However, the diagrams do yield a simple method of visual comparison, which may be useful as long as its limitations are kept in mind.

It is again possible to rank the skulls in the morphological sequence *Trogonophis*-*Pachycalamus*-*Diplometopon*-*Agamodon* (also see table 2). The three major trends in the overall shape of the skull demonstrated by this are (1) a shortening of the skull, (2) an angulation of the facial versus the occipital region, with a consequent spatulate widening of the rostral tip, and (3) a relative broadening of the occipital region, with consequent lateral displacement of the semicircular canals. The deformed coordinate diagrams confirm these trends and indicate that the angulation of the skull is achieved partly by an increase in the parietal height.

The diagrams also give a very good indication of the differences in the relative deformation of the various cranial elements of the "advanced" forms. This suggests the superficial nature of the similarity between the skull of *Diplometopon* and that of *Agamodon*, and shows that the "intermediate" condition of *Pachycalamus* cannot be interpreted as the relict stage of a phylogenetic pathway. The external similarity of the skulls has been produced by changes of different parts.

Beyond the trends in the shape of the entire skulls, the morphological "series" also demonstrates several, quite possibly correlated, changes of individual elements. There are the decrease in the length of the tooth-bearing aspect of the maxilla and in the number of maxillary teeth, the reduction of the participation of the ectopterygoid on the palatal plane (to the apparent total loss of this bone in *Agamodon*), and the increased exposure of the frontal on the facial plane.

A quite remarkable series of changes occurs in the size and arrangement of stapes and extracolumella. There is, first, a tendency towards an enormous enlargement of the stapedia foot-plate. Second, the columellar portion increases in size and extends laterally beyond the level of the quadrate. Finally, the cartilaginous, rod-shaped extracolumella, which initially lies next to the mandible, thickens, shortens, expands vertically, and

¹ This resemblance prompted Fürbringer (1900, p. 619) to include *Trogonophis* and *Blanus* in his provisional subfamily "Trogonophinae s. Amphisbaenidae oxyurae." He contrasted this group to the "Amphisbaeninae s. Amphisbaenidae amblyurae" under which heading he lumped the genera with vertically or horizontally compressed skulls.

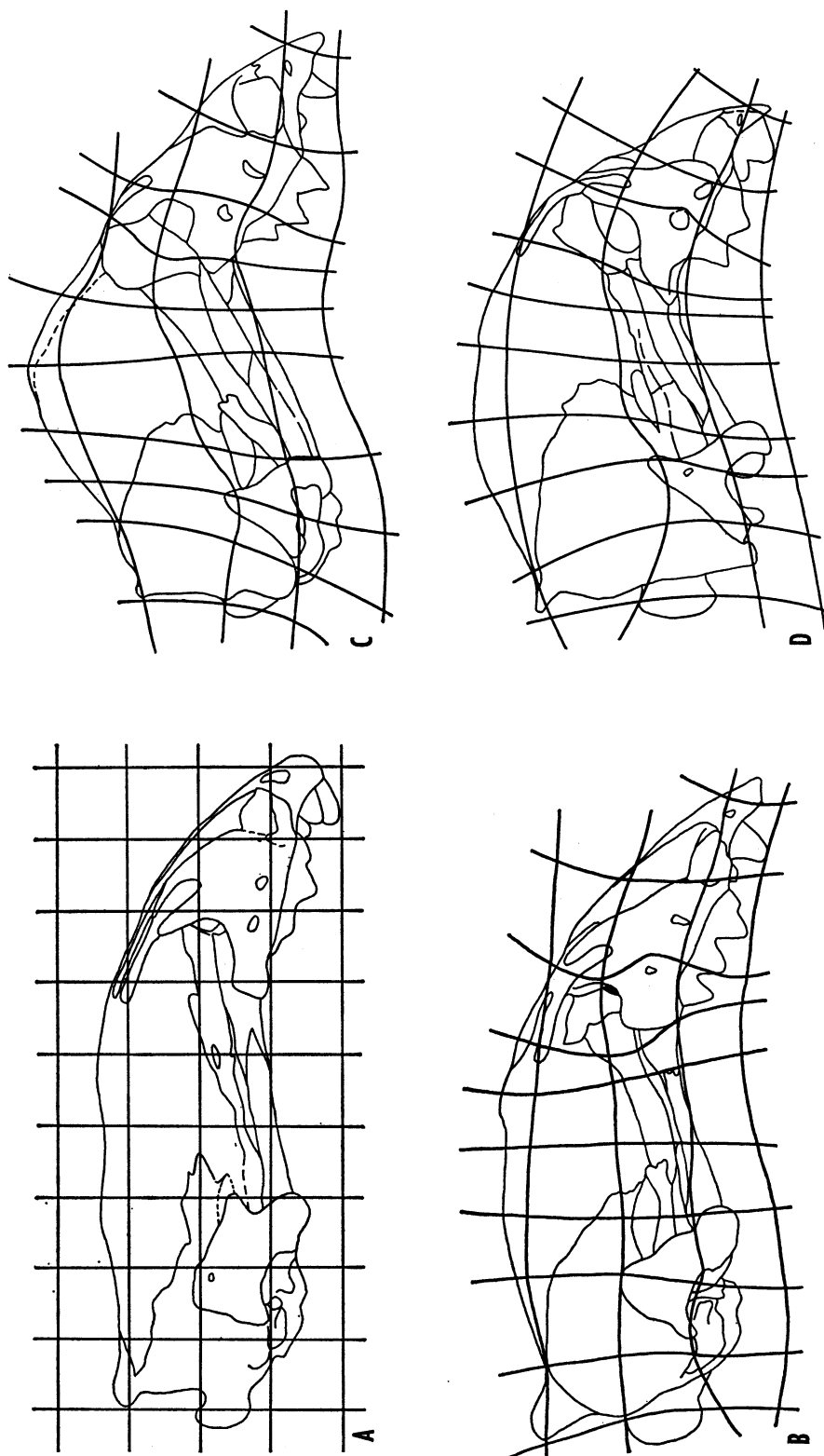


FIG. 8. Outline (lateral) views of the skulls of the four species of the Trogonophinae, with superimposed deformed coordinate grids to show nature of changes that have occurred in these skulls. A. *Trogonophis wiegmanni* used as standard for comparison, as this is probably the most primitive of the species. B. *Pachycalamus brevis*. C. *Diplometopon zarudnyi*. D. *Agamodon anguliceps*.

ossifies. The result is a triangular bony plate (fig. 14) that articulates with the columella, lies lateral to the mandibular articulation, and ties into the soft tissues adjacent to the upper and lower jaws.

The simple condition that exists in *Trogonophis* has been previously described by Smalian (1884, p. 193) and Versluys (1898, p. 91), the latter referring to calcification of the extracolumellar cartilage. An essentially similar situation has also been described for *Amphisbaena alba* (Camp, 1923, pp. 317, 342), *A. caeca* (Camp, *ibid.*), *A. fuliginosa* (Smalian, *ibid.*; Versluys, 1898, 1903, 1936; Camp, *ibid.*), and *Anops* (= *Anopsibaena*) *kingi* (Smalian, *ibid.*). In *Rhineura floridana* (Camp, *ibid.*) the rod-shaped extracolumella has a small, bony, proximal portion. Only in *Monopeltis capensis* (Kritzing, 1946, p. 189; and personal observation) is there a very elaborate, yet cartilaginous apparatus. These reports suggest that the condition in *Trogonophis* is the one most widely distributed in the pleurodont amphisbaenids, and hence presumably primitive.

It might be mentioned in passing that the possible embryonic origin and function of these structures have given rise to considerable speculation. Peters (1882, p. 583, for *Agamodon*) believed the distal element to be the *Hammer* (malleus), while Smalian (1884, p. 193) suggested that it might be the jugal. Fürbringer (1919, 1922) stated that it represented the epihyal. This was in contrast to Versluys' (1903, p. 157) tentative suggestion (based on his 1898 study) that the structure represented a true extracolumella, a suggestion that has been accepted by most subsequent authors (Camp, 1923; Versluys, 1936; Zangerl, 1944; Romer, 1956). The functional interpretations of this structure are discussed in the second part of the present paper.

The skulls of the several species are next described in detail.

TROGONOPHIS

The skull of this species (see fig. 9) has been rather poorly figured and described by Wagner (1841) and Gervais (1853).¹ Figures and

¹ The plate numbers of Gervais' paper were apparently transposed so that all references to plate 15 apply

descriptions of the entire skull are presented by Zangerl (1944) and Vanzolini (MS), while Smalian (1884), Versluys (1898), E. Fischer (1900), Lakjer (1927), Bellairs and Boyd (1947), Pratt (1948), and Bellairs (1949, 1950) comment on or figure only specific regions or structures.

The skull of *Trogonophis* is very elongate, with the ratio of parieto-occipital to facial length almost two to one. The facial plane starts its ventrad swing very gradually, and the major change in orientation takes place anterior to the supraorbital margin.

The dorsal view shows that the posterior processes of the maxillae flare sharply outward, so that the skull is wider here than at the occipital lobes. The elongate lobes and the posterior projection of the occipital condyle indicate that the skull is carried with the axis of the cranial section parallel to the main axis of the body. The line of the jaws slopes slightly downward with the skull *in situ*.

The vertical process of the premaxilla is large and rectangular and has a smooth dorsal surface. The process runs dorsad and caudad between the two nasals and has a short dentate junction with an anterior process of the parietal. Such contact seems unique to this genus among amphisbaenids (figures in Vanzolini, MS; and personal observation). The anterior portion of the premaxilla spreads out only slightly and then narrows to form a relatively solid, pointed rostrum. Two well-marked foramina pierce the sides of the premaxilla.

The ventral aspect of the premaxilla has a raised semicircular edge forming a continuous margin around the tip of the upper jaw. There is one bluntly rounded, slightly curved, large, central tooth, flanked on each side by a smaller single tooth element with two cusps,² customarily referred to in the literature as two teeth. It was not possible to determine whether this represents two distinct but fused

to plate 14 and vice versa. The skull of *Trogonophis* is thus shown as figures 3-4 of plate 14 and referred to in the text as figures 3-4 of plate 15.

² This tendency towards a larger number of premaxillary teeth, i.e., five instead of three, appears to be another primitive character, because almost all amphisbaenines listed by Vanzolini (MS) have five or seven teeth on the premaxilla.

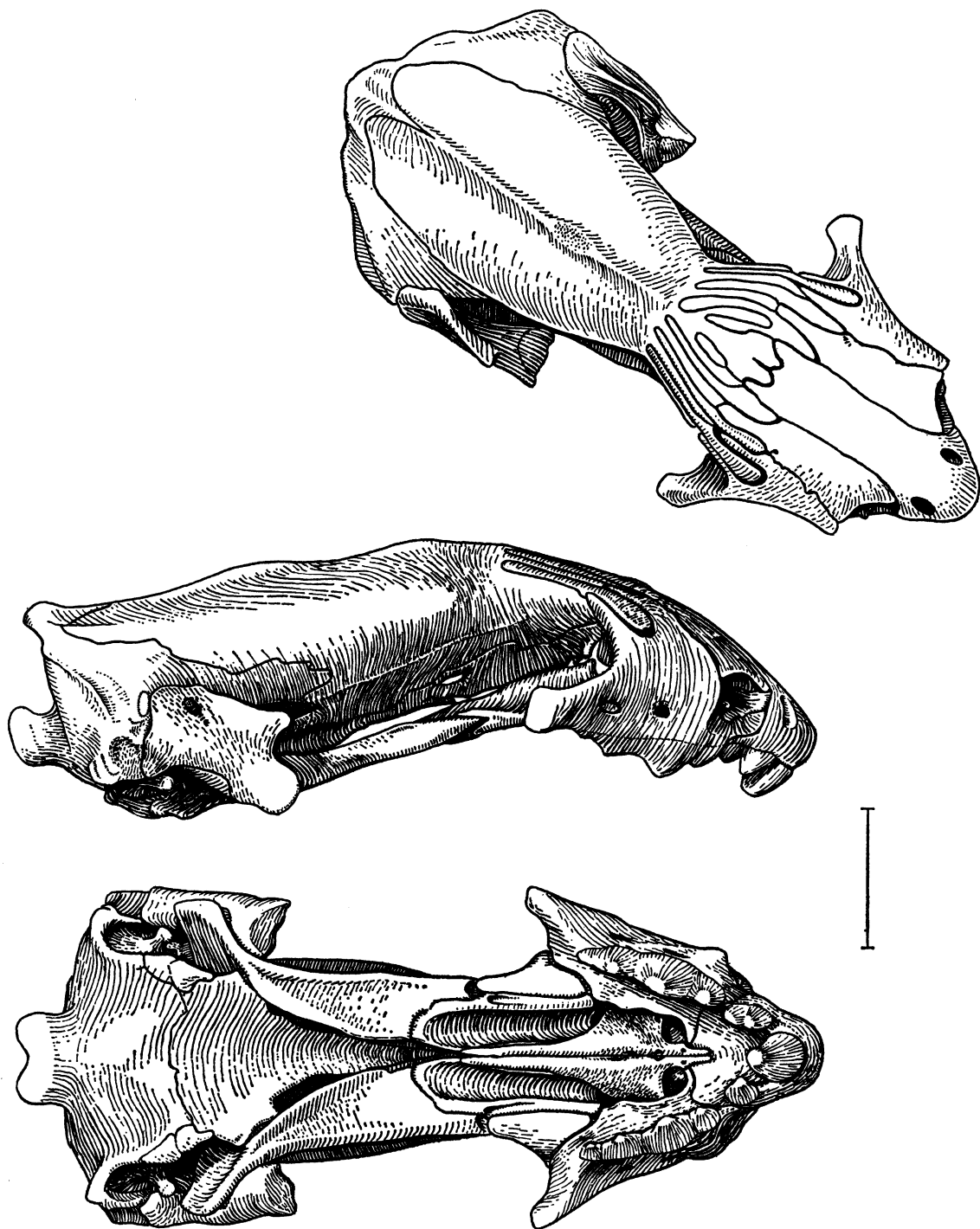


FIG. 9. Views of the skull of *Trogonophis wiegmanni* (M.C.Z. No. 27373). The dorsal view is taken normal to the facial surface. It is believed that the parieto-occipital sutures are adequately represented in this view. The line equals 2 mm. to scale. Drawn by P. Adams.

teeth or a single bicuspid tooth. One specimen (M.C.Z. No. 27373) showed only a single cusp on the left side.

The thin bony lamellae present in the ventrolateral surface of the nasal opening were interpreted as greatly enlarged septomaxillaries by E. Fischer (1900, figs. 1–5, 7, 8) and Zangerl (1944, p. 440). Their position is best shown on the sectional views published by the former.

The nostrils open forward. They are roofed by the parallel-sided nasals, each of which has a single digital process entering into the frontals. Laterally the nasals touch the dorsal edges of the maxillae, which have displaced them from participation in the rounded but clearly apparent canthus rostralis.

The frontals are separated by the anterior process of the parietal. Their participation in the dorsal surface is minor. The dorsal surface consists of two sets of interlocking fingers, interdigitating with the processes of nasal, maxilla, and parietal. The frontals appear superficially as a series of "splinters" rather than as a single bone, as the parietal digits may be in contact with those of the nasals. The interdigitations of each side slant posteromedially, running parallel to the edge of the supraorbital roof.

A short medial process of the maxilla forms the floor of the naris. The posteroventral process of the maxilla (= jugal of Lakjer, p. 167, fig. 58, as well as Vanzolini, MS, p. 19; though no suture was present in my specimens) flares sharply laterad. This process is very large and presents a triangular aspect in lateral view.

The ventral edge of the maxilla supports four teeth, of which the second is very much the largest. The tooth bases appear fused. Three of the teeth are pointed and slightly compressed, while the second (and largest) tooth is very much flattened and bears a definite, twin-edged cusp. One of the Algerian specimens sent me by Bellairs had the crowns of the teeth worn down to flat surfaces.

The palatal process of the maxilla swings medially and forms a shelf next to the tooth-bearing edge. Anteriorly the process inserts dorsal to the palatal process of the premaxilla. Mediad the maxillary process joins the lateral and anterolateral wings of the vomer in circumscribing the orifice for Jacob-

son's organ, from which the premaxilla is excluded.

The vomer extends caudad as a narrow tongue lying ventral to the medial edge of the trough-shaped palatine. It is pierced by a very faint medial foramen. The vomer forms the roof of the internal naris (pars posteriore choanarum) which lies just anterior to the palatine trough. Anteriorly the vomer sends a peculiar vermiform process between the wings of the premaxilla.

The palatine sends an elongate, tongue-shaped process dorsal to the medial shelf of the pterygoid. The process runs parallel to the midline and extends to the level of the quadrate articulation. The ectopterygoid takes up a large area on the palatal plane.

The basipterygoid process lies medial to the ventral tips of the quadrates, and the surface of articulation faces laterally. The vertical edge of the pterygoid rises sharply from the level of the basipterygoid articulation, changing the major axis of the bone from the horizontal to the vertical. A new horizontal shelf forms at the posterior quarter of the pterygoid and participates in a narrow articulation with the medial and posteroventral surfaces of the inclined quadrate.

The parietal forms the roof and much of the side of the anterior brain case. The premaxillary process of this bone forms its only contribution to the facial plane. There is a clearly marked central keel, which starts from the level of the orbit, with a brief dilation after the anterior third of its length. From here the keel continues caudad onto the very narrow and elongate processus ascendens, where it attains maximum height. The posterior lobes of the parietal extensively overlap the dorsal surface of the occipito-otic capsule, an overlap that may be demonstrated by the treating of the skull with essential oils. The processus ascendens must not be considered to be an actual process here. Because the cranial plates overlap widely rather than join by suture, the processus is actually that portion of the supraoccipital exposed between the two posterior lobes of the parietal. There is no cartilaginous plug or foramen apparent at the very tip of the processus. A sharply defined ridge runs along the side of the parietal, dorsal and parallel to its suture with the orbitosphenoid.

The supraoccipital crest presents an obtuse angle from the rear, and its folds continue laterally to the edges of the skull. The U-shaped condyle is strongly produced and projects posteriorly beyond the crest. The bottom of the U is somewhat indented owing to a reduced participation of the basioccipital. The sutures between basioccipital and exoccipital fuse in adults and can be determined only in juveniles (U.S.N.M. No. 12318). The condylar tips flare dorsad and posteriorly, so that they lie immediately posterior to the horizontal midline of the foramen magnum. Strut-like processes angle laterodorsally from the anterior face of the condylar pedestal and join the lateral walls of the foramen magnum. Each strut is pierced by a single foramen at the level of the condylar top. This foramen may serve for the N. vagus and glossopharyngeus (Bedriaga, 1884, p. 48).

The front and outside angle of the orbit contains a small prefrontal, in some specimens covered almost completely by the superior process of the maxilla. The descending lamella of the frontal is very large, but much of it is masked by the external plates of the parietal and orbitosphenoid. The latter bone forms the ventrolateral portion of the brain case and stretches posteriorly up to the level of the foramen for the Gasserian ganglion (Zangerl, 1944, p. 424), from the edge of which it is excluded by the junction of basisphenoid and parietal.

The epipterygoid (fig. 10) is a very slender bony rod that rises anterodorsally from a suture with the pterygoid and extends to the parietal by a ligamentous connection. Bellairs (1950, p. 899, pl. 1, fig. B) first described this element from sections, and it should be mentioned that it was not found (most probably "prepared away") in the first skulls and was located only by a careful regional dissection for this purpose.

The occipital lobes bulge laterally but are narrower than the flaring tips of the maxillae. The specimen (or possibly specimens) illustrated by Lakjer (1927, p. 166, fig. 58) and U.S.N.M. No. 12318 show a straight suture crossing the base of the skull at the level of the posterior tips of the pterygoids. This marks the division between basisphenoid and basioccipital. A pair of small elements flanks each lateral extremity of the suture, lying

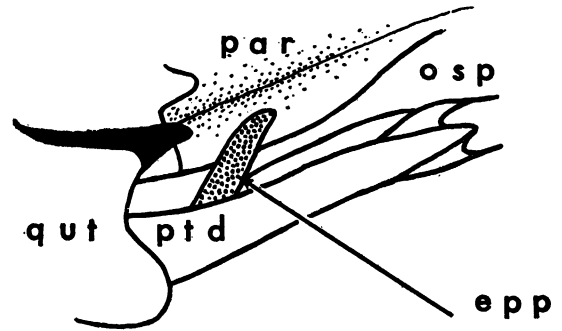


FIG. 10. Lateral view of *Trogonophis wiegmanni*, to show size and position of ectopterygoid (stippled).

Abbreviations: epp, epipterygoid; osp, orbitosphenoid; par, parietal; ptd, pterygoid; qut, quadrate.

anteromedial to the stapedial plate. Lakjer considered these to be basioccipital and basisphenoid epiphyses, Zangerl referred to part of them as "elements x" (1944, p. 421), while Vanzolini (MS, p. 14) believed the (anterior?) pair to be homologous with the basitemporals of birds and crocodilians.

Bedriaga (1884, p. 49, figs. 11, 12) first described and figured the semicircular canals of *Blanus* from cranial dissection. Parts of these canals are visible through the semi-transparent dorsolateral and posterior surfaces of the occipito-otic lobes of *Trogonophis*, which they circumscribe. A comparison with Bedriaga's description was possible only after the use of a similar destructive technique. This was carried out on one side of a single specimens of *Trogonophis*. The horizontal canal here lies slightly dorsal to the quadratic articulation. It passes caudad to the region of the pro-otic process, whence it swings sharply medioventrally. The crus commune of the vertical canals lies at the level of the horizontal canal, and the two ascending branches diverge here, passing dorsad as parallel but discrete tubes. They may be seen through the foramen magnum. The two vertical canals reach the dorsal extremity of the lobe at closely adjacent points. (Prior to the dissection it was impossible to determine whether the externally visible portions represented a single canal or parts of two separate canals.) From here they diverge at an angle of 120 degrees, the anterior vertical canal running anterolaterally

along the forward extent of the lobe and the posterior canal angling posterolaterally to the supraoccipital crest and descending ventrolaterally along the back of the lobes. The externally visible portions of the three canals seem to be in contact at their extremities.

The stapes is located asymmetrically near one end of a very large, oval foot-plate. The columellar process is thin and short and in lateral view can be seen just ventral to the posterior articulation of the quadrate. The cartilaginous extracolumella, stated to be calcified by Versluys (1898, p. 91), extends ventral to the angle of the mouth (not attaching to this, as stated by Versluys) and continues as a fan-shaped pad of connective tissue that attaches to the skin along the posterior portion of the mandible. A very few strips of connective tissue leave the bundle earlier (more caudad) and rise sharply to attach to the skin along the side of the maxilla. The various connective-tissue bundles are separated from the skull and the mandible by a thick mass of labial glands.

The quadrate has a very peculiar appearance. Its central portion is shaped like an arrowhead, pointing anteroventrally at an angle of approximately 45 degrees. The two-pronged posterior end bears against a convex, anteroventral, articulating surface recessed into the lateral aspect of the occipito-otic lobes, so that the quadrates have only a slight lateral spread beyond these. The dorsal edge of the quadrate extends anteriorly as a thin triangular plate, so that the dorsal edge of the quadrate is parallel to the long axis of the skull. A small foramen pierces the plate near the dorsal end of its base. The wide and rounded distal end of the quadrate extends mediad to provide the cylindrical articular facet for the mandible. The posterior aspect of the distal end also articulates with the laterad-curving vertical plate of the pterygoid.

PACHYCALAMUS

The skull of *Pachycalamus* (fig. 11) was described and figured in somewhat diagrammatic fashion in Vanzolini's papers (MS; 1951, fig. 11). As his views are taken at slightly different angles from mine, there are several minor differences.

The skull is very much shorter than that of

Trogonophis, with the ratio of parieto-occipital to facial length one to one, and of length to greatest width two to one. The facial plane again shows a gradual curvature, though the angle between rostral tip and occipital crest is 115 degrees.

The dorsal view shows that the skull of *Pachycalamus* lacks the prominently flaring posterior processes of the maxillae, so that the skull is widest at the occipito-otic lobes. *In situ* the skull is carried with the occipitoparietal plate slightly inclined to the horizontal.

The vertical process of the premaxilla is enormous and extends anteriorly and laterally to cover the nares and take up the entire rostral region. There is some surface sculpturing on the anterodorsal face of the spatulate tip, and four foramina lie at the bottom of the grooves. The ventral aspect of the premaxilla has a tooth-bearing pedestal that is set back some distance from the anterior edge. There is a large central tooth flanked on each side by a single smaller one. All have rounded tips.

No septomaxilla is apparent from the outside.

The general pattern of sutures is clearly shown on the facial surface. The canthus rostralis is poorly defined. The supraorbital ridges swing mediad behind the orbits to meet the parietal ridge which is but weakly expressed anteriorly. The ridge increases in size posteriorly and ascends at full height onto the processus ascendens. The dorsoposterior wing of the maxilla is in contact with a process of the parietal, thus excluding the frontal from the supraorbital shelf. There are no supraorbital foramina.

The dorsal portion of the maxilla appears to have been slightly reduced and shifted posteriorly when compared with *Trogonophis*. It forms only the posterior part of the indistinct canthus in its articulation with the frontal. The posteroventral process is very prominent and forms the anterolateral wall of the orbit. The ventral edge of the maxilla bears three full-sized teeth, of which the anteriormost is the largest. There is a small accessory cusp, or small fourth tooth, on the front of the row. The teeth show little lateral compression but have notably rounded tips.

The palatine again forms a deep trough.

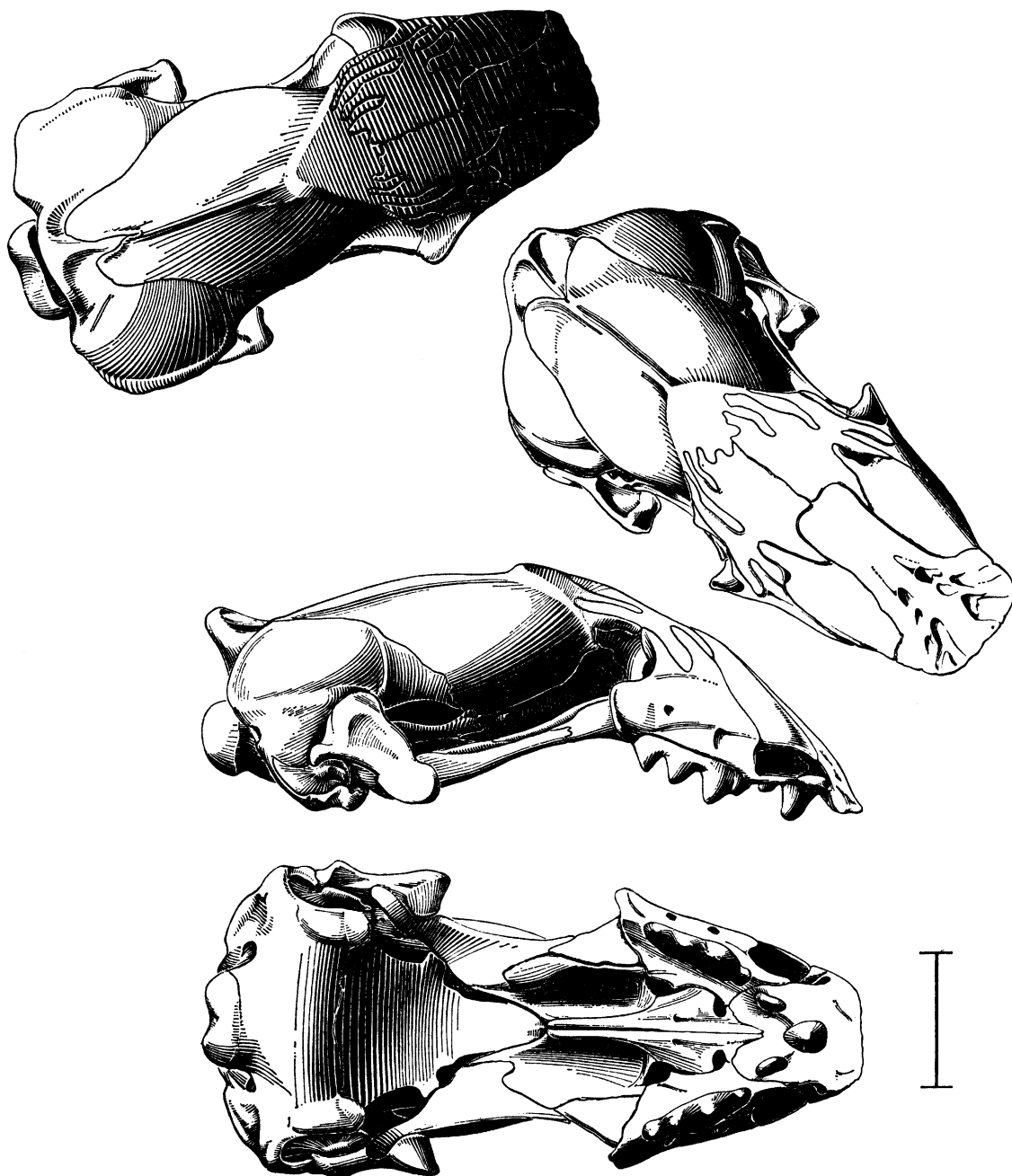


FIG. 11. Views of the skull of *Pachycalamus brevis* (A.M.N.H. No. 73424). Two dorsal views are shown, one normal to the facial surface and the other normal to the parieto-occipital surface. The objects shown in adjacent views have been rotated 90 degrees to conform to standard drafting practice. The lateral view is shown as if the long axis of the body were horizontal. The line equals 2 mm. to scale. Drawn by S. B. McDowell.

The pterygoids spread widely, leaving a central gap. This makes the basipterygoid processes reach laterally so that they are clearly seen in ventral view. The posterior wing of each pterygoid swings 90 degrees around the posterior aspect of the quadrate, so that the extreme ends point laterally.

The basal portion of the skull is completely fused in my specimens. The condyle is strongly produced and U-shaped. As in *Trogonophis* it is flanked by a single foramen on each side.

A clear fold marks the anterior limit of the occipito-otic lobes. The externally visible portions of the semicircular canals appear as an isosceles triangle that has been applied to the surface of the lobe. They are almost entirely restricted to the laterodorsal aspect thereof.

The descending lamella of the frontal is very large. The anterior opening from the orbit into the brain cavity is partially hidden by the posterior edge of the maxilla. The sharply defined fold of the parietal leaves the edge of the supraorbital roof and passes ventrad immediately posterior to the orbit. There is neither a prefrontal nor an epipterygoid.

The quadrate lacks the triangular plate shown by *Trogonophis*, but is as deeply recessed into the side of the occipito-otic lobe. Its posterior tip bears a peculiarly scrolled wing that fits into a notch of corresponding shape. The stapedial foot-plate of *Pachycalamus* is much larger than that of *Trogonophis*, but the columellar portion is short. The extracolumella is still cartilaginous, but widened anteriorly, and relatively more of the connective tissue fibers tie it to the skin along the upper jaw.

DIPLOMETOPON

The skull of *Diplometopon* (fig. 12) is remarkably short and broad, the ratio of length to greatest width (at the occipital lobes) being three to two. Its dorsal surface is sharply angled. The anterior, flattened, shovel-shaped, facial surface, consisting of the exposures of premaxilla, nasals, and frontals, joins the posterior and slightly shorter, saddle-shaped, parieto-occipital portion which ends over the very prominently bulging occipital lobes. There is an angle of about 130

degrees (110 degrees minimum between rostral tip and occipital crest) included between the two sections. In the living animals (fig. 14) the skull is held with the parieto-occipital surface subtending one-half of the angle (to the longitudinal axis) as does the facial surface. The spatulate edge of the premaxilla thus lies almost normal to the probable direction of motion, and the tooth line of the jaws slopes anteroventrally at an angle of 30 degrees.

The vertical process of the premaxilla is of the same size as that of *Pachycalamus*, but narrower anteriorly. The exposed surface of the ascending process is slightly constricted in the middle. Its anterior portion spreads laterally and forms a spatulate process over the full width of the snout. Ventrally the premaxilla forms a pedestal for the large, central, forward-curved tooth. Two posterior wings form a bridge to the anterior processes of the maxillae and form the ventral circumference of the nares. The ventral surfaces of these wings each bear a single minute tooth. The posteriormost portions of the wings curve in medially, their junction being displaced forward by the anterior tips of the vomers. The central portion of the ascending premaxillary process is scored by a pair of deep grooves, which are pierced by foramina apparently connecting with the nasal cavity.

No septomaxillaries may be noted externally.

The dorsal portion of the premaxilla and of the nasals flanking it forms a plane very strongly inclined to the long axis of the skull. There is a bend at the top of the nostrils, and the surface from here to the frontoparietal suture is also perfectly plane, though inclined at a somewhat lesser angle.

The nasal-premaxillary articulation runs in a smooth curve. The posterior edge of the nasal is deeply interdigitated with the frontal, a finger of the nasal inserting into the frontal almost one-third of the frontal length. Laterally the nasal forms the dorsoposterior edge of the naris, which lies below the canthus rostralis, but opens anteroventrally.

The frontals have a smooth central suture. Laterally they contribute to the supraorbital shelf which forms a continuation of the strongly marked and overhanging canthus

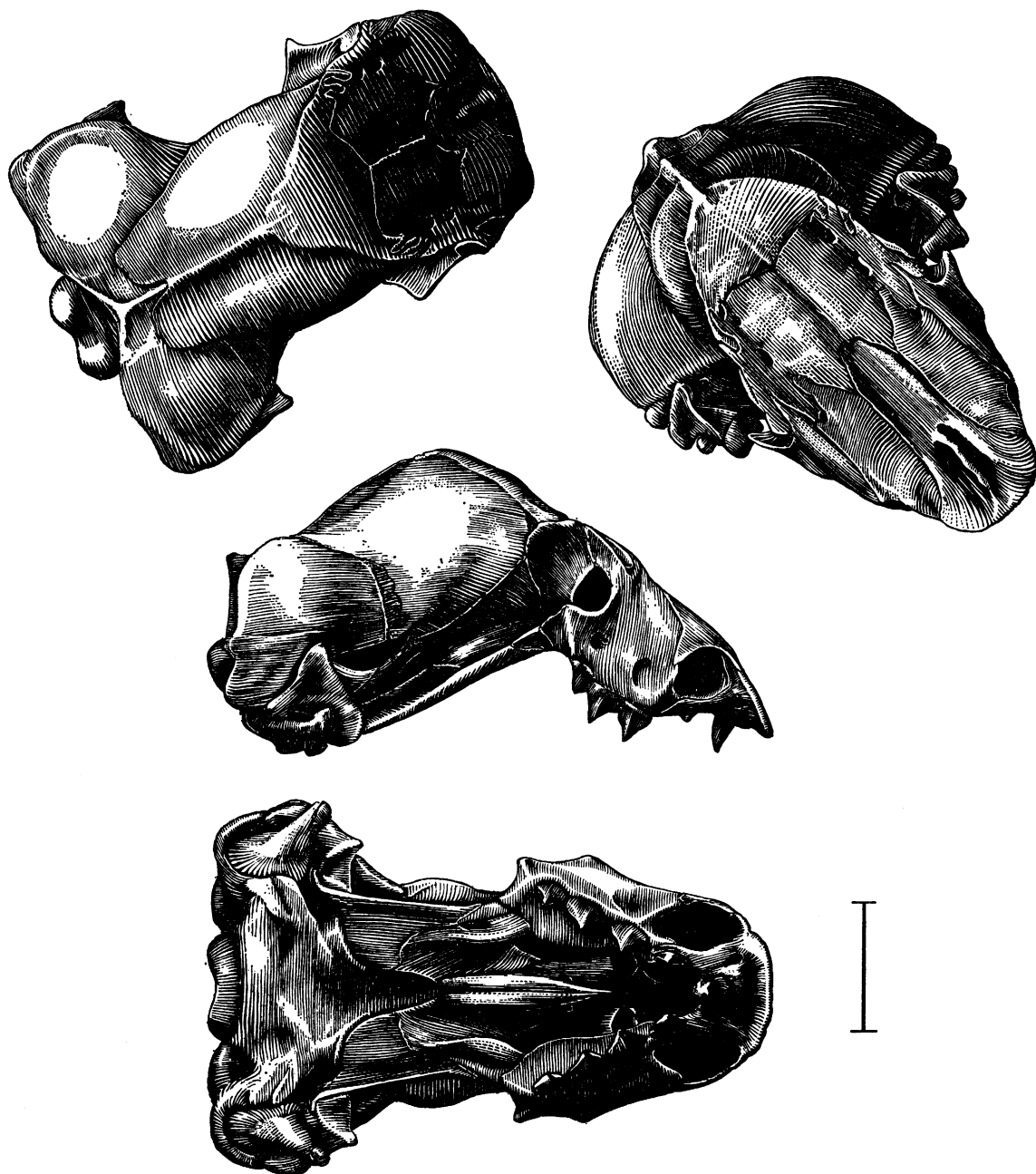


FIG. 12. Views of the skull of *Diplometopon zarudnyi* (C.N.H.M. No. 74007).
Conventions as in figure 11. Drawn by S. B. McDowell.

rostralis. The parietal articulation of the frontals is reasonably smooth in the center but is again interdigitated on both sides. These interlocking structures do not run normal to the main line of the junction but rather appear to extend radially outward from a pair of centra on the midline of the frontals. This suggests that they may function to strengthen the edge and roof of the orbit against stresses tending to twist or bend the skull around the long axis. The upper plate of each frontal is laterally pierced by two or three supraorbital foramina which may vary in size and relative position.

The frontals send down two lateral lamellae and thus form an almost complete ring around the forebrain. Dorsally these descending lamellae contribute to the posterior edge of the supraorbital ridge and continue down the medial wall of the orbit, immediately posterior to the large anterior opening. Their posterior suture with the parietal forms the start of the raised ridge that runs diagonally down the inside of the orbit at an angle of about 45 degrees.

There is no prefrontal and no epipterygoid.

The ascending plate of the maxilla is short and high; it reaches outward and upward to form the anterior edge of the canthus rostralis. The canthus continues posterior-medial to join the parietal ridge. The maxilla is pierced by two foramina, and its posterior processes surround the laterofrontal aspect of the orbit. The posterodorsal process of the maxilla forms the anterolateral portion of the supraorbital ridge, and the posteroventral process of the maxilla swings sharply laterad along the bottom of the orbit, where it also bears a diagonal keel. On one side of one of the specimens (C.M. No. 33504) the lower process appears to be a separate bone. This might provide evidence for Vanzolini's (MS, p. 19) suggestion, mentioned above, regarding the existence of a jugal fused to the maxilla in this location.

The ventral surface of the maxilla supports a row of three teeth with fused bases, thus presenting the appearance of a single tricuspid tooth. The first tooth is the largest, the second slightly smaller, and the third but one-half to two-thirds of the size of the first. Each tooth is provided with a sharp edge and

minor keels which run up both its lateral and medial faces.

The vomer extends caudad as a narrow tongue lying ventral to the medial edge of the trough-shaped palatine. It is pierced by a single foramen about midway along its length and forms the roof of the internal naris (*pars posteriore choanarum*), which lies just anterior to the palatine trough.

The palatine shelf of the maxilla is extended posteriorly by the ectopterygoid, by the *pars lateralis* of the palatine, and by the pterygoid. The ectopterygoid is a small bone that takes up a triangular space on the superficial palatal plane and sends an ascending process into the bottom of the orbit. The pterygoid forms the lateral edge and medial surface of the palatal plane. Anteriorly, the pterygoid plate lies ventral to the palatine, while its posterior edge rests against the basipterygoid process.

The anterior portion of the pterygoid is a smooth plate, without vertical processes. Immediately posterior to the basipterygoid process the rapidly narrowing pterygoid gives rise to a high, triangular, dorsal process which cannot be seen on the drawings. This effectively changes the major axis of the bone cross section from the horizontal to the vertical. The only remaining trace of the anterior horizontal plane is a thickening of the ventral edge of the bone. The triangular wing wraps around the posteroventral aspect of the quadrate, providing an extremely rigid articulation. This stabilizes the palate and makes for additional rigidity of the mandibular suspension.

The anterior portion of the parietal has a triangular surface on the facial plane. Just beyond the joining ridges of the canthus rostralis, the parietal swings downward on both sides to form the major portion of the brain case. The central keel is well marked and continues onto the *processus ascendens* of the supraoccipital, a sizable portion of which bone is exposed posteriorly.

The elements of the occipito-otic region and bottom of the brain case are fused in adult specimens and difficult to analyze without disarticulating the skull, an action that was precluded by the scarcity of specimens. Description is again restricted to the externally visible portions of the various

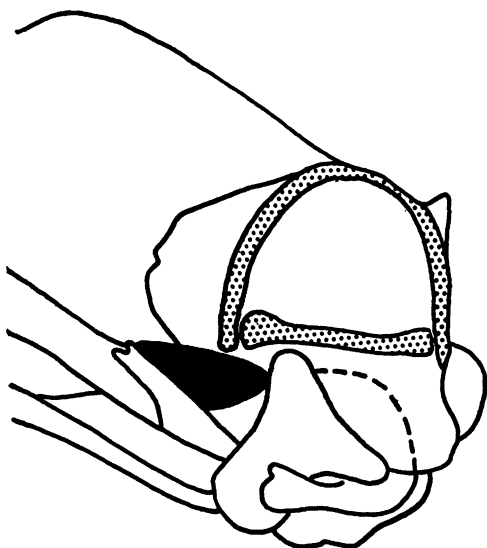


FIG. 13. Diagrammatic lateral view of the occipital region of *Diplometopon zarudnyi*, to show approximate position of superficially visible semicircular canals (stippled area), as well as outline of posterodorsad portion of fenestra ovalis (dashed line).

bones. The occipito-otic plates swing forward and laterally, thus forming the enormously bulging lobes which almost double the width

of the skull in this region. The pre-otic fold is sharply defined just anterior to the line of overlap of the parietal.

The orbitosphenoid lies posterior to the descending lamella of the frontal and extends below the ventral edge of the parietal to the foramen for the Gasserian ganglion, from which it is excluded by a narrow process rising from what appears to be the lateral wing of the basiparasphenoids.

The quadrate is similar to that of *Pachycalamus* but more clearly triangular and not so deeply recessed into the occipito-otic lobe. A sharp ridge runs down the anterior edge of the quadrate. This ridge becomes higher ventrally, as the apex of the triangle is neared. The ventralmost portion of the quadrate is widest. It articulates with the mandible, and its medioventral surface also forms the articulation with the pterygoid.

The superficially visible semicircular canals are indicated in figure 13. This figure emphasizes the truly startling size of the canal system in *Diplometopon*. The anterior vertical canal parallels the fold marking the edge of the occipito-otic lobe and ascends to a point just beyond the posterior tip of the parietal. Here it is replaced (in the superficial region) by the posterior ascending canal,

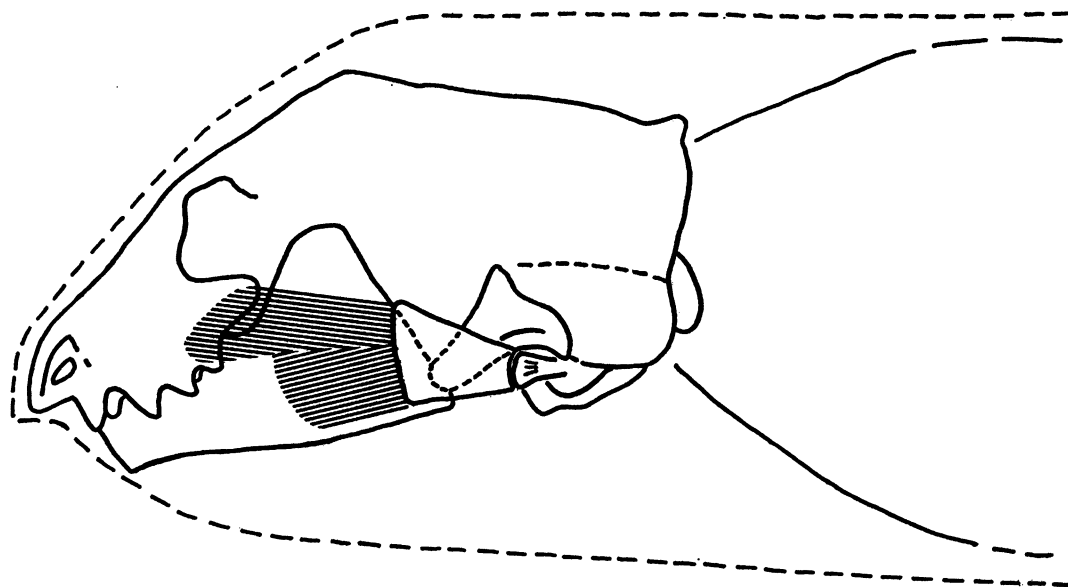


FIG. 14. Outline view of the head of *Diplometopon zarudnyi*, to demonstrate position of skull and size and location of extracolumella. The two bundles of dense connective tissue are shown hatched. They attach to the skin of the upper and lower lips.

which swings sharply ventrad around the back of the lobe. The horizontal canal seems to touch the ventral extremes of the vertical canals. It swings around the lateral extension of the lobe just dorsal to the articulation of the quadrate. It might be noted that the superior portion of the stapedial foot-plate continues into a pocket underneath the quadratic articulation. This pocket approaches quite closely to the lateral extremity of the horizontal canal and may be mistaken for a branch thereof.

The stapes is enormous and rises from a very large and solid foot-plate which closes the fenestra ovalis and is maintained in position by the overlapping rims of the latter. With the stapes *in situ* the columellar portion extends laterally beyond the quadrate, passing through a notch in the ventral portion of this bone. The columella terminates distally with a strong head that articulates with the caudal portion of the triangular, plate-like extracolumella (fig. 14). This is fairly thick at the point of articulation but thins rapidly towards its anterior edge. The entire rostrad portion of the extracolumella is tied into a very thick bundle of connective tissue that divides anteriorly. The dorsal portion is inserted into a thin fascia over the pre-orbital glandular tissue labial to the maxilla, while the ventral portion inserts into the thickened skin along the side of the mandible by means of a similar, but more fragile, fan-shaped connection.

AGAMODON

The skull of *Agamodon anguliceps* (fig. 15) was first figured by Peters (1882, figs. 6-8). It is even shorter and has a sharper angle between occipitoparietal and facial planes than that of *Diplometopon*. The rostrad tip of the facial shield forms an angle of less than 90 degrees with the occipitoparietal plane. As the skull is held in approximately the same position as that of *Diplometopon* (see fig. 14), the tip of the facial shield would ordinarily lie almost normal to the direction of motion.

The vertical process of the premaxilla is much wider and shorter than that of *Diplometopon*. It also differs in having a prong-shaped rather than a simple articulation with the frontal. The anterior portion of the pre-

maxilla is spatulate and similar in shape to the same bone in *Diplometopon*. The ventral pedestal and lateral wings bear a single tooth each, differing from those in *Diplometopon* only by their more rounded shape. The vertical process is pierced by two central foramina as in *Diplometopon*, but their grooves are not so regular. Extensive sculpturing is produced by a second set of foramina as well as by four (or six) sets of parallel grooves. No septomaxilla is apparent.

The frontonasal and frontoparietal articulations are again very strongly interdigitated. Their individual processes are proportionately longer than those of *Diplometopon*. There are no supraocular foramina.

The anterior aspect of the maxilla agrees well with *Diplometopon*; however, the posterior one shows some definite changes. These and the changes in the proportions of the elements of the palatal plate appear to be caused by the extreme angulation of the skull.

The ventroposterior process of the maxilla swings sharply inward. It is much less developed than is the corresponding member in *Diplometopon*, and a splinter-like element initially interpreted as the ectopterygoid lies above it in the larger (here illustrated) specimen. The bone in question has been reduced to a tiny triangle on the palatal plane. It lies outside the lateral edge of the palatine and dorsal to and between the tips of maxilla and pterygoid. Peters neither mentioned nor figured this element, and the region in question is shown as a posterior wing of the maxilla. His type was the largest specimen of the genus ever recorded, and more than 50 per cent longer than the larger (M.C.Z. No. 10784) of the two specimens examined by me so that it is possible that the sutures in question had fused. The fact that the smaller specimen (M.C.Z. No. 38697) shows the region incompletely ossified, without either bone or center of ossification, would suggest that the structure in question either represents an artifact or is an anomaly.

There are only two maxillary teeth, fused to a single base in the same manner as described for *Diplometopon*. Each bears a triangular cutting edge, but the actual cusp of the tooth is located on the posterior portion of the anterior tooth and on the anterior

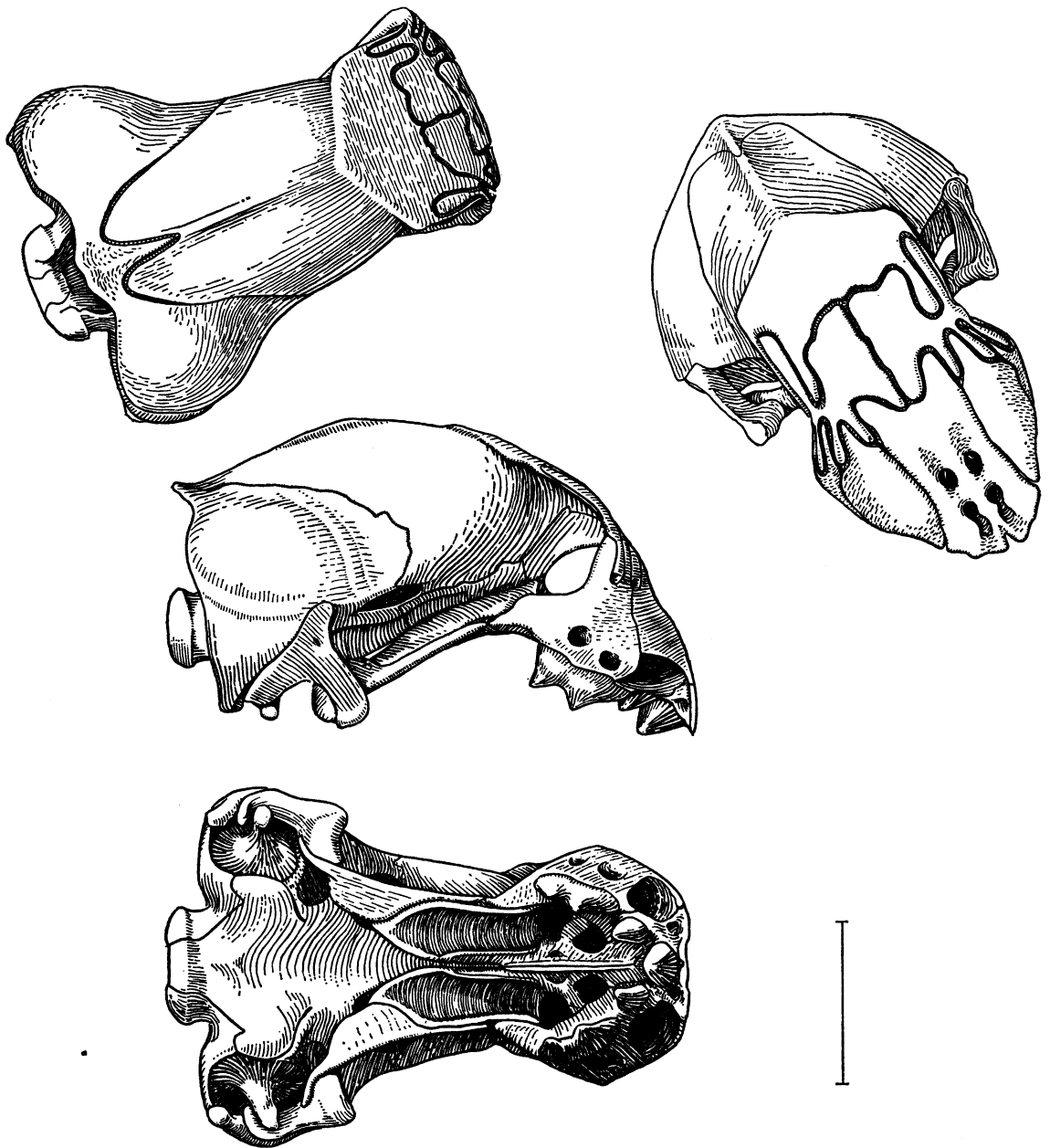


FIG. 15. Views of the skull of *Agamodon anguliceps* (M.C.Z. No. 10784). Conventions as in figure 11. The line equals 2 mm. to scale. Drawn by P. Adams.

portion of the posterior tooth, so that the cusps are closely adjacent. There appears to be a longer front than rear shoulder, but the secondary cusp of the smaller posterior tooth mentioned by Peters (1882, p. 324) is not present on either of my specimens.

Because nothing seems to be known of tooth

replacement in acrodont amphisbaenids, if indeed there is such a thing, it might be of interest to mention that the teeth of both maxillae of the larger specimen (M.C.Z. No. 10784) had semilunar openings on their lingual aspects. After preparation, which involved a two-minute cleaning in concentrated

Chlorox (5% commercial sodium hypochlorite), the teeth were found to be hollow shells, very poorly fused to the maxillae. Those of one side broke off, leaving a portion of the maxilla without teeth or any evidence of replacement teeth. It may be that the semilunar openings are usually found in *Agamodon*. Peters, however, does not mention these, and the other skull examined for this study showed no similar openings on the maxillary teeth. However, there were openings below teeth of the mandibular row of other acrodont amphisbaenids in several cases. Whether these "alveoli" are but foramina for the passage of nerves and blood vessels,¹ or, as seems more likely, are but a temporary stage of the replacement cycle forms another subject in need of investigation.

There is neither a prefrontal nor an epipterygoid.

The posterior tongue of the vomer is very much reduced in the specimens at hand and neither so long nor so wide as that shown by Peters. The anterior tip of the pterygoid takes up but a very narrow bar on the ventral surface of the palatal plane, and the palatine makes a proportionately larger contribution to the roof of the mouth than it does in *Diplometopon*. The medial wings of the pterygoid are much smaller, even though there is again some difference between my specimens and Peters' drawing, which shows the pterygoid much more robust. The posterior portion of the pterygoid again undergoes a change in cross section and bends around the inside of the quadrate, the curved process providing a rigid support for the mandibular articulation.

A greater portion of the parietal extends onto the facial plane, and the lateral interdigitations of the parietal form more than 80 per cent of the supraocular roof. They fall little short of meeting the posterior processes of the maxillae. The central keel of the parietal starts a short distance beyond the beginning of the cranial plane, where the strongly marked extensions of the two canthi rostralis join. The keel rises to its greatest

height approximately two-thirds of the distance to the processus ascendens. Only a faint keel continues onto the supraoccipital, of which the whole posterior edge is bent smoothly upward. A diagonal keel runs down the lateral plate to the top of the foramen for the Gasserian ganglion. Peters' figure 7 gives the view normal to the facial plane, so that on first inspection it appears to be at variance with part of this discussion.

The occipital lobe of *Agamodon* does not bulge so prominently as that of *Diplometopon*, but the position of the semicircular canals is more clearly marked by slightly bulging lines. The proportion of the parietal to occipitals and the general aspect of the latter are the same, except that the proportions of the external aspects of the semicircular canals differ. These are similar rather to those of *Pachycalamus* in forming an isosceles triangle applied to the surface of the lobe and in the restriction to the laterodorsal aspect thereof. The posterior canal marks the extreme posterior edge of the occipital shield.

Remarkable is the fact that the bulge of the occipital lobes has been changed, so that, instead of being at the midpoint, the point of greatest cranial width is rather at the posteriormost part of the lobe. This fact should be kept in mind when one reads the second part of the present paper, in which the function of this extreme widening of the skull is discussed.

The condyle is very similar to that of *Diplometopon*. The sutures between basioccipital and exoccipitals are clearly apparent in my specimens, though they seem to have fused in the specimen illustrated by Peters.

The visible portion of the descending frontal lamella is entirely restricted to a narrow strip on the inside of the orbit. The parietal wing descends posterior to it, and below this lies the narrow orbitosphenoid which is even more reduced here than in *Diplometopon*.

The shape and arrangement of the quadrate-columella-extracolumella assemblage are roughly the same as in *Diplometopon*. The quadrate of the figured specimen of *Agamodon* seems comparatively small, but Peters' figure suggests that this may be but individual variation. The extracolumella of my smaller specimen is only partly ossified.

¹ This hypothesis is prejudiced by the apparent presence of additional foramina, possibly for the dental lamina, piercing the maxilla through the tooth-bearing surface.

TABLE 2
CHARACTERS OF SKULL AND MANDIBLES IN THE TROGONOPHINAE

	<i>Trogonophis wiegmanni</i>	<i>Pachycalamus brevis</i>	<i>Diplometopon zarudnyi</i>	<i>Agamodon anguliceps</i>
Skull				
Over-all shape				
Ratio of length to width	3/1	2/1	3/2	3/2
Ratio of frontal to parietal length	1/2	1/1	3/2	2/1
Minimum angle between rostral tip and occipito-parietal crest	120°	115°	110°	90°
Existence and position of individual elements				
Epipterygoid	Present	Absent	Absent	Absent
Prefrontal	Present	Absent	Absent	Absent
Septomaxilla	Present	?	?	?
Ventral exposure of ectopterygoid	Entire	Reduced	Reduced	None—bone absent?
Participation by frontal on supraorbital shelf	None	None	Present	None
Supraorbital foramina	Absent	Absent	Present	Absent
Teeth				
Shape	Conical, faintly grooved	Cylindrical, with faint lateral compression, rounded tips	Laterally compressed, edged	Laterally compressed, edged
Premaxillary—number	1+4 (3)	1+2	1+2	1+2
Maxillary—number	4	1+3	3	2 (3 ^a)
Extracolumella	Cartilaginous, rod-shaped	Cartilaginous, anteriorly widened	Ossified, triangular	Ossified, triangular
Mandible				
Angle between base and posterior edge	75°	75°	75°	90°
Retro-articular process	Short	Absent	Absent	Faint
Ratio of distance caudal of tooth row to length of tooth row	0.65	0.75	0.50	0.35
Depression of articular surface below tooth line as per cent of mandibular height	0.35	0.28	0.65	0.57
Dentary—tooth number	8 (7-9)	6	6	5

^a *Fide* Peters (1882).

MANDIBLE

GENERAL COMPARISON

The mandibles of the four species seem to be unusually bizarre even for those of amphisbaenids. They are flat, relatively

plate-like structures, with a reduced retro-articular process or none at all. Their high coronoid ramus gives them a startlingly mammal-like appearance on superficial inspection.

Among the acrodont forms *Trogonophis*

has the simplest and probably least specialized jaw, with the lowest coronoid ramus and the largest number of teeth. Only a few, rather poorly marked trends can be discerned through the other forms (table 2). The clearest ones concern the decrease in the number of teeth and in the relative length of the tooth row, both clearly related to the similar changes in the skull. A definite increase may also be noted in the extent in which the tooth line is separated from the glenoid fossa. There also is a decrease in the size of the always small retro-articular process and an increase in the size of the symphyseal shelf. None of these characters furnishes trends in the same sense as do the first two, because their changes do not proceed in the sequence *Trogonophis* - *Pachycalamus* - *Diplometopon* - *Agamodon*. They rather underline the fact that such a sequence may be established for only a limited number of characters.

TROGONOPHIS

The mandible of *Trogonophis* (fig. 16) is similar to the mandibles of the other species here examined, as it is relatively high and long in relation to its width. However, the resulting plate-like structure is not plane but twists mediad ventrally. The mandibular symphysis consequently recedes ventrally, and there is a small symphyseal shelf formed by the ventrad junction of the mandibles. The characters diagnostic for the mandible of this species are the medium-sized, gradually ascending, and dorsally rounded coronoid ramus, the elongate and low tooth-bearing region, the very unspecialized teeth, and the well-defined, but small (when compared to those of rhineurine species), retro-articular process. The posterior edge of the mandible is extended ventrally beyond the ventral edge of the anterior portion so that not only the retro-articular process, but also half of the mandibular fossa, lies below this.

The dentary bears seven to nine, generally eight, teeth that are closely crowded together. The tooth bases adjoin, appearing as a single unit that shows little surface differentiation or constriction, though cleavage planes between the individual teeth can be seen upon careful examination. The cusps are relatively low, lower than the base, and seem to have been eroded in certain specimens. The tips

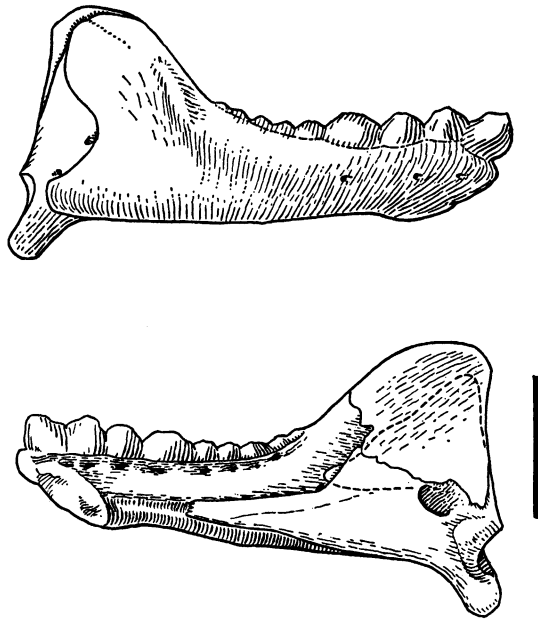


FIG. 16. Views of the right mandible of *Trogonophis wiegmanni* (M.C.Z. No. 27373). Top labial, bottom lingual. The line equals 2 mm. to scale. Drawn by P. Adams.

are conical, with faint lateral compression and a pattern of fine grooves radiating from the tip, particularly on the lingual aspect. The two anterior teeth are highest and appear to curve forward. The third tooth is slightly lower, while the fourth is still lower and by far the widest of the entire series. The fifth and sixth teeth are very much reduced in height, and the seventh, eighth, and ninth are little more than nubbins on the tooth ridge.

A dentary canal enters the central cavity of each of the four anterior teeth and opens as a lingual foramen in the groove ventral to the tooth base. There is a faint indication of similar foramina below the posterior teeth, but no canals could be traced, nor were any central cavities visible within the tooth bases.

Three (Meckelian?) foramina, two large anterior and a small posterior one, open on the labial face of the dentary. A ridge, the development of which shows some individual variation, starts below the last three teeth and continues posterodorsad parallel to the dorsal edge of the dentary. The ridge attains

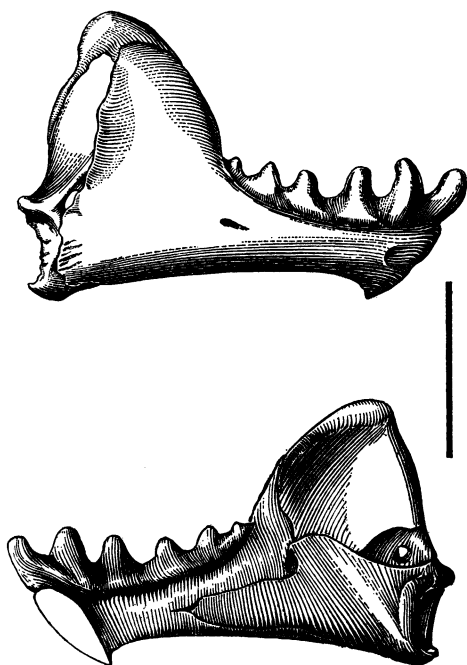


FIG. 17. Views of the right mandible of *Pachycalamus brevis* (A.M.N.H. No. 73424). Top labial, bottom lingual. The line equals 2 mm. to scale. Drawn by S. B. McDowell.

its maximum size just posterior to the last tooth and may overhang posteriorly in this region.

The Meckelian canal is closed lingually along most of its length. Anteriorly this closure is formed by the prearticular, a bone that posteriorly is in contact with the lower edge of the coronoid and is fused to the articular. The coronoid is exposed labially along the entire top of the coronoid ramus.

The surangular is pierced by two foramina, one foramen just opposite the apex of the articular facet, and the second in the center of the ramal fossa at the point of its most rostral lateral exposure.

PACHYCALAMUS

The mandible of *Pachycalamus* (fig. 17) shows the shortest relative tooth length and highest coronoid ramus among the four species examined. Consequently, it has the least depression of the articular surface below the tooth line. The anterior tip of the mandible is bent medially, and the symphyseal shelf

is clearly expressed. The shelf projects ventrad from the front of the faintly concave ventral edge of the mandible. The ventral edge of the glenoid fossa projects beyond the ventral edge of the mandible, and there is no retro-articular process.

The six teeth are of oval cross section, with rounded tips. The anteriormost projects anterodorsad and is slightly curved near its tip. The next three teeth decrease in size, the fourth and fifth are approximately equal, and the sixth is but a nubbin. The second, third, and fourth teeth also curve but not so markedly as the first. With the mandible *in situ*, this curvature of the teeth directs them normal to the biting surface. The bases of the several teeth appear to be fused, and the cusp height is less than the base height except for the first tooth.

A groove in the lingual surface of the dentary lies immediately ventral to the fused tooth base. A series of shallow depressions, one for each tooth, lies within the groove. The labial foramina are two in number and lie ventral to the second and sixth tooth. There is no ridge on the labial surface of the dentary.

The surangular has a vertical ridge parallel and just posterior to the rear edge of the dentary. The surangular foramen can be seen through the gap between these two bones just above the glenoid fossa.

The cup of the glenoid fossa extends medially, and its thickness is far greater than that of the anterior portion of the mandible. No definite sutures can be noted, but a faint line (or rather a difference in texture or transparency) indicates that the articular forms the inside (bearing surface) of the fossa as well as the lingual surface of the articular boss.

The pre-articular is relatively short and ends below the second tooth.

DIPLOMETOPON

The coronoid process of *Diplometopon* (fig. 18) is not so high as that of *Pachycalamus*, but the mandible differs from that of the latter species in having a sharply ascending tooth line, so that the distance between the contact line of the teeth and the glenoid fossa is far greater. The fossa is located at

the ventral edge of the mandible, so that there is no retro-articular process. The symphyseal shelf is very poorly developed.

The six teeth show decided lateral compression, and their cusps have marked anterior and posterior edges. They appear triangular in lateral view and seem to have fused into a single row. The anterior three are of equal size, and the last three decrease in sequence.

A groove lies ventral and parallel to the line of tooth fusion, and a series of foramina at its base mark the openings of the dental canals. The anterior labial (Meckelian) foramen (sometimes emerging as a pair of canals leading to a single fossa) opens near the tip of the dentary. The posterior and much smaller foramen lies near the posterior end of the tooth row.

The Meckelian canal (which seems to open on the labial side in all these species) is closed anteriorly on the lingual side. The increasing gap between the overhanging sides of the dentary is closed by the pre-articular. Posteriorly there is a rise of the dorsal margin of the canal, so that the entire coronoid ramus is hollow.

The coronoid of *Diplometopon* is as large as that of *Pachycalamus*, though slightly less of it is exposed in labial view. It does cover most of the lingual surface of the coronoid ramus. A thin anterior wing of the surangular extends dorsad between coronoid and dentary. The exact size of the wing cannot be determined without destructive dissection. It appears to be limited ventrally at the level of the glenoid fossa. Posteriorly the surangular is fused to the articular. Just dorsal to the glenoid fossa the surangular is perforated by two foramina, of which the dorsal foramen is much the larger.

The articular is apparently restricted to the glenoid fossa proper, although the sutures are fused, and description must be uncertain. The glenoid fossa forms an elongate cylindrical surface projecting medially out of the mandibular plane.

The triangular pre-articular appears to fuse to the articular below the lip of the glenoid fossa. The pre-articular forms the ventral edge of the Meckelian fossa, anterior to which it sends a very thin plate dorsad to

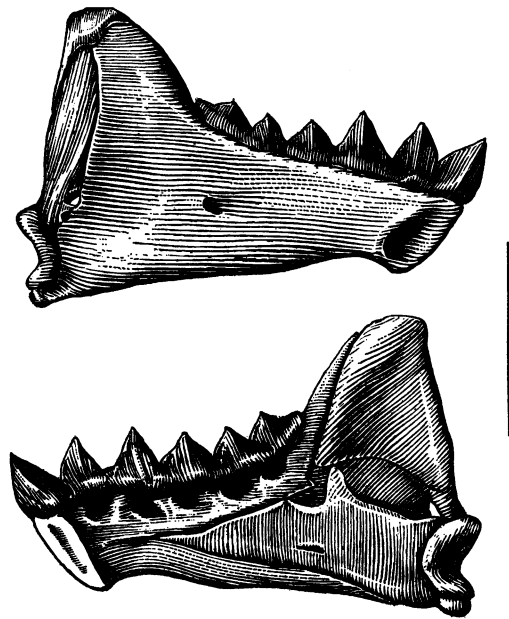


FIG. 18. Views of the right mandible of *Diplometopon zarudnyi* (C.N.H.M. No. 74007). Top labial, bottom lingual. The line equals 2 mm. to scale. Drawn by S. B. McDowell.

the ventral edge of the coronoid. A small foramen pierces the pre-articular near its midpoint.

AGAMODON

The mandible of *Agamodon* (fig. 19) is the most striking among the mandibles of the species discussed, mainly because of the relatively large region taken up by the tooth row. The tooth line swings posteriorly in an ascending curve rather than a straight line, but is not displaced so far dorsad to the glenoid fossa as is that of *Diplometopon*. The fossa itself lies slightly higher than in the latter form, so that there is an indication of a retro-articular process at the posteroventral apex of the mandible. There is a large symphyseal shelf.

In shape the individual teeth are similar to those of *Diplometopon*. The forward-slanting first tooth is by far the largest, and the following three teeth are only one-half as high and rise vertically. The last tooth is much reduced in size and curves sharply backward, so that it seems to fold into the anterior edge of the coronoid ramus. The teeth seem to

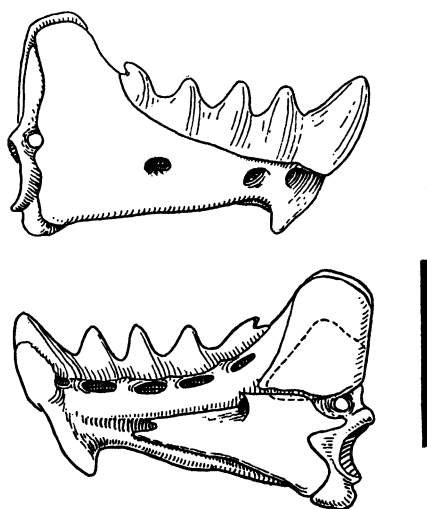


FIG. 19. Views of the right mandible of *Agamodon anguliceps* (M.C.Z. No. 10784). Top labial, bottom lingual. The line equals 2 mm. to scale. Drawn by P. Adams.

have fused, but a faint fracture or junction line can be seen between each pair. The first teeth of the two mandibular rami are flattened where they are in contact with each other.

There are three labial (Meckelian) foramina that are discrete and do not open into the bottom of a single groove as in some of the previous forms. A series of large fossae is aligned below the individual teeth. Only narrow struts of bone rise between these to abut the points where two teeth adjoin. The teeth seem to be hollow and very poorly fused to the tooth-bearing edge.¹

The coronoid and surangular show little difference from the condition described for *Diplometopon*. However, only a single foramen, rather than a pair of foramina, is exposed in the surangular between the top of the glenoid fossa and the posterior edge of the dentary. What seem to be the articular sutures are not fused in my specimen, and it can be seen that the articular covers only the articulating surface of the glenoid fossa and does not extend dorsad beyond the level of the surangular foramen.

¹ Some possible implications of this phenomenon are discussed above in the description of the skull of this species.

ANTERIOR VERTEBRAL COLUMN

GENERAL COMPARISON

The vertebral column of the acrodont species forms the topic of a separate study. However, certain aspects of the functional analysis, which is presented in the second part of the present paper, make it desirable to describe certain modifications at this time. The description emphasizes modifications of the anterior column as a unit and is restricted to those details immediately related to the functional discussion.

The anterior vertebral column of all four species is characterized by (1) the presence of high neural arches with elongate neural spines, (2) the presence of hypapophyses, and (3) a general shortening of the length of each vertebra. The neural arches of the anterior region project farther caudad than the posterior ones, so that they lie dorsad to the centrum of the following vertebra. The atlas is composed of a pair of neural-arch halves and a midventral hypocentrum (scheme a-1; Remane, 1936, p. 104). The axis of all species but *Agamodon* bears two hypapophyses (scheme b-4; Remane, 1936, p. 104).





There is a very definite trend towards a shortening of the anterior column (fig. 20) from *Trogonophis* to *Pachycalamus*, *Diplometopon*, and *Agamodon*. There is also an increase in the height and number of the neural spines (table 3). The most highly modified condition is encountered in *Agamodon* in which the second and third vertebrae appear to have fused into a single unit. In *Trogonophis*, *Pachycalamus*, and *Diplometopon* the increased height of the neural spines has been achieved by the addition of a mid-dorsal plate. In *Agamodon* it is produced solely by the angulation and posterior elongation of the neural-arch roof.

TROGONOPHIS

The neural arches of this species angle posterodorsad, and the spines are expressed as a series of midarch ridges, of little more height than the thickness of the neural-arch roof. The height of the spines diminishes caudad.

The hypapophyses project from the extreme posterior edges of the centra. The first ribs are carried by the fourth vertebra rather

TABLE 3
CHARACTERS OF THE ANTERIOR VERTEBRAL COLUMN IN THE TROGONOPHINAE

	<i>Trogonophis wiegmanni</i>	<i>Pachycalamus brevis</i>	<i>Diplometopon zarudnyi</i>	<i>Agamodon anguliceps</i>
Vertebrae bearing hypapophyses	1-8	1-7	1-8	1-11
Vertebrae bearing neural spines	2-8	2-7	2-20+	2-20+
Shape of neural arch in cross section				
Postcranial unit bearing first rib	4	4	4	3
Composition of axis				
Neural arches	2	2	2	2+3
Pleurocentra	1+2	1+2	1+2	1+2+3
Hypocentra	2+3	2+3	2+3	2+3+4

than the third as in *Amphisbaena*, *Rhineura*, and other forms.

The atlas and axis of *Trogonophis* show a typical lizard-like condition. The axis is fused in the adult, and only the faintest discontinuity indicates the separate origin of the first hypapophysis. The axis of a juvenile specimen (U.S.N.M. No. 12318) retains discrete sutures, and it may be confirmed that the posterior pleurocentrum (p2), completely fused with its neural arch (na2), is discrete from the anterior pleurocentrum (p1) that forms the odontoid process. The two hypocentra (h2, 3) form the hypapophyses and contribute to the ventral portion of the centrum. The posterior hypocentrum (h3) of the juvenile has already started to fuse to pleurocentrum 2, which is of interest as all more posterior hypapophyses of the specimen have already fused to the point at which the sutures are no longer apparent.

The elongate cartilaginous point of the odontoid process fits into and articulates with the central region of the U-shaped (in cross section) occipital condyle and projects between the two dorsal (exoccipital) horns thereof. The process is concave in sagittal, and convex in horizontal, section. This arrangement coupled with the deep condylar cup provides a relatively stiff yet strong head joint.

PACHYCALAMUS

The general arrangement of the anterior column is similar in *Pachycalamus*. The most

notable differences lie in the shape of the neural arches and spines. These are triangular in dorsal view, with the spines produced by a sharper angulation of the neural arches and by much higher ridges than those of *Trogonophis*. The dorsal tip of the spines terminates in a heavy protuberance which is most strongly expressed on the fifth and sixth vertebrae.

The hypocentrum of the axis is very much smaller than that of *Trogonophis* and is only partly visible in lateral view. The odontoid process of the axis is more elongate, and the two hypocentra have fused into a single ventral plate, containing a pair of central cavities. The third vertebra is very short, and its neural spine is very close to that of the axis.

DIPLOMETOPON

The anterior neural arches of *Diplometopon* are triangular in dorsal view and similar to those of *Pachycalamus*, except that the overlap onto the posterior vertebra has disappeared by the seventh vertebra. The anterior vertebrae have a much more steeply gabled neural arch than the posterior ones. All the spines bear a heavy dorsal protuberance. The extreme height and very gradual disappearance of the spines along the column give this species an entirely different aspect from that of the previously described ones. The close arrangement of the anterior vertebrae would seem to reduce dorsoventral flexibility.

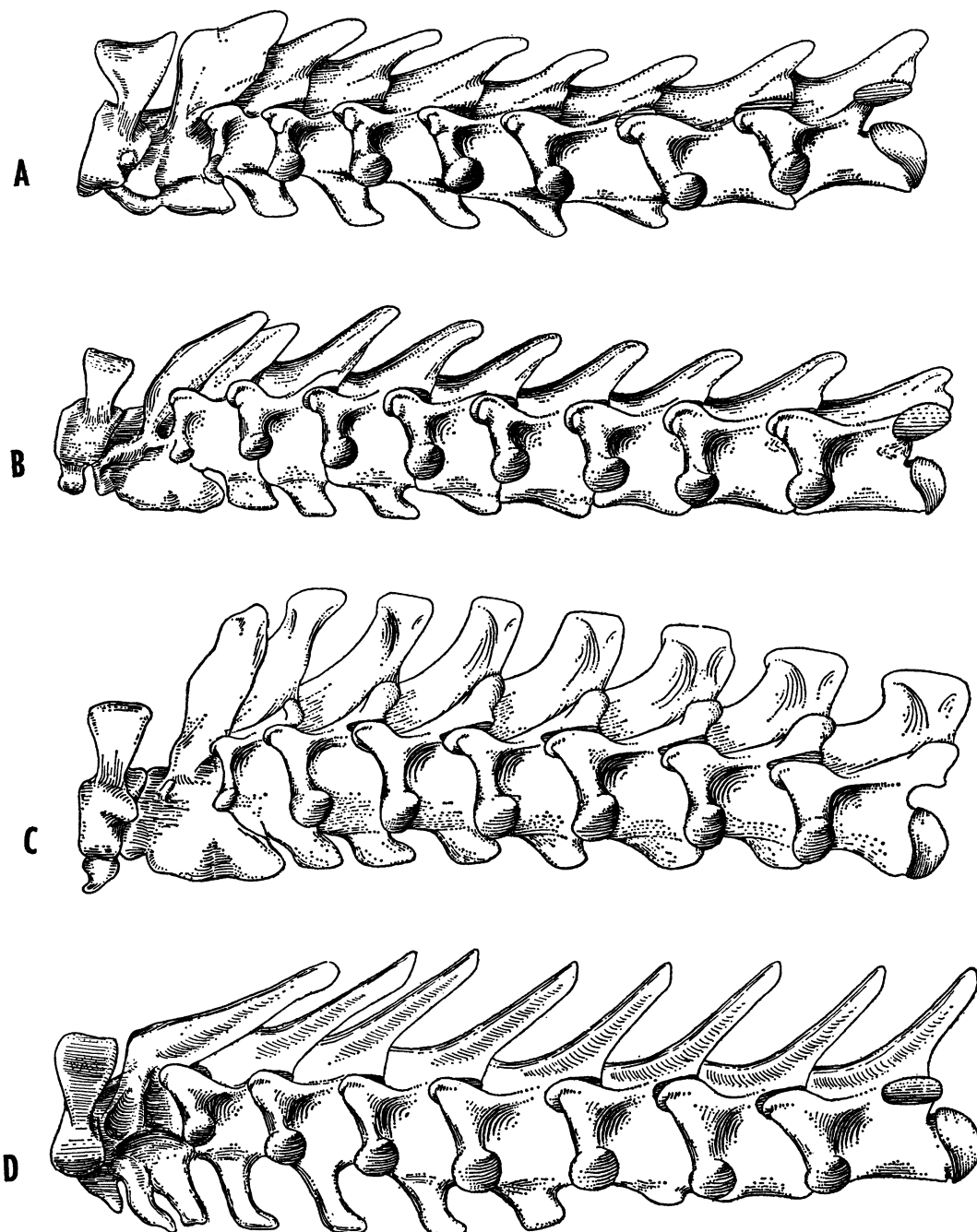


FIG. 20. Lateral views of cervical and anterior thoracic vertebrae. A. *Trogonophis wiegmanni* (M.C.Z. No. 27373). B. *Pachycalamus brevis* (A.M.N.H. No. 73424). C. *Diplometopon zarudnyi* (C.N.H.M. No. 74007). D. *Agamodon anguliceps* (M.C.Z. No. 10784; several broken parts restored from M.C.Z. No. 38697). Drawn by W. A. Auffenberg and R. O. Beach.

The hypocentrum of the atlas is relatively large and bears a prominent, cranially directed ventral process. The neural-arch halves of the atlas have prominent transverse processes, while those of the axis are much smaller and *in situ* are located immediately posterior to the atlantean ones.

The juvenile specimen C.A.S. No. 84588 differs from the adults in retaining an unfused axis and demonstrates that the participation of various components does not differ from the condition described for *Trogonophis*.

AGAMODON

The anterior column of *Agamodon* would seem to be the most highly specialized one among the columns of the acrodont species. The neural spines consist of flat, square-ended plates that angle sharply dorsad at approximately 60 degrees and represent an extension of the neural arch proper rather than a separate shelf or spine. There is no protuberance at the dorsal tip. Caudad the spines become shorter and their inclination is reduced, though they continue well into the thoracic region. The shortening and increased height of the anterior vertebrae seem to produce a decided reduction of dorsoventral flexibility.

The axis of *Agamodon* (fig. 21) is of particularly startling appearance. It seems to have fused with the next posterior vertebra so that it includes three pleurocentra (p1, 2, and 3). While the sutures between the posterior sections are fused in both specimens, the above conclusion was arrived at on the following evidence:

1. The presence of three distinct hypapophyses. The anterior pair of these still show the suture lines in M.C.Z. No. 10784, while the posterior one is fused to the body of the vertebra, as are all the hypapophyses of the postaxial vertebrae.

2. The presence of a vertical ridge running down the middle of the vertebral body, with a transverse process protruding from its midheight. The anterior transverse process has disappeared because of the caudad shift of the articulating surfaces of the atlas on the odontoid process. A small but distinct element may still be discerned (on M.C.Z. No. 10784) on the site normally taken up by the transverse process, a site that is now part of the articulating surface (and hence invisible in the lateral view of the articulated column).

3. The presence of a faint vertical fold or line of fusion as well as of a large foramen in the center of the vertebral body, just anterior to the vertical ridge. A continuation of this

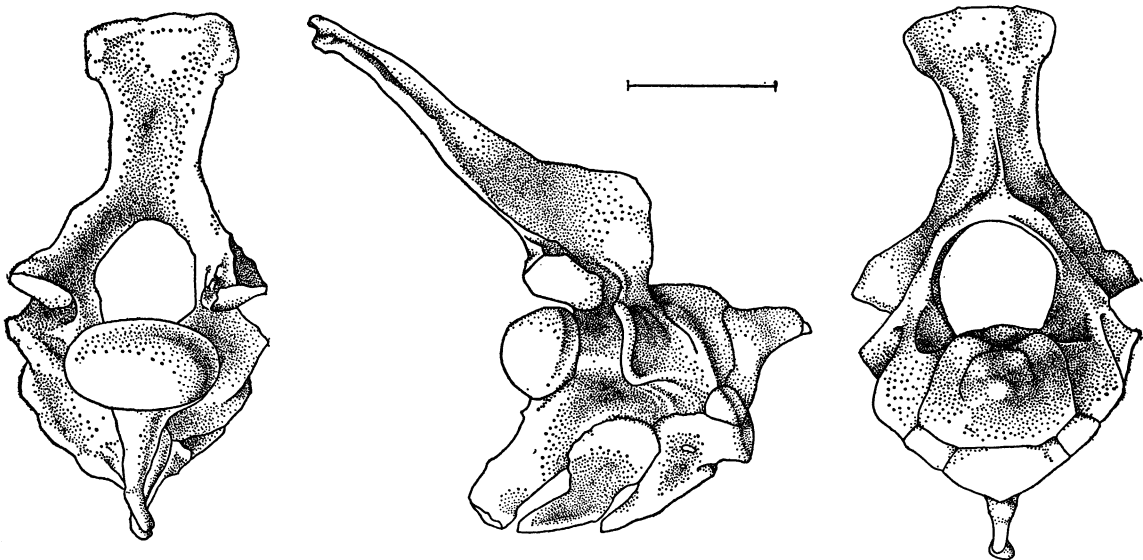


FIG. 21. Anterior, lateral, and posterior views of the fused second and third vertebrae of *Agamodon anguliceps* (M.C.Z. No. 10784). The line equals 1 mm. to scale. Drawn by M. Franson.

line angles dorsad onto the neural arch. It is possible to trace a suture across the neural arch in M.C.Z. No. 38697.

4. The presence of a fully developed rib on the "first," instead of second, postaxial vertebra. This is the only instance of this in the subfamily.

If the interpretation that fusion has occurred is correct it would represent a unique situation in amphisbaenids, with neural arches 2 and 3, pleurocentra 1, 2, and 3, hypocentra 2, 3, and 4 all contributing to the formation of the axis. It might be interesting to investigate the possibility of the existence of a similar condition in *A. compressus* and *A. arabicus*.

HYOID

Knowledge of the reptilian hyoid was summarized by Fürbringer (1919, 1922), while Camp (1923), Richter (1933), and others have figured additional species of lizards since that time. Of the species discussed here, the hyoid of *Trogonophis* was figured or discussed by Smalian (1884), Fürbringer (1919, 1922), and Richter (1933), and that of *Agamodon* by Peters (1882). Zavattari (1910) figured only the hyoid musculature (of *Agamodon*).

The hyoids of the four acrodont species (fig. 22) were prepared by dissection. Tissue identification was checked in several cases by gross differential staining with methylene blue and alizarine. If the variety of patterns described for various amphisbaenids is considered, the acrodont patterns are remarkably similar. In each case the hyoid consists of the cartilaginous corpus, processus lingualis, cornua hyalia and cornua branchialia II, and the ossified cornua branchialia I. Differences are shown only in arrangement and relative length of the arms and processes. It might be mentioned that breaks or fracture lines in the cartilaginous matrix form the source of spurious differences. Such lines can be noted particularly at the base of arms or at similar loci of stress concentration (or fusion?). These lines seem to be artifacts produced by partial desiccation of this extremely fragile material (compare pl. 4, fig. 16, of Bedriaga, 1884, with pl. 6, fig. 22, of Smalian, 1884; both show the hyoid of *Blanus*).

In the series from *Trogonophis* to *Pachy-*

calamus to *Agamodon* there exists a trend towards reduction in the length and simultaneous widening of the cornua branchialia I, as well as an increase in the length of the cornua branchialia II. *Diplometopon*, however, has relatively longer cornua branchialia I than does *Pachycalamus*. *Diplometopon* and *Trogonophis* are, furthermore, the only forms in which these horns swing sharply outward, including an obtuse rather than an acute angle.

The hyoid of *Trogonophis* is notable only in its relatively short second branchials and distinctly elongated first branchials and by the angled rather than gradually curved cornua hyalia. The hyoid of *Pachycalamus* may possibly be distinct in the angle included between the first branchial horns and in the shape of the tips of the hyoid horns.

In *Diplometopon* the corpus lies ventral to the anterior portion of the trachea, and the cornua branchialia turn dorsad and embrace the lateral aspects of the trachea. The rod-shaped processus lingualis points towards the mandibular symphysis. The cornua hyalia swing rostrad from the sides of the corpus, and their cylindrical arms end in plate-like sheets next to the lingual edge of the mandibles. The cornua branchialia I attach to the corpus by suture and then swing posterolaterad in an anteriorly concave curve. These bony horns are white, or rather colorless, in alcoholic specimens and thus differ from the opaque pink of the cartilaginous portions. The cornua branchialia I contain a central cavity. In the juvenile specimen C.A.S. No. 84588 they have just started to ossify. Two of the specimens dissected had the first branchial horns proceeding posteriorly at a slightly smaller included angle than the one shown in figure 22.

The hyoid of *Agamodon* differs from that of *Diplometopon* by its longer and narrower over-all shape, and by the blade-like extensions on the tips of the cornua branchialia I. These horns are shortened to one-half of the relative length of those in *Diplometopon*.

PECTORAL GIRDLE

The only trogonophine pectoral girdle previously described is that of *Trogonophis* which has been figured or commented upon by Wagner (1841, pl. 13, fig. 23), Fürbringer

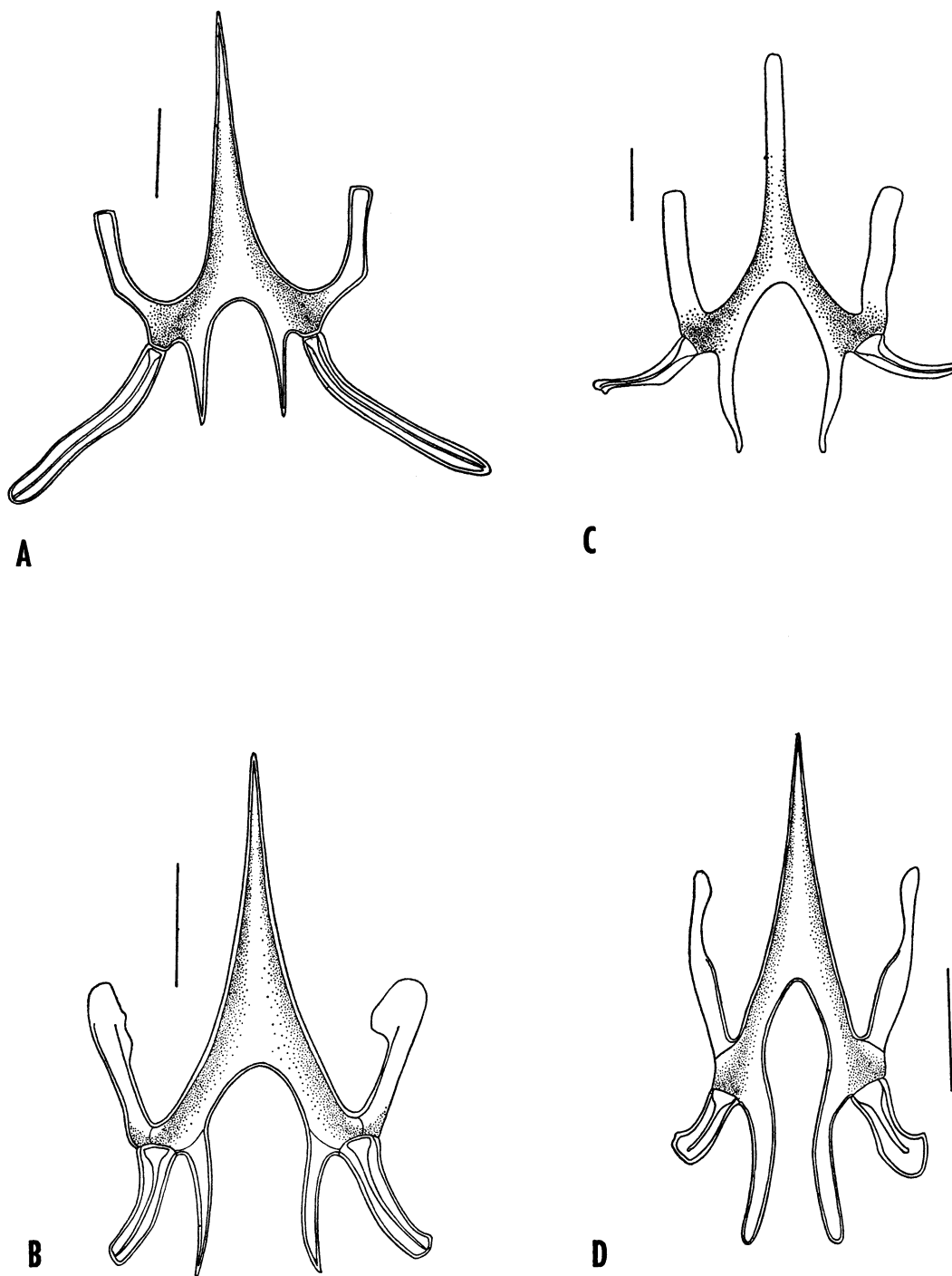


FIG. 22. Hyoids. A. *Trogonophis wiegmanni* (M.C.Z. No. 27373). B. *Pachycalamus brevis* (A.M.N.H. No. 73424). C. *Diplometopon zarudnyi* (C.N.H.M. No. 74007). D. *Agamodon anguliceps* (M.C.Z. No. 10784). The line equals 1 mm. to scale. Drawn by P. Washer.

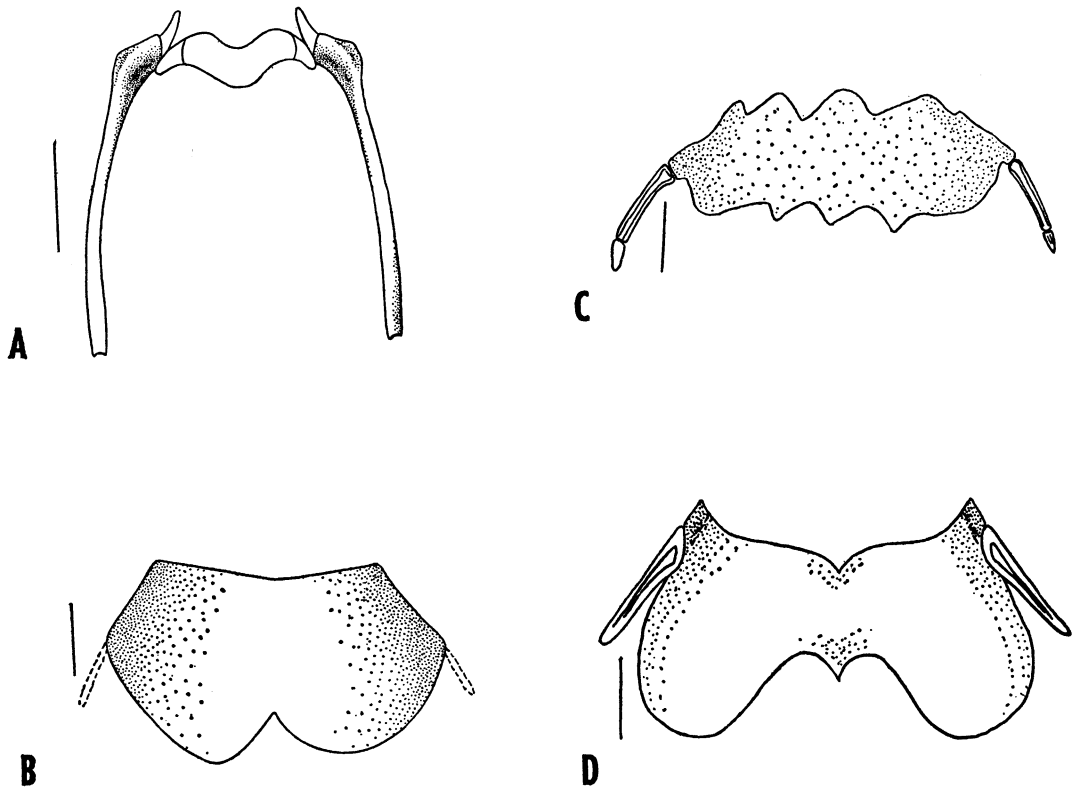


FIG. 23. Shoulder girdle remnants of the four species of the Trogonophinae. A. *Trogonophis wiegmanni* (M.C.Z. No. 27373). B. *Pachycalamus brevis* (A.M.N.H. No. 73424). C. *Diplometopon zarudnyi* (C.N.H.M. No. 74007). D. *Agamodon anguliceps* (M.C.Z. No. 38697). The line equals 1 mm. to scale. A and B drawn by P. Washer.

(1870, p. 75), Smalian (1885, p. 194), Fürbringer (1900, p. 261), Müller (1900, p. 32) and Zangerl (1945, p. 768¹). As the condition found in *Trogonophis* differed from that exhibited by any pleurodont species, it was accorded considerable attention.

In *Trogonophis* (fig. 23A) the girdle is composed of three elements: a cartilaginous central yoke, the sternum, and a pair of lateral rods, the scapulocoracoids (Fürbringer, 1900). The sternum lies immediately below the skin, while the two lateral elements are but loosely tied to it by the ligamentum sternocoracoideum and are quite deeply sunk into the musculature. The scapulocoracoids are bony and have a central canal and an approximately circular cross section. Anteriorly

¹ Zangerl mentioned that he was unable to find the pectoral girdle in his cleared and stained specimens and suggested that it might have been removed during the skinning process.

they curve mediad, and their proximal tips are widened as if to provide attachment surfaces for muscle fibers. A small medial element attaches to the anterior aspect, though this may be but an expanded terminal cartilage.

While the other acrodont genera differ strikingly in general appearance, it is possible to derive their condition from that exhibited by *Trogonophis*. In each case there is a large but thin, central, cartilaginous plate which may have or lack single or jointed lateral appendages. The central cartilaginous plate quite probably corresponds to the sternum, and the lateral elements to Fürbringer's (1900) scapulocoracoid. Whether the distal portions of the lateral elements are remnants of the scapula proper or rather secondarily separated portions of the fused scapulocoracoids is open to question. Confirmation of these suppositions would of course involve

embryological and myological study of the region.

It is again possible to establish a morphological series, this time one running *Trogonophis*-*Diplometopon*-*Agamodon*-*Pachycalamus*. The terminal position of *Pachycalamus* is suggested by the almost complete reduction of the scapulocoracoids in this species. These elements are indicated only as traces of unossified connective tissue on the lateral extremities of the simple, cartilaginous sternal plate. The above sequence differs from the sequences suggested by every other character here discussed. It indicates the danger of using "degeneration rates" of "useless" structures in the establishment of phylogenies and furthermore reemphasizes the fact that modifications of diverse structures need not proceed in parallel.

The large but thin cartilaginous sternum found in *Pachycalamus*, *Diplometopon*, and *Agamodon* is immediately apparent on removal of the skin of the posterior throat region. The sternal plate lies on the ventral surface of the neck musculature and is loosely tied to this by connective tissue. The plate is semitransparent and of almost the same color as the underlying musculature, though it may turn black upon exposure to air.

In *Diplometopon* the sternum has an irregular outline and is generally asymmetrical. It has a pair of very definite bony appendages that attach to its anterior corners and slant posterodorsad *in situ*. These scapulocoracoids are rod-shaped and divided into unequal portions by a pair of sutures. Unstained they differ from the cartilaginous central plate by their pinkish color, their central canal, and by a texture and rigidity approaching those of the ribs. The distal element is small, and it is impossible to be certain about the presence of a central cavity. Though the scapulocoracoids were tied into the muscles of the sides, their exact method of attachment was not studied. They had not yet ossified in the (109+10 mm.) juvenile.

The girdle of *Agamodon* is similar to that of *Diplometopon* in that it consists of a cartilaginous sternum and a pair of bony lateral appendages. Yet the shape of the plate differs decidedly, and the lateral bony elements are much shorter and single. They are set at a sharp angle to the sternum and ascend

sharply into the lateral musculature.

It must be mentioned that the lateral elements were either absent or went unnoticed on the first specimen examined (M.C.Z. No. 10784). There thus exists the possibility that these degenerate structures may be exposed to considerable variation.

MISCELLANEOUS TOPICS

A check of the literature disclosed two items that seemed to suggest special modifications within this subfamily.

DERMAL INNERVATION

As far as known, all amphisbaenids except *Blanus* (which has but one annulus) have two dermal annuli per trunk segment. Camp (1923, p. 399) quoted Smalian (1884, as 1885) to the effect that *Trogonophis* "is fundamentally different from the New World forms (*Amphisbaena*, *Anopsibaena*, *Rhineura*) for each segment of the skin is innervated by a separate nerve (Rami lateralis of ventral branches of spinal nerves)." He cited the example as furnishing possible evidence for a reversal of the usual pattern of skin metamorphism.

Camp was unfortunately incorrect, both on the factual point and in the Smalian citation. Smalian actually wrote (1884, p. 137): "wie bei der spanischen Form (*Blanus*) treten die Nerven in die Mitte der Hautringe ein; doch herrscht in so fern Alternation, als ein Ring einen Nerven bekommt, der andere eines solchen entbehrt" (italics mine). Innervation was checked for *Trogonophis* (U.S.N.M. No. 12318), *Pachycalamus* (U.S.N.M. No. 60653), *Diplometopon* (M.C.Z. No. 57176, C.A.S. No. 84599), and *Agamodon* (M.C.Z. No. 38697), as well as for a large number of other species of amphisbaenids, and was found to be single throughout.

REDUCTION OF RIGHT LUNG

Bedriaga (1884, p. 63) found only a single lung in *Trogonophis*, while Smalian (1884, p. 189) correctly stated the right lung to be but two-thirds of the length of the left.

Butler (1895) in his classical paper on lung-reduction patterns in elongate Squamata reported on 11 species of amphisbaenids. For all amphisbaenine (*Amphisbaena*, *Blanus*, *Anops*=*Anopsibaena*) or rhineurine (*Mono-*

peltis, *Lepidosternon* = *Leposternon*) genera the right lung was referred to as "small," rudimentary, or absent. It was only for the two acrodont species that the length of the right lung was sufficient to be expressed as a fraction of the left. Summarizing values from the literature and personal observation, we get:

Trogonophis

Smalian, approximately $\frac{2}{3}$; Butler, 0.60; U.S.N.M. No. 12318, 0.58
Range, 58–65%

Pachycalamus

Butler, 0.25, 0.33; U.S.N.M. No. 60653, 0.26
Range, 25–33%

Diplometopon

C.A.S. No. 84588, 0.30; M.C.Z. No. 57176, 0.25
Range, 25–30%

Agamodon

M.C.Z. No. 38697, 0.40
Range, 40%

The summary indicates that all trogonophine genera are characterized by the presence of a partially functional right lung, another item characterizing them as a group. This lung is largest in *Trogonophis*, a genus the primitive position of which is indicated by several other characters. As the ancestral stock of the Trogonophinae undoubtedly had two fully functional lungs, the minor degree of reduction would reinforce the conclusion that *Trogonophis* retains a relatively unspecialized character pattern. It is also of interest to note that the left (read right) lung of *Bipes canaliculatus*, a member of the only limbed, and hence presumably fairly primitive, amphisbaenine genus, is listed by Meckel (1819, p. 222, as *Chirotus*) as 20 per cent of that of the right (read left). While the right lung of this form is thus proportionately larger than that of any other species of pleurodont amphisbaenid, it is more reduced than the right lung of any trogonophine.

TAXONOMIC CONCLUSIONS

The preceding descriptions were designed to permit decisions on certain questions regarding the relations of the acrodont amphisbaenids. The more immediate of these were: 1. Is *Diplometopon zarudnyi* a good species of acrodont amphisbaenid? 2. What other species are there within the Trogonophinae? 3. What are the relations of these species to one another? 4. What are the relations of these species to the pleurodont amphisbaenids? It was hoped that the last two questions would indicate whether or not the Trogonophinae (*sensu* Vanzolini) represented a natural grouping. All these questions had to be considered on the basis of the recent forms here discussed, as no acrodont amphisbaenids have been reported from the fossil record.

1. It is possible to give an affirmative answer to the first question. *Diplometopon* is definitely acrodont and, while allopatric to the other acrodont species, is markedly distinct from them in a variety of major characters.

2. The limitations of the available material make it more difficult to issue an absolute answer to the second question. *Trogonophis wiegmanni*,¹ *Pachycalamus brevis*, and *Aga-*

modon anguliceps undoubtedly represent valid species. There is some doubt regarding the assignment of *Agamodon compressus* and *A. arabicus*. No specimen of either species was available for examination, nor was it possible to examine *A. anguliceps immaculatus*, which Loveridge (1941) had placed in the synonymy of *A. compressus*.

A study of all available literature citations tended, however, to confirm Loveridge's hypothesis that at least two valid species existed in the genus *Agamodon*. Thus *A. anguliceps* and *A. compressus* appear to be sympatric, as the former has been reported (Anderson, 1901; Calabresi, 1915; Scortecchi, 1931) from the two sites (Brava and Mogadish) at which *A. compressus* has been collected (Boulenger, 1897; Calabresi, 1915). Of the characters listed as differentiating these two forms, I should have most confidence in the presence of the laterally upturned cephalic shields in *A. compressus*. Secondary characters would be the lateral compression of the body, the presence of 144 to 160 rather than 127 to 137 annuli on

¹ Hediger (1935, p. 13) presents reasons for the possible presence of a second and unicolored species of this genus in Morocco.

the body and of 22 to 23 rather than 15 to 19 annuli on the tail (table 1).

In the establishment of this hypothetical scheme, it is necessary to take exception to Loveridge's assignment of *A. anguliceps immaculatus* Calabresi, 1927, to the species *A. compressus*, an assignment that was apparently made for the reason that the count of body annuli of the type (143) was much closer to that of *A. compressus* than to that of *A. anguliceps*. Calabresi was a careful worker and had seen both species (Calabresi, 1915, 1927). She should certainly have been able to distinguish them by the form of the head shields and the lateral compression of the body. Her type, furthermore, had 18 caudal annuli, four fewer than the lowest known count for a specimen of *A. compressus*. The type locality of the race was Afghedud, more than 300 miles north of any previous record for either species. Geographic variation may thus be involved, and it is suggested that *immaculatus* be retained as a race of *A. anguliceps* until more material becomes available.

Similar problems exist in the determination of the status of *A. arabicus*, a species known from the type only. In head shape and number of caudal annuli this species reminds one of *A. anguliceps*. It might be considered to be a race continuing a possible northward trend towards increased number of body annuli and greater lateral compression, were it not for the rather aberrant arrangement of the minor cephalic shields. This arrangement incorporates such factors as a vertically split ocular scale. The species had best be maintained until additional specimens from Arabia or the horn of Africa, or from both areas, become available.

3. The three species described within the genus *Agamodon* appear to form a satisfactory generic assemblage. They share such characters as the azygous frontal scale and the peculiarly modified scalation of the dorsal and ventral sulci. No character now known suggests that the assemblage is unnatural.

Pachycalamus brevis, *Diplometopon zarudnyi*, and *Trogonophis wiegmanni* are here shown to differ from *Agamodon (anguliceps)* and from one another in a number of ways, with major characters differentiating between these species in virtually every organ system examined. The differences are suffi-

cient to leave little doubt of the generic distinctness of these species.

It has been suggested that the four forms here discussed be included in a single genus and that the existing differences be pointed out by the erection of subgenera. Such a procedure would imply a closeness of relation that almost certainly does not exist. The present arrangement appears adequate and is therefore retained.

4. Beyond the fact that these species represent distinct genera it is possible to make some further statements regarding their probable relation to one another and to the remaining amphisbaenids.

Vanzolini (MS, 1951) divided the amphisbaenids into three subfamilies: the pleurodont Amphisbaeninae and Rhineurinae, and the acrodont Trogonophinae. The amphisbaenines were stated to trend towards lateral compression of the head, and the rhineurines towards dorsoventral compression of the head. The trogonophines, of which Vanzolini recognized only *Trogonophis*, *Pachycalamus* (with a range including Persia) and *Agamodon*, were separated primarily because of their acrodont dentition. The present study confirms the conclusion that the acrodont species form a natural group, as they share a considerable number of additional characteristics.

The first and most important item from my point of view is the demonstration of a specialized and different mode of burrowing coupled with the various characteristics that make this possible (see second section of this paper). Among these morphological features are the shortening of the skull and its division into two planes, the "widening" of the occipital region, the enlargement of the ascending process of the premaxilla, the shift of the bones roofing the orbit, which involves the wide dorsal exposure of the frontals and loss of the prefrontals, and the reduction in length of the tooth-bearing bones coupled with the simultaneous reduction in the number of teeth and the shortening of the anterior cervical vertebrae. Another characteristic, possibly correlated with a change in the mode of burrowing, is the enlargement of the stapes and extracolumella and the ossification of the latter. The acrodont amphisbaenids also share the relatively short and stout body, the

presence of a cartilaginous sternal remnant, the sizeable remnant of the right lung, the hyoid with cartilaginous cornua hyalia and cornua branchialia II as well as ossified cornua hyalia I, and finally the lack of caudal autotomy.

The very distinctness of the acrodont species makes it probable that they should be accorded full family status (as already proposed by Taylor, 1951, and Hoffstetter, 1955). This decision has been deferred to a subsequent paper, as it has not yet been possible to examine a sufficient number of the pleurodont forms.¹

In regard to the list of trogonophine "characteristics," it must be kept in mind that it represents a character pattern towards which the specializations appear to lead. Many of these characters are shown most clearly in *Diplometopon* and *Agamodon*, the most highly modified genera of the subfamily.

Trogonophis is almost certainly the most primitive or generalized acrodont genus. While it shows traces of all mentioned modifications, it retains a quite generalized structural pattern. Its head shape is more or less rounded, with only a beginning of the rostral shovel. The scutellation demonstrates such relatively primitive characters as contact between the nasals, few enlarged head shields, tendency towards a nuchal band of reduced scales, and strongly expressed lateral sulci. The skull shows premaxilla-parietal contact and strong reduction of the exposed frontal surface. It has prefrontals and epipterygoids and the highest number of teeth among acrodont forms. The extracolumella is cartilaginous and retains a fairly generalized arrangement. There is almost no shortening of anterior vertebrae, and both right lung and shoulder girdle show minimal reduction.

A character that could not conveniently be checked on the present material might also indicate the primitive nature of this species.

¹ It has also been suggested by Matthey (1949, p. 192) that the acrodont species represent a group of independent origin from the other amphisbaenids. This suggestion was based primarily on differences in chromosome arrangement observed in an examination of two (*Trogonophis wiegmanni* and *Rhineura floridana*) of the more than 100 species of amphisbaenids. An extrapolation of this order hardly deserves further comment.

Lynn and Komorowski (1957) in their discussion of the amphisbaenid thyroid mention a bipartite gland in *Trogonophis* as well as in all amphisbaenine and rhineurine species examined by them. *Diplometopon* (the only other trogonophine they examined) had a single gland. They unfortunately overlooked the implications of this fact, possibly because they followed the *lapsus calami* in Romer (1956, p. 564) by which *Diplometopon* is assigned to the subfamily Amphisbaeninae.

A further interesting point about *Trogonophis* is contained in Hediger's (1935) report of the birth of live young by this species, one of the two known cases in the amphisbaenids (Loveridge, 1941; 1955, p. 177).² Hediger reported that one of the embryos was still provided with a "sausage-shaped" yolk mass that stretched along its body. It would be useful to check this point in the other acrodont species, though the phenomenon of "ovoviviparity" does not exhibit any particular constancy in the Squamata.

Several of the characteristics of *Trogonophis* suggest that it may be structurally primitive not only within the Trogonophinae but also within the amphisbaenids in general. Its shoulder girdle is remarked upon (above) as showing the least reduction of the shoulder girdles of any non-limbed amphisbaenid species, its eyes are less degenerate than those of most members of this group (Angel and Rochon-Duvigneaud, 1942a, p. 166, 1942b, p. 256; Bellairs and Boyd, 1947, p. 91), its right lung shows the least reduction, and it is unique in the group in the possession of an epipterygoid. It is also the only amphisbaenid having the premaxilla in contact with the parietal, though such contact would seem to be a specialized rather than a primitive characteristic. These items cast some doubt on Vanzolini's suggestion (MS, p. 103) that the Trogonophinae may have originated from the "*Blanus-Bipes*" line. It is hoped that this matter can be discussed in a future paper.

² Bellairs (*in litt.*) advises me that he collected large numbers of *Trogonophis* at two places on the Algerian coast at times of the year when other reptiles were breeding, but never found a specimen containing recognizable embryos. He therefore thinks that the species may possibly be oviparous, at least in part of its range.

If *Trogonophis* is accepted as the most primitive acrodont genus, *Agamodon* and *Diplometopon* must be considered the most highly specialized. In spite of their superficial resemblance in head shape, they represent two distinct lines of specialization, as indicated by their many differences. Their resemblance in such characters as the presence of a bony, plate-like extracolumella can be considered the result of parallel adaptations to similar sets of requirements.

Pachycalamus seems in many respects to be intermediate between *Trogonophis* and *Agamodon*. Vanzolini (MS, p. 103) mentions it as a possible ancestor "in the morphological

sense at least" of the latter. However, *Pachycalamus*, though structurally closer to *Agamodon* than to *Diplometopon*, has been shown to possess many characteristics in no way intermediate between *Trogonophis* and *Agamodon*, which indicates that such a superficial morphological sequence may not approach the phylogenetic one very closely, and that *Pachycalamus* has evolved for a considerable distance from the ancestral stock leading to *Agamodon*.

Figure 24 depicts a dendrogram indicating the probable relationships of the four genera. Beyond this it is possible only to hope for a fossil record.

SUMMARY LIST OF SPECIES

The list of species is intended solely as a summary of taxonomic and distributional information. Detailed descriptive material inherent in the discussions and tables has not been repeated. The synonymies have been simplified by the omission of all general citations already listed by Loveridge (1941).

Only for the genus *Diplometopon*, for which no previous summary was available, has a complete bibliography been given.

Generic diagnoses are omitted from this paper, as it seems futile to separate "generic" and "specific" characters for the three monotypic genera, and only a single species of the

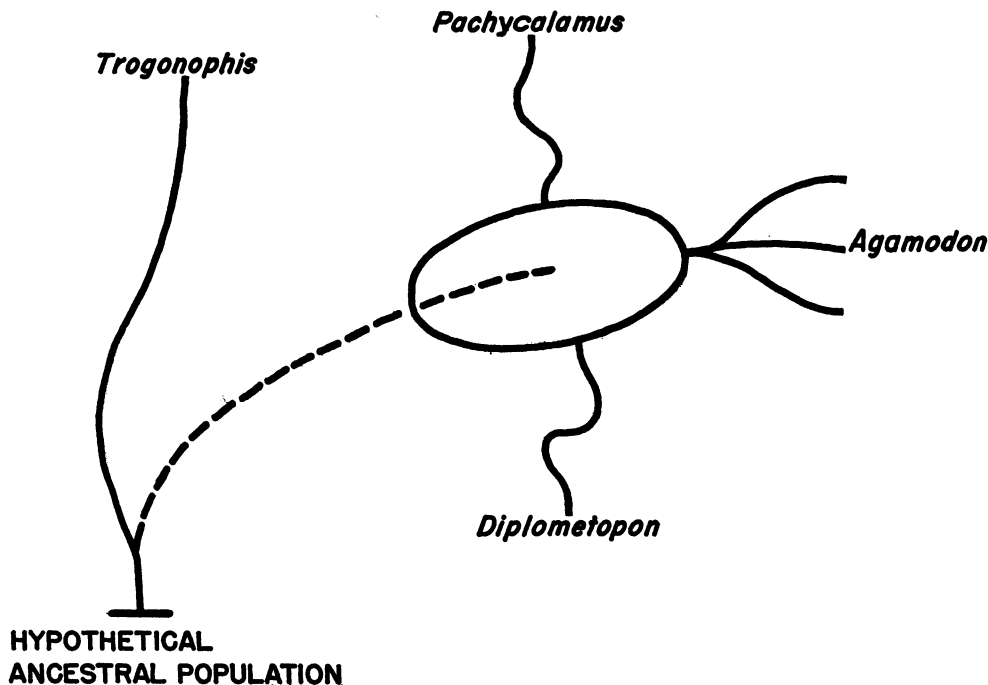


FIG. 24. Dendrogram indicating probable relationships of the four species of the Trogonophinae.

genus *Agamodon* has been examined thus far.

Specimens cited by museum number under Locality Records were examined by me unless preceded by an asterisk (*).

***Trogonophis wiegmanni* Kaup, 1830**

Trogonophis wiegmanni KAUP, 1830, p. 880.
Type locality: Unknown.

Amphisbaena elegans GERVAIS, 1835, p. 113.
Type locality: Algeria, Tangiers, and Zafarin Islands.

Trogonophis wiegmanni maroccana WERNER, 1931, p. 280. Type locality: Chella, Rabat; Agadir; Fes, Djebel Taghat; Morocco.

Trogonophis wiegmanni, LOVERIDGE, 1941, p. 360. *Trogonophis w. maroccana* is untenable as well as being a synonym of *A. elegans*.

RANGE: Northwest Africa: Morocco to Tangiers, west to Tunisia.

LOCALITY RECORDS: (Modified from Loveridge, 1941). *Tangiers*: No data, M.C.Z. No. 6001; Tanger. *Spanish Morocco*: Larache; Mellila; Tetuan; Tifazor; Zafarin Islands. *French Morocco*: No data, U.S.N.M. No. 12318; Agadir; Azimour; Berguent; Bin el Ouidane (Saint-Girons, 1953); Casablanca; Chella; Dar Anflous; Djebel Taghat; Dradek; El Aioun; Fedala; Fenzou, M.C.Z. No. 7430; Fez; Fort Gurgens; Guercif; Imi n' Tanout; Koreina; La California; La Chiffa; Maidnet; Mogador; Oued Akreuch; Oued n' Fis; Oues-san (Hediger, 1937); Rabat; Salé; Sidi Abd el Djellil; Sidi Ali; Sisi Slimani; Tamaruth Valley; Taourirt; Uezzan. *Algeria*: No data, A.M.N.H. Nos. 1102, 1103; Ain el Hadjar; Ain Temouchent; Alger; Arzeu; Batna; Batterie espagnole; Biskra; Blidah; Bone; Budshia; Cap Matifu; Castiglione (Bellairs and Shute, 1954); Djebel Mourdjado, M.C.Z. No. 27373; Hamman Meskoutine; Hussein Dey; La Calle; Laghouat; Maison Carrée; Mecheria; Oran; Polygone; Rachgoun Island; Sebdu; Sidi Douma; Tebessa (Hediger, 1935); Tichy (Bellairs and Shute, 1954); Tiemcen. *Tunisia*: Tamesmida.

***Pachycalamus brevis* Günther, 1881**

Pachycalamus brevis GÜNTHER, 1881, p. 462.
Type locality: Socotra Island.

Pachycalamus brevis, LOVERIDGE, 1941, p. 364.

RANGE: Socotra Island, Indian Ocean.

LOCALITY RECORDS: (After Loveridge, 1941). *Socotra Island*: No data, A.M.N.H. Nos. 73423, 73424, M.C.Z. No. 10785;

Hadibu Plain, U.S.N.M. No. 60653; Dahamis and Homhil; Haggier Mountain; Jena-aghah; Tamarida.

***Diplometopon zarudnyi* Nikolski, 1907**

Diplometopon zarudnyi NIKOLSKI, 1907, p. 277.
Type locality: Nasrie in Arabistano ("Perse"). One from the collection of N. A. Zaroudny.

Pachycalamus zaroudnyi, BOULENGER, 1920, p. 352. New combination, made without discussion.

Diplometopon zarudnyi, SCHMIDT, 1939, p. 60. Species returned to original genus pending revision of the family.

Diplometopon zarudnyi, HAAS, 1957, p. 71. Record of 29 specimens.

TYPE LOCALITY: Stielers' "Hand-Atlas" (Gotha, 1930/1931) lists two sites named "Nasrije" within the range of this species. One is the town generally referred to as An Nasiriya on the Euphrates in Iraq, and the second is on the Karun River in southwestern Iran (formerly Persia). The Karun site lies in the old province of Arabistan and is almost certainly the type locality. Ahwaz is closely adjacent to the Nasrije on the Karun and the United States National Museum record (U.S.N.M. No. 121594) indicates that the species is still found there.

RANGE: Extreme western Iran, southern Iraq, Kuwait, the northern half of Saudi Arabia, Trucial Oman.

LOCALITY RECORDS: *Iran*: Ahwaz, U.S.N.M. No. 121594; Nasrije (Nikolski). *Iraq*: Baghdad, *S.M.F. No. 54365; Hindia Dam, *S.M.F. (specimen not numbered). *Kuwait*: Shaiba Lezait? (Boulenger, 1920). *Saudi Arabia*: Between Hadj and Tebuk (Haas); Trans-Arabian pipeline, M.C.Z. No. 57176; Ras el Mishaab, U.S.N.M. No. 132401; Manama (Boulenger, 1920); Al Hasa District, Qatif Oasis, C.N.H.M. No. 64429; Al Jubail (Schmidt, 1939); Dharan, C.A.S. Nos. 84274, 84405, 84406, 84501, 84529, 84534, 84539, 84559, 84588, C.N.H.M. Nos. 41955, 74007, U.S.N.M. No. 139414 (Haas); Abqaiq, C.A.S. Nos. 84343-84347, 84349-84354, 84373, C.M. Nos. 33503-33506,¹ C.N.H.M. No. 74008 (Haas); Shimal, C.A.S. No. 84426 (Haas); Doha Dalum, C.A.S. No. 84454 (Haas); Khadud Spring, U.S.N.M. No.

¹ C.M. No. 33504 has been recatalogued as M.C.Z. No. 54360.

127998. *Trucial Oman*: South of Selwa, C.M. No. 33522; Sharja (Haas).

***Agamodon anguliceps* Peters, 1882**

Agamodon anguliceps PETERS, 1882, p. 580. Type locality: Barava (= Brava, Somalia).

Agamodon anguliceps immaculatus CALABRESI, 1927, p. 27. Type locality: Afghedud, Somalia.

Agamodon anguliceps, LOVERIDGE, 1941, p. 365. *Agamodon a. immaculatus* assigned to *A. compressus*.

RANGE: Somalia, eastern Ethiopia.

LOCALITY RECORDS: *Somalia*: No data, M.C.Z. No. 10784 (Mocquard, 1888); Chisimajo (Scortecci, 1929); Mofi, near Chisimajo (Lönnberg and Andersson, 1913); Jumbo (= Gumbo), Lower Giuba (Boulenger, 1909); Alessandra (Scortecci, 1931); Brava (Peters, 1882; Boulenger, 1897; Anderson, 1901); Lugh (Boulenger, 1897); inland from Mogadish, M.C.Z. No. 38697 (Calabresi, 1915; Scortecci, 1931); Mogadish (Scortecci, 1940); Mahaddei (Calabresi, 1927); Afghedud (Cal-

abresi, 1927). *Ethiopia*: No data, *N.M.B. No. 13480.

***Agamodon arabicus* Anderson, 1901**

Agamodon arabicus ANDERSON, 1901, p. 140. Type locality: Al Khaur, Arabia.

RANGE: Known from the type only. This was collected at Al Khaur, in Abian County, Yemen, which is 40 miles northeast of Aden and 20 miles west of Shukra (Thomas, 1900, p. 96).

***Agamodon compressus* Mocquard, 1888**

Agamodon compressus MOCQUARD, 1888, p. 133. Type locality: Comalis (= Somalia).

Agamodon compressus, LOVERIDGE, 1941, p. 367. *Agamodon anguliceps immaculatus* included in synonymy.

RANGE: Central Somalia.

LOCALITY RECORDS: *Somalia*: No data (Mocquard, 1888); Brava (Boulenger, 1897); Mogadish (Calabresi, 1915).

KEY TO THE SPECIES OF ACRODONT AMPHISBAENIDS

The presently known species of acrodont amphisbaenids can, on the basis of external characters, be recognized by the possession of a large rostral covering the entire width of the dorsoventrally flattened snout (or by a slightly smaller rostral with enlarged nasals in contact behind it), by the presence of more than 40 segments per midbody annulus, by the absence of well-defined nuchal or lateral folds separating head from body, and by the absence of enlarged ventral scales in the pectoral region. (The diagnosis may occasionally be inadequate for specimens of *Trogonophis*. These can be recognized by their distinctive color pattern as shown in pl. 45.)

1. Head rounded; rostral takes up only a small portion of face, nasals in contact behind it; faint vertebral and strong lateral sulci; no pre-anal pores . . . *Trogonophis wiegmanni*
Tip of head horizontally depressed; rostral tip of snout spatulate, with horizontally edged rostral taking up more than 25 per cent of

- facial plane; dorsal or ventral sulci only; pre-anal pores present or not 2
2. Only two enlarged cephalic shields (rostral and very large frontal); dorsal and ventral sulci made up of multiple rows of modified scales (*Agamodon*) 3
More than two enlarged cephalic shields; dorsal and ventral sulci simple, between two rows of segments 4
3. Cephalic shields plane; body rounded in cross section; 127-143 annuli on body, 15-19 on tail *A. anguliceps*
Cephalic shields plane; body laterally compressed in cross section; 161 annuli on body, 18 on tail (type only) *A. arabicus*
Edges of cephalic shields upturned; body strongly compressed laterally; 144-160 annuli on body, 22-23 on tail
. *A. compressus*
4. Dorsal and ventral sulci; interlabial scale present; anal pores in both sexes
. *Diplometopon zarudnyi*
Ventral sulcus only; no interlabial present; anal pores in males only *Pachycalamus brevis*

A FUNCTIONAL INTERPRETATION OF THE AMPHISBAENID ADAPTIVE PATTERN

THE ADAPTATIONS OF THE AMPHISBAENIDS are manifold and almost proverbial. The peculiar nature of these adaptations has given rise to some very startling phylogenetic speculations and has elicited a variety of comments regarding supposed functional or adaptive significance. One of the most remarkable of these tales is the oft-repeated story that the amphisbaenids progress above the surface of the ground by vertical rather than horizontal undulations.

Vanzolini (MS), in his revision of the amphisbaenids, demonstrated two distinct methods of burrowing in the pleurodont amphisbaenids and attempted to correlate these with his subfamilies Amphisbaeninae and Rhineurinae. The amphisbaenines had more or less lateral compression of the head and were supposed to burrow by swinging the skull laterally around the head joint. The rhineurines had vertically compressed snouts and were supposed to displace the soil by a dorsoventral movement of the head. Their gular folds would facilitate movement of the head on the body, while the enlarged pectoral shields provided a wear surface.

No functional scheme was proposed for the Trogonophinae, though Vanzolini was aware of and commented on the fact that these species, superficially so similar, differed from the rhineurines in a number of ways that went beyond the character of the dentition. The investigation of the Trogonophinae, presented as the first part of the present paper,

prompted a reëxamination of this question.

While no live specimens of any of the acrodont species were available for study, it was possible to obtain a series of live *Rhineura floridana* and *Leposternon microcephalum*. The observation of these forms, in the laboratory, the dissection of a number of other genera, and a survey of the literature suggested that it might be useful and even necessary to go beyond the immediate problem of the trogonophines and analyze the general adaptive pattern of the amphisbaenids.

The present section of this paper is therefore divided into three parts: (1) a general *Fragestellung* of the major problems of a subterranean existence, (2) an analysis of the actual pattern of adaptation in a single species (*Rhineura floridana*), and (3) a functional reconsideration of the modifications exhibited by the Trogonophinae.

The present analysis is considered to be preliminary on all three levels, designed mainly as an initial approach to and statement of some of the problems. It is intended in no small part as a guide to further studies of specific aspects and groups of amphisbaenids; some such studies are already well under way as this is written. The preliminary nature of the analysis cannot be emphasized too strongly, and particularly the third portion thereof must remain tentative until it can be checked by the observation of living specimens.

THE PROBLEMS OF A SUBTERRANEAN EXISTENCE¹

Among the many problems relating to the behavior of a subterranean animal are five about which I should like to speculate here. Such selection does not imply that these five are the only problems encountered by these

reptiles, but rather that they seem to be those involving special tasks for a subterranean animal. The five problems (which are in truth complexly interrelated) have been more or less arbitrarily delimited for the sake of convenience in discussion. They involve (1) locomotion, (2) orientation and recognition of the nature of the environment and of food, (3) food and water intake, (4) protection of the body and its orifices from the extraneous influences of the environment,

¹ In this discussion the term "burrower" is used to refer to species that make their permanent abode underground. The discussion does not apply to the denizens of the air-ground interface (i.e., various toads and such snakes as *Heterodon* and *Bitis*, which hide under a superficial layer of sand).

and (5) reproduction. Many of the factors considered here will be found to be strongly influenced by the nature of the substrate.

LOCOMOTION

Locomotion actually covers three subjects: movement on the surface of the ground, the traverse of an existing passage or tunnel, and the production of a new passage through the substrate. The first subject poses no problems of a burrowing nature, except that the need for occasional surface locomotion might limit the degree of burrowing modification that would be selectively advantageous.

It is almost axiomatic that the amount of work involved in transporting a solid body through a dense medium will be directly related to the cross-sectional area of the body and thus to the volume displaced. This means that forms with a high ratio of diameter to length must compensate by a more efficient digging apparatus, by a more efficient energy source (possibly a higher metabolic rate), or by both. The establishment of a permanent set of tunnels, excavated and extended over a period of time, is also possible. This reduces the energy output per unit time but still permits rapid passage throughout a territory. Yet another attack on the problem lies in the reduction of the ratio of diameter (or cross section) to length, i.e., in an elongation of the body. This involves certain problems of its own, but has been the method utilized by most fishes,¹ as

¹ The relative position of the cloaca (or of the posterior limit of the coelomic cavity) has no effect on the validity of the present argument. Its forward shift in certain fishes is possible only because of the entirely peculiar nature of locomotion in an aqueous medium. Here the frictional resistance of the anterior part of the body (cross-sectional as opposed to surface drag) is insufficient to militate against the use of a "long column" body structure. The driving forces may then be exerted at any point of the column, and the actual site of their application may be determined by other considerations.

All the most efficient burrowers among the squamates have extremely short tails. This is true for the Typhlopidae, Leptotyphlopidae, and Aniliidae among others. However, the fossorial representatives of the Anguillidae, Scincidae, and Teiidae often have quite long tails. It is believed that this long-tailed condition may be correlated with four other factors. These are (1) their recent descent from a limbed stock in which a long tail might have definite advantages, (2) the advantages of autotomy to a creature living near the surface, (3) the fact that a high percentage of these species seem to be re-

well as by the Gymnophiona, Urodela, and Squamata, and is the one to be dealt with here.

In first considering the movement of a burrower through an existing tunnel or opening, we are dealing with a special type of subterranean locomotion. Any animal must exert a force on the substrate in order to move. Subterranean existence only complicates this. First there is the need for a locomotor apparatus that does not significantly increase the cross-sectional area of the individual. Next there is an advantage to an ability to exert the force at any point of the (360°) periphery. Finally there would always seem to be a definite selective advantage in the ability to back up, i.e., to reverse the direction of motion without turning around.

However, there exists a further requirement the importance of which is far from secondary. This is the need for a continuous locomotor apparatus, rather than for one restricted to isolated segments of the body or even to the anterior end alone. While it is relatively simple to drag an elongate body through a straight tube of slightly larger diameter, the drag forces, and with these the stresses within the vertebral column, increase disproportionately with each bend of the tube and consequently with the relative length of the body. Each time the body is dragged around a bend it tends to assume the arc of the curve, and the forces acting to straighten it increase the friction along the inside surface of the curve. The increase in frictional drag due to such a bend increases the forces promoting straightening of any other bend between it and the site of motor action, which further increases the drag forces encountered here. The problems encountered in rostral movements are minor when compared to those involved in backing up. These may be approximated by a consideration of the difficulty of forcing a limp rope through a twisted tube, particularly one with a roughened internal surface.

The ability to move the body along a tunnel is not the only locomotory require-

stricted to special substrates such as dry sand, which shares some of the attributes of an aqueous medium, and (4) the fact that some are poor burrowers occupying tunnels not of their own making.

ment for a successful subterranean existence. This would be sufficient only if the organism were to inhabit the tunnels of some other animal. To be most effective, a subterranean creature must be able to excavate its own burrow and thus become independent of spaces of questionable suitability supplied by forms with differing requirements.

A tunnel can be produced either by the breaking up and subsequent removal of the substrate or by its temporary or permanent displacement or compaction. In the first case the excavated material is carried to the mouth of the tunnel and piled at or near it (as is done by most burrowing mammals, birds, and certain annelids and arthropods). Temporary displacement occurs by the raising of the surface of an uncompacted and reasonably incompressible substrate (this is used by *Neoseps* and other "sand swimmers"). In this case the tunnel seems to collapse the moment the burrower passes. Permanent tunnels are generally made by compacting the displaced material into the walls of the burrow.

The structural requirements for permanent displacement are: (1) a penetrating tip or anterior end with a contour that permits maximum cutting or initial penetrating action, (2) a mounting for this tip that will permit the transmission of constant or intermittent forces along the long axis of the animal, preventing buckling and always orienting the tip at the proper angle of attack, and (3) a method of exerting forces at right angles to the tunnel walls in order to compact the displaced material. In order to reduce unnecessary contact and frictional drag the third requirement must be fulfilled in such a manner that the resulting tube is slightly larger than the diameter of the body of the animal.

ORIENTATION AND FOOD RECOGNITION

The main problem here is due to the opacity of the substrate, which effectively eliminates sight. The variety of orienting and other functions performed by the eye must be taken over by other structures. The extent to which such substitution becomes necessary is demonstrated by the facility with which the eyes tend to become reduced or to disappear altogether in fossorial creatures,

which indicates that they probably do not retain much visual function.

The main tasks imposed upon the other senses will then be (1) general orientation, i.e., gravitational orientation and the differentiation between left and right turns, (2) recognition of the texture, humidity, and temperature of the substrate, (3) location of prey, both at a distance and when it is close enough to be seized, (4) information about possible predators in the environment, and (5) location and recognition of the opposite sex.

FOOD AND WATER INTAKE

The mouth must be located in such a position that it is protected during digging yet may be opened and used effectively, either within a tunnel or near its end. Certain burrowers, of course, feed on the surface and simplify these problems, but the manner of opening the jaws is particularly important in the case of those elongate limbless burrowers where the size of the head determines the size of the tunnel.

There must be provision for the absorption of water from saturated air or from a moist substrate. Alternatives would be the ability to tunnel down to the water table, to use surface water, or to rely on metabolic water.

PROTECTION OF THE BODY AND ITS ORIFICES

Even when enemies sufficiently strong (or large) to excavate the entire burrower are ruled out, the problems of protection against action of the substrate and against small predators remain. The first item must include wear resistance or a capacity for the replacement of the integument and a method for preventing the entrance of substrate particles into the nostrils, mouth, cloaca, and sensory openings. The second item would require special protective devices such as a plug for the tunnel. It may be assumed that many predators or small unspecialized carnivores will find the burrower by tracing it along its tunnel. Even when the initial contact is at the burrower's midbody, the burrower may be able to move fast enough along the existing tunnel to present the enemy with front or rear. Because the very nature of subterranean life precludes a reversal of position, there

would be a definite selective advantage to the ability to defend or at least protect both of its ends. Beyond this there should be provision to keep such enemies from bypassing the burrower's ends along the tunnel.

REPRODUCTION

Here there are three unusual problems: (1) The sexes must encounter each other in a three- rather than a two-dimensional zone. (2) Prenuptial play and copulation would involve special problems in a tunnel. (3) Eggs and young within the body of the female would have to be protected during burrowing.

THE PATTERN OF ADAPTATION IN *RHINEURA FLORIDANA*¹

Rhineura floridana (Baird), 1858, is a species of amphisbaenid restricted to the sandy soils of northern and central Florida. It is a highly adapted burrower with vestigial eyes (Eigenmann, 1902) and feeds on a number of small arthropods and earthworms (Allen and Neill, 1954). As nominate representative of the Rhineurinae it possesses the horizontally spatulate snout, the nuchal fold, and traces of pectoral shields that are all characteristic of that group.

LOCOMOTION

Even superficial observation of this species demonstrated a startling difference in rates between locomotion through a solid medium (packed wet sand) and travel along an existing tunnel. While no exact measurements have yet been made, the estimated difference is of the order of 100 times. Travel along the tunnel proceeds with almost equal facility backward and forward. There seems to be some lateral undulation within the tunnel, providing contact points at which the skin momentarily remains stationary. As the amphisbaenid skin is far more loosely attached to the vertebral column than is that of other Squamata, it is possible for the column to be moved past the skin at any point and for a

The selection of a suitable incubation site would of course pose no additional problems to a burrower. Data regarding breeding behavior, eggs, and young, as well as the embryology, of amphisbaenids are almost entirely lacking. One of the very few observations of amphisbaenid courtship was made by Doumerge (1901, p. 246), who noted two specimens of *Trogonophis* moving over each other on the surface of the ground. This observation suggests that mating occurs on the surface, but some further observations would be desirable, because the specimens were not sexed and no copulation took place.

considerable distance. The muscular attachments insert on the skin over an arc of 320 degrees and run both cranial and caudad.

The motion appears to proceed in a relatively jerky manner. The motion of the skin must be reversed relative to the column, and longer sections are involved than in the "caterpillar movement" of certain of the heavy-bodied snakes. The fact that contact takes place at a number of discrete points and is not continuous may be elegantly demonstrated by having the specimen cross a cavity within the substrate or climb through a plastic tube.

This whole process is in essential agreement with the observations of Kaiser (1955) on *Leposternon*. What is not in agreement with this author's observations is the manner in which the skin is stretched. In *Rhineura* the interannular raphes are flexible and of limited elasticity. Stretching of the skin does not take place here. It thus seems that the situation is exactly opposite to that described for *Leposternon*. The dermal muscle fibers keep the segments of an annulus more or less curved, and the "stretching" of the skin proceeds by means of a change in the curvature of the segments to a greater radius, or by complete extension of these. Kaiser's statement that the weakness of the dermal musculature precludes its functioning in locomotion ignores the fact that any single raphe of the skin is loaded only by the forces required to bend or contract the two adjacent annuli. Forces required to advance the body proper are imposed on the skin solely at its station-

¹ The observations remarked on here were excerpted from a continuing study. They were carried out on specimens in specially constructed cages that were filled with various substrates and designed to permit the observation and modification of the activities of the animal.

ary contact points with the substrate. Here they are immediately transmitted to the slips of the *M. costocutaneus* and *M. vertebrocutaneus*.

The segmentation of the skin provides an additional advantage. The annuli ring the body and give an equal friction contact around its entire periphery. Because the annuli can move as units, it becomes possible for dorsal contact at one point to be translated into ventral or lateral contact at the next. The tight connection of the segments of an annulus makes, however, for but a limited amount of radial expansion or contraction. Such limitation seems to be the reason for the presence of specially modified sulci. Those of *Rhineura* are restricted to the posterior half of the body and are invisible on a plump and fully fed and watered individual.

In digging a new tunnel, or in extending an old one, *Rhineura* proceeds in an entirely different manner from that described above. Almost all the action is concentrated at the anterior end. The process may be subdivided into two steps: a ramming motion driving the head into the tunnel end, and a dorsad rotation of the head around the head joint compacting the substrate and widening the tunnel.

When *Rhineura* moves into an area where the tunnel is slightly or completely obstructed, the specimen holds its head downward, with the rostral tip at or but slightly dorsad to the ventral surface of the body. As soon as the tip strikes an obstruction, a single or a series of battering or ramming blows occur which drive the head into the substrate up to the junction point of facial and parietal surfaces. The ramming movement starts with the post-nuchal segments closely contracted and the nuchal folds closed. The post-nuchal segments appear to maintain firm contact with the substrate. The animal next makes a sudden forward movement of the head, a movement that proceeds until the kinetic energy of the head is completely absorbed by the substrate. The interannular nuchal sulci unfold during this stroke, i.e., the head moves while the post-nuchal integument remains stationary. The forward motion of the column proceeds with a minimum of non-essential friction with the tunnel walls, as most of the integument remains stationary.

The penetration is shortly followed by a contraction of the long muscles of the nape. This contraction rotates the head around the severely modified atlas-axis joint and also bends the chain of anterior vertebrae. The magnitude of the force exerted during this swing was commented on by Kaiser (1955), who mentioned that *Leposternon* was capable of breaking a glass tube through which it was crawling. The dorsad sweep ends with the head slightly raised above the dorsal surface of the trunk. The head then swings ventrad and the cycle is repeated.

Owing to the manner in which the two tendons attach to the ridge between facial and parietal portions of the skull, the action of only one of the muscle groups, or the unbalanced action of both, swings the skull laterally as well as dorsad. Such motion does not seem to be an unusual occurrence, and a *Rhineura* held in the hand can easily swing the head in a circle. The specimens observed while they were digging in the test cages always used the dorsoventral movement as long as they remained submerged. Only when breaking through to the surface (when feeding on insects as described below) did they swing the head in a circle and thus provide the tunnel with a funnel-shaped (or counter-sunk) orifice.

FUNCTIONAL ANALYSIS OF DIGGING MOVEMENTS

Even a very much simplified consideration of the digging or excavating cycle permits one to trace a number of quite simple mechanical adaptations. The questions that might most usefully be asked are: Why does penetration take place in a series of battering movements rather than in a continuous push? Why is the head held with the rostral edge at or near the ventral surface of the body? What is the advantage of a digging procedure involving an upward or, for that matter, a sideways sweep, if the head must first be rammed into the substrate in either case?

Of these the first question is easiest to answer. The unbalanced force applied to the substrate in any system equals the mass acted upon times the acceleration (of the moving body). The greater the initial velocity of the body of the animal the higher is the (negative) acceleration component of the equa-

tion and, with this, the force. On the same principle a pile driver operates by the repeated dropping of an object that would be insufficient to effect penetration by its weight alone.

A further advantage lies in the fact that the period of positive acceleration, i.e., the time required to attain maximum velocity, may be longer than the period of negative acceleration. This makes for a slower rate of acceleration, and for a reduced force to be exerted by the muscle system. It also reduces the longitudinal reaction force between skin and tunnel wall, a reduction the importance of which is further commented on below.

The two remaining questions can be answered only by recourse to a simple consideration of the forces imposed on the rhineurine head during the ramming and sweeping cycle.

The force that must be exerted to push a solid body into a homogeneous substrate may theoretically be expressed by a relation such as:

$$F = f(D^2) + f(D^x)$$

in which F stands for the force required; $f(D^2)$, for a function of the maximal displaced area; and $f(D^x)$, for a function of the maximal contact perimeter. The logical derivation of this relation is far from simple. In the absence of model tests it is possible to be certain only that the force will equal some sort of exponential function of the diameter. The area effect function $f(D^2)$ of the suggested equation represents the fact that the penetrating force increases with the cross-sectional area (i.e., as the square of the diameter), in the same way as the work increases proportionately with the displacement. The perimeter effect function $f(D^x)$ represents the compression or compacting effect, which also probably increases disproportionately with the diameter ($x \neq 1$).

With the use of the example of penetration by a circular cylinder tipped by a regular cone of height h , and the simplifying assumption that the diameter of the cylinder = 1 [in which case $f(D^2) = f(D^x) = f(D^n)$], it is possible to plot a graph (fig. 25) showing the approximate forces required to ram the cone-tipped cylinder into the substrate to a depth d . Certain facts can be ascertained from this graph:

1. $f(D^{x=1})$ increases linearly from the origin (point of initial penetration) to depth $d=h$ and remains constant thereafter, owing to the fact that the maximum diameter in contact with the substrate is the effective diameter for this function at any point.

2. $f(D^{x>1})$ increases exponentially from the origin to point $d=h$ and remains constant thereafter.

3. The curves from 0 to h show by inspection that the average force that must be exerted through this distance is less than half of the force to be continuously exerted from h to $2h$ or, for that matter, from h to l , when l equals the length of the cylinder.

The work done increases exponentially from 0 to h and linearly thereafter at the maximum rate. None of these statements is affected by a change in the exponents of the equation.

The force involved in the preceding discussion is the force ramming the head into the substrate. This force acts in parallel to the long axis of the body of the burrower, which means that a portion of the posterior body must transmit the reaction forces to the tunnel wall. Part of such transmission may be handled by the contact of the curved body against bends in the tunnel, but some if not all of the force is normally handled by pressing a portion of the skin against the tunnel wall. The tendency for slippage is very great, particularly in a tough yet friable medium such as wet sand, with relatively high impact and packing resistance, yet low shear strength. Anything that reduces the longitudinal force required for unit penetration then possesses decided selective advantage.

Rhineura has solved the problem by developing the highly mobile head joint and the elongate tendon-muscle assembly mentioned above. Figure 26 shows the osseous, muscular, and dermal elements in position for the ramming and for the digging strokes, while figures 27 and 28 summarize the forces acting on the skull in each of the two movements. Figure 27 shows the manner in which the unequal angulation of the dorsal and ventral surfaces produces an unbalanced downward component when a longitudinal force is applied at the head joint. (Forces are shown summed at midpoints of areas on

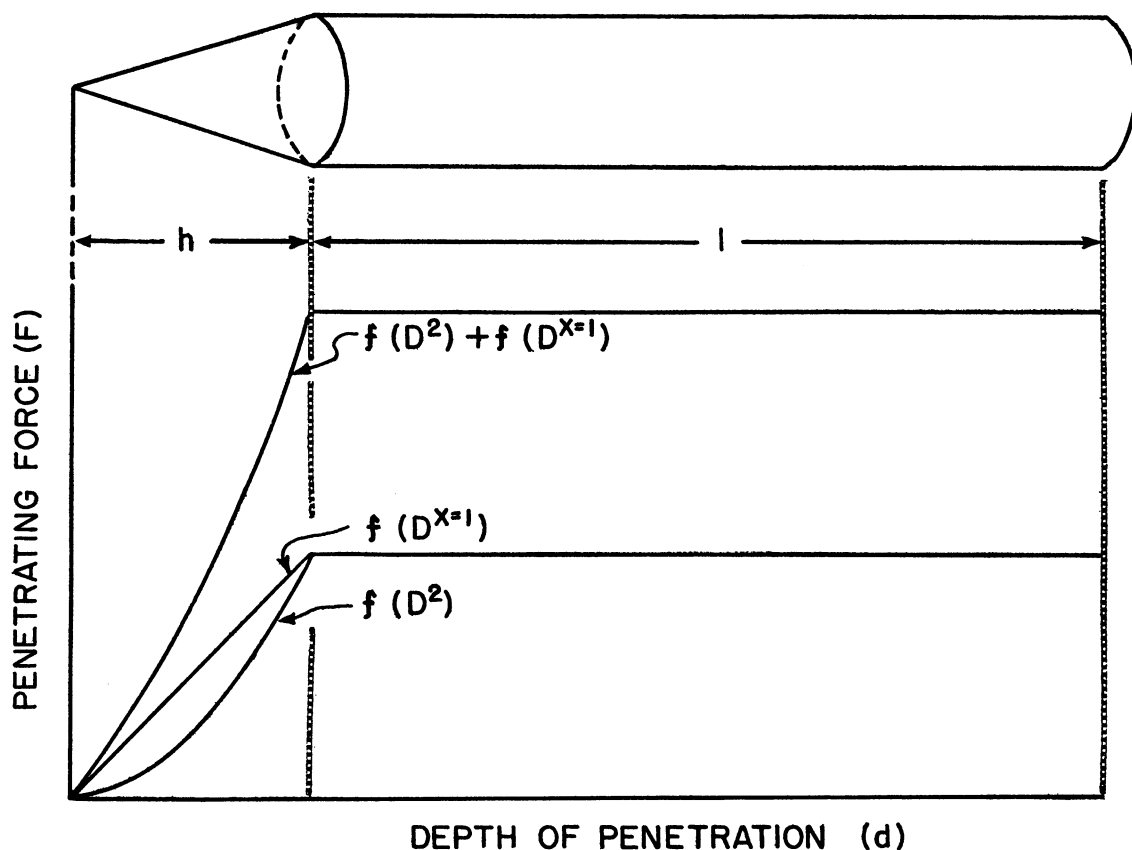


FIG. 25. Graph to show the theoretical force (F) required to ram a cone-tipped cylinder into a substrate to the depth d.

which they act and the analysis is referred to a two-dimensional system for purposes of simplicity.) This slight ventrad deflection assures that the ramming stroke stops at the ventral tunnel surface so that the excavating stroke covers the entire tunnel height. The disproportionate development of the dorsal musculature also makes for a simple correction of undue ventrad movement. The positioning of the head finally reduces the forces acting on the jaw suspension and oral opening.

Figure 28 shows the forces acting during the upstroke. It may seem that the skull is rotated around the atlas-axis joint by the contraction of the various slips of the *M. capitivertebralis*. Their forces are transmitted to the skull by the two tendons inserting on the cross-parietal ridges. As the movements involve rotation rather than displacement, there are only slight longitudinal

components. These forces actually tend to pull the body cranial in the tunnel after the facial plane has passed the parallel to the longitudinal axis.

The nature of this muscular insertion is furthermore much more effective than are the arrangement and insertion of the ramming muscles. The most characteristic attribute of animal muscle is that it exerts its force only during the contraction phase. This then establishes tension stresses within the connecting tendons. Compression stressing can be attained only by the attachment of muscles to rigid elements.¹ It is this fact that made the existence of some type of rigid

¹ The only exception is the case of sphincters, the ends of which join to form a ring. Such muscles seemingly exert their force at right angles to the direction of contraction. While such is actually not the case, they do operate under mechanically disadvantageous circumstances.

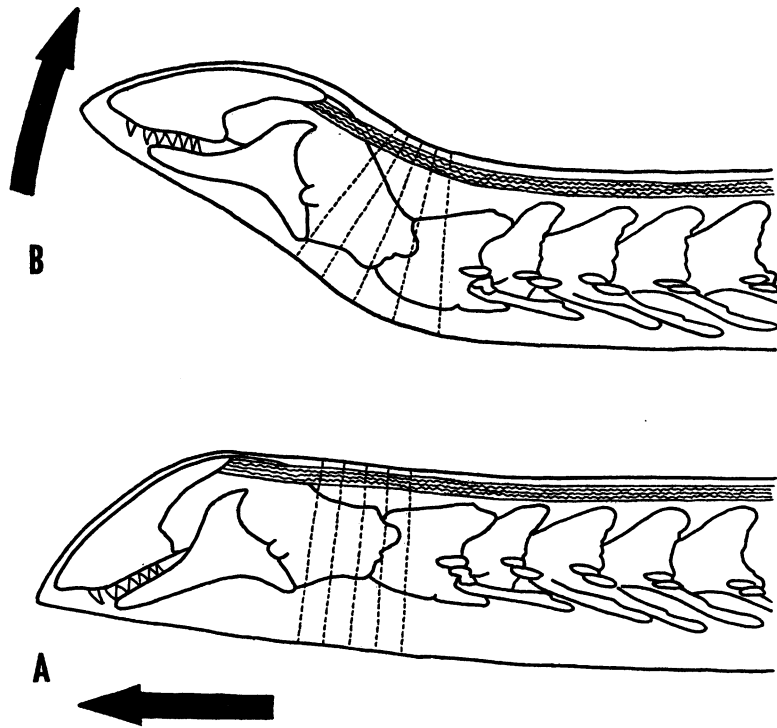


FIG. 26. Diagrams to show relation of skull, vertebral column, nuchal ligaments (wavy lines), and integument (nuchal folds shown as dashed lines) during burrowing movements in *Rhineura floridana*. The solid arrow shows direction of skull movement. A. Ramming stroke. B. Digging or elevating stroke. Drawn by E. Coogle.

skeleton a prerequisite for many modes of life. It also allows the deduction that the greatest efficiency is attained by having a muscle act parallel, or close to parallel, to the direction of effected motion.

The ramming action must then be powered by the contraction of those slips of the *M. costocutaneus* and *vertebrocutaneus* that insert on the stationary portion of the skin in contact with the wall of the tunnel. As the extent of this section of skin is necessarily limited by and dependent on local conditions, so also is the maximum force that can be produced by this means. Any slippage between wall and integument detracts further from the efficiency. In contrast, the action of the nuchal musculature is an entirely internal affair, acting within the closed system of the body and exerting its force between two points of the axial skeleton. As the muscle is feathered, its origins can be spaced over any number of body segments and the total force

consequently amplified.

During the vertical upstroke the pectoral region is in contact with the opposite tunnel wall, and it is here that the vertical reaction forces are passed to the "ventral" tunnel wall. This is easily observed in the test cage as the pressure compacts the tunnel surface so that the packing action proceeds around the entire periphery.

Evidence for the hypothesis that the vertical upsweep of the head serves primarily to reduce the force necessary for the ramming stroke is offered by the fact that *Rhineura* does not use the upsweep when digging through loose soil near the surface. Under these conditions and those involving other uncompacted media the specimens push their way through the substrate by ramming movements powered by lateral undulations of the body within the tunnel.

It may also be of interest to mention a possible origin for the story that the amphis-

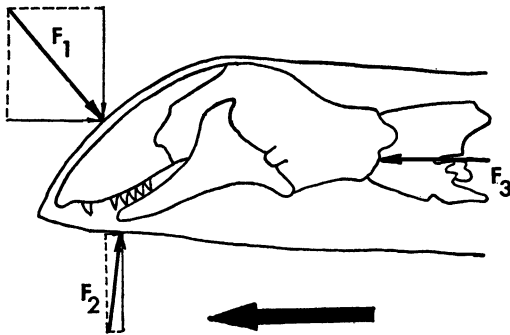


FIG. 27. Static diagram of cephalic region, to show relation of forces acting on the skull at a given instant of the ramming stroke in *Rhineura floridana*. The propelling force (F_3) acts at the head joint and is assumed to be applied parallel to the long axis of the body. F_1 is the major resistance, which in this case acts on the facial surface. F_2 is the theoretically required vertical force maintaining the head in position, i.e., counteracting the vertical component of F_1 . This vertical force may, of course, be provided by contraction of the muscles attaching to the nuchal ligaments. The analysis is two-dimensional for the sake of clarity. All these diagrams show static forces with the system at rest. In order to effect motion, it would be necessary to have the force in the direction of motion (F_3) larger than the resisting forces. The force term of the acceleration equation applies *only* to the unbalanced vectors.

baenids progress by vertical undulations. When *Rhineura* is placed upon a smooth surface it moves off by a modified rectilinear movement (Lissmann, 1950), with slight lateral undulations. The head quarters the ground until it finds a point of discontinuity where burrowing can be started. A definite force is necessary for the initial ramming thrust, and *Rhineura* obtains this by bending the anterior portion of the body into a vertical loop, which is brought over the head. The weight of this loop provides the necessary penetrating force. To a casual observer such actions may well suggest travel by vertical undulation.

ORIENTATION AND FOOD RECOGNITION

The eye of *Rhineura* is entirely useless for shape vision, but some light sensitivity does seem to exist. The specimens appeared to be negatively phototropic, a point upon which experiments are presently in progress. When

kept in narrow cages made of two parallel sheets of glass three-quarters of an inch apart they dug their tunnels on the shaded side, and moved from this when the cage was illuminated from the opposite side. When both sides were illuminated, the specimens dug central tunnels that only rarely touched either side.

When the specimens traveled through the tunnel system, the head was generally dorsal side up, although the posterior portion of the body might be twisted 180 degrees or more. The head and anterior body followed slowly when the entire cage was rotated through 180 degrees. While no experiments have been carried out on *Rhineura*, or on any other amphisbaenid, tests on other squamates (Trendelenburg and Kühn, 1908) have confirmed that the capacity for such orientation lies in the semicircular canals. Their relatively large size in amphisbaenids may then indicate a particular emphasis on one of the more important of the remaining orientational devices.

It is not yet known to what extent such factors as the temperature and humidity of the soil and the gravity-induced pressure assist in the orientation process, or how they influence the habitat selection of the species. The requirement for a relatively moist substrate (Bogert and Cowles, 1947) may indicate that the species has a fairly low activity temperature, as it has been observed (Geiger, 1950, p. 149) that the ground temperature drops more sharply in moist soils than in dry. The data of Bogert and Cowles confirm the sharp drop in soil temperature, though the two specimens taken by them were encountered near the surface in a zone of relatively high temperature. The complex interrelation of the various limiting factors is shown particularly well by Miller's (1944) ecological study of the "sand swimming" lizard *Anniella*. Careful and well-designed experiments will be needed to separate these items.

Bogert and Cowles (1947, p. 22) also commented on the amazing accuracy with which a specimen of *Rhineura* managed to direct itself to clusters of termites that had tunneled into the sand from the surface, but did not decide whether olfactory or auditory cues were used. The present observations seem to indicate that the initial stimulus is offered by auditory cues, because the amphisbaenids in

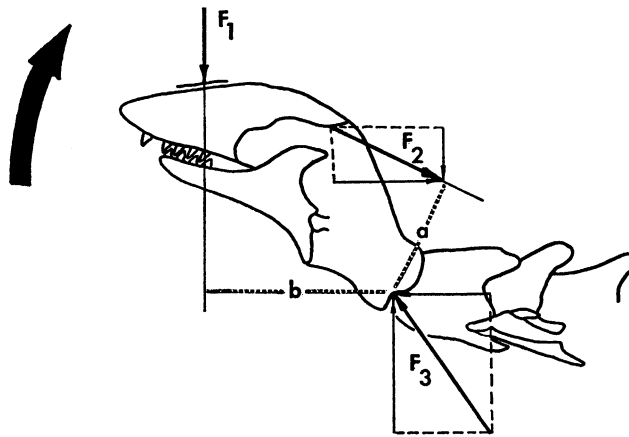


FIG. 28. Static diagram to show relation of forces acting on the skull at a given instant during the upstroke of the head in *Rhineura floridana*. The position at which F_1 is exactly vertical is illustrated here. The skull is assumed to rotate about the condyle. Summation of movements about the axis of rotation yields the equation $F_1 = a/bF_2$. The vertical component of F_3 ($F_3^v = F_1 + F_2^v$) represents the force transmitted to the tunnel wall by the pectoral shields. Here, as in figure 26, the vertebral column is shown stationary to simplify analysis. All other conventions as in figure 27.

the lower tunnels became active before the odor might be expected to have diffused to this zone. All surface tunnels were destroyed before several of the feeding sessions in order to prevent the spread of the odor or of termites through the tunnel system, yet the amphisbaenids still started moving towards the prey after a similar interval.

Once the animal had approached a position closely adjacent to the prey, the tongue began to be everted after each thrust of the head (Bogert and Cowles, 1947, p. 22). My specimens tunneled completely through a termite hole and then retreated 3 to 5 cm. The retreat action was often elicited by contact of the neck or body with a termite. The retreat was then followed by a slow secondary advance during which the tongue was used regularly. Most of the prey captures observed occurred during this phase of the feeding process. When termites were allowed to walk on the unbroken surface of the packed moist sand, the *Rhineura* often penetrated the surface, widening the exit by a circular swing of the head. The tongue was used continuously,

and feeding was occasionally observed while the head was above the surface. Termites often fell into such open pits.

The different cues used by *Rhineura* in localizing distant prey and recognizing such prey when adjacent to the head may well be related to the peculiar structure of the amphisbaenid ear. The outer and middle ear regions are entirely missing. The stapedial portion of the columella articulates with a cartilaginous or ossified extracolumella which runs along the outside of the head and ties into heavy pads of connective tissue underlying and tied intimately to the skin along the angle of the jaw and along the labial side of the maxilla and dentary. It has repeatedly been remarked in the literature and could be confirmed by personal observation that any movement of the skin moves the loosely positioned stapes. Versluys (1898) felt that the ear had lost its function in the amphisbaenids. However, Camp (1923, pp. 313, 343) stated that the amphisbaenid outer ear is not a degenerate structure but a highly specialized one and may serve as a micro-

phonic device to pick up noisy prey. Furthermore Kritzing (1946, p. 190) described synovial joints between the stapedial footplate and the margins of the foramen ovale and suggested that sound waves are probably transferred from the ground to inner ear via this mechanism.

It seems probable that some auditory capacity is retained by these animals, though it is unlikely that the organ as constituted would pick up airborne vibrations. Such a capability is almost certainly ruled out because of the energy required to vibrate the massive pads of tissue on the sides of the jaws, particularly as there is no trace of any membrane or similar pick-up device. However, the organ would be quite effective for the detection of low-frequency, soil-borne vibrations, such as those produced by the digging activities of other burrowers or the scrape of a chitinous exoskeleton against sand grains. The substrate contact would have to be unbroken for such a purpose and the side of the head pressed against the tunnel wall. The padding of the "cheeks" might well serve to provide a certain elasticity to the area and thus make for a better contact with an irregular surface.

While any such apparatus would pick up soil vibration, it is not at all clear how the directional element is attained. It may be that the two sides of the amphisbaenid give differential readings, either simultaneously or in sequence, but further observations are necessary to clarify this point.

In any case the "ear" could serve only to notify the animal of the presence of prey and possibly of the directional bearing thereof. It would be most effective at a distance, and of little or no use for the exact location of a food animal that was walking down the same tunnel millimeters ahead of the *Rhineura*. Olfactory clues would have to be employed at short range, and it is at this stage that *Rhineura* has been observed to make most use of its tongue.

The sensory problem would theoretically involve recognition of the texture of the substrate. The extracolumella has also been mentioned in connection with some such function. It appears more probable, however, that the suitability of the substrate is evaluated on the basis of cues furnished by

dermal receptors and on the basis of the force required for penetration.

Rhineura is also particularly sensitive to a disturbance of the soil due to the digging motions of another animal or foreign object. Even a slight disturbance of the substrate produces an immediate retreat reaction. When several specimens are kept in the same cage, they apparently do not react to one another's burrowing movements, except in the case of immediate contact. It is not known whether the extracolumellar apparatus, the entire integument, or both are involved in the perception of these major soil vibrations.

FOOD AND WATER INTAKE

The matter of water intake is most interesting, and Bogert and Cowles (1947, p. 21) have provided some simple yet suggestive experiments. They demonstrated the striking rapidity with which *Rhineura* loses moisture in dry sand, and that the species desiccates to the point of death within 24 hours. It can regain the necessary water when placed in moist sand and does not need to drink. The authors suggest that this water absorption takes place through the skin, an interesting though apparently not unique adaptation in modified squamates.

The humidity requirement would restrict the species to fairly moist sand. (The air in interstices and tunnels will remain nearly 100 per cent saturated as long as any free, i.e., neither bound nor absorbed, surface moisture remains.) My specimens occasionally burrowed through dry areas in the test cages, but always retreated to the moist zones. Only after the sand in the cage had desiccated completely did the specimen leave the tank across the (always open) surface. Neither Bogert and Cowles nor the present author ever observed *Rhineura* to drink from a water dish in the manner described by Bedriaga (1884, p. 33) for *Blanus*, though it is conceivable that it may have done so. The distinct reliance on a moist substrate places these species in a peculiar position among the terrestrial squamates, most of which are far better adapted to dry conditions.

Feeding generally occurs after the prey has been maneuvered against a tunnel end. The

mouth of *Rhineura* is located on the ventral surface of its head and is protected by the overhanging rostrum. It is opened by muscle action on the extensive retro-articular processes of the mandibles. When the prey (annelids and small arthropods) is seized, the head is held with the rostral tip slightly dorsad of the central line of the body. Such action seems to remove the need for applying excessive forces on the mandible, because the downward action of this structure can take place in an excavated region. There is thus little need for movement of the mandible against the substrate. That the mandible is capable of being opened against external resistance is indicated by occasional observations. The action is facilitated by the long retro-articular processes which serve to increase the mechanical advantage of the muscles opening the jaws.

The gape of small lizards directly affects the maximum size of prey that can be mastered, as the gape determines the nature of the initial bite, the effectiveness of crushing or chewing motions, and the swallowing process. The gape may theoretically be increased by cranial kinesis, which raises the tip of the upper jaw. The ingestion of food items may also be affected by a downward change in the suspension point of the mandible, thus adding a caudad vector to the forces imposed on captured food items.

Versluys (1912) in a classic paper reviewed the various kinetic mechanisms of reptiles and also commented on the mesokinetik (i.e., movement between frontals and parietals or frontals and nasals) condition in amphisbaenids. Versluys had dissected *Amphisbaena* and *Trogonophis* and also used a dried skull of *Leposternon*. He described extensive movements of the tip of the snout, but suggested reëxamination of his findings, particularly those on *Leposternon*, with fresh material. Kritzinger (1946, p. 192), in a discussion of the cranial anatomy and kinesis of *Monopeltis capensis*, on the basis of two sets of serial sections, described a well-defined line of bending between frontals and parietals of this rhineurine species. His figure 7, however, shows the anterior process of the parietal interdigitating between the two sheets of each frontal. The text comments that the bones are joined only by loose connective tissue and

should be able to move relative to each other.

The degree of motility predicated by Kritzinger was extreme enough to suggest reëxamination of this matter. The dissection of an adult alcoholic specimen of *Monopeltis c. capensis* (M.C.Z. No. 21319, from Kimberley, Union of South Africa) did not disclose any particular motility between the various elements mentioned, and the cranial capsule and palate were found to be composed of discrete elements solidly joined. This finding is not unexpected, but still requires checking on fresh material of various age groups as there may well be some ontogenetic variation.

Beyond this it is necessary to consider stress patterns set up in the skull by different activities, such as ramming, lifting the head to pack the soil, and biting. Depending upon the angle of the head, the frontoparietal suture is in compression and downward flexure during the ramming stroke, in compression and upward flexure during the bite, and in tension and downward flexure during the vertical movement. The peculiar interlocking sutures described in Kritzinger's study appear to act as reëncforcements of the skull roof. They limit bending and stabilize the various elements during burrowing, yet still permit readjustment of the bones for purposes of growth. This point could even be confirmed for partially decalcified juvenile skulls of *Diplometopon* and *Agamodon*, though the slight flexure of the facial shield here occurred at the frontonasal rather than the frontoparietal sutures.

In *Rhineura* the mandibular suspension point lies below the contact line of the teeth, which is the exact opposite of the condition described by Stöcker (1957) as a crushing adaptation. In both cases there has been added an anteroposterior component to the jaw closing movement. In *Rhineura* the closing movement is caudad and possibly assists the ingestion of the food.

PROTECTION OF THE BODY AND ITS ORIFICES

Wear of the integument is provided for by ecdysis as in all squamates. The problems of abrasion and wear are accentuated by the sandy medium in which *Rhineura* digs its burrows. Much of the wear is concentrated

on the cephalic shields, and the dermis is thicker here than on the midbody annuli, though not so noticeably as in the heavily keratinized cephalic spades of forms such as *Monopeltis* and *Anopsibaena*.

Vanzolini (1951, p. 84) pointed out that fusion of cephalic shields tended to reduce friction and that such reduction of friction was the probable cause for such fusion on heavily wearing surfaces. Further examination seems to confirm his hypothesis. In *Rhineura* the reduction in scale number and increase of scale size take place not only on the head, but also on the pectorals. Figure 28 indicates that these scales bear the vertical component of F_3 during the upward stroke of the head, and are also exposed to sliding wear during the rostral movements of the integument.

The head is modified in having the eyes protected by a continuous dermal cover (Brille), in having the nostrils hidden below and behind the rostral shield, and in having the lower jaw recessed behind the projecting labial fold of the upper. The nostrils are, furthermore, recurved internally and covered by a protective fold. The large Harderian gland takes up most of the orbit and drains into the nasal cavity and through it into the mouth (Eigenmann, 1902, p. 536). The secretion may serve to keep the nasal passages clean. There are of course no external ear openings.

The cloaca is located on the ventral surface of the body, at a point where this retains its maximal diameter. It is thus exposed

to the entry of soil particles during both forward and reverse movements. The anterior lip of the cloaca slightly overlaps the posterior. The bordering scales enter the slit and line its walls. There appears to be a cloacal sphincter at their inside edge. Both of these structures tend to keep foreign particles from entering and possibly damaging the cloacal cavity. The species is further adapted by the ability to prolapse the anal region during excretion, an eversion that provides a simultaneous cleaning effect.

It is finally necessary to consider protection of the ends against small generalized predators or, rather, the blocking of the tunnel to prevent the passage of such animals and their attack on the midbody region. The head is fairly well adapted in this respect. When it is moved downward it blocks the tunnel with a keratinized shield underlain with dense connective tissue and bone. Any attack on this elicits an upward swing that might well crush a small animal against the tunnel wall. The rhineurine tail is flattened, and its dorsal surface is covered with an alternating arrangement of large and small caudal tubercles which appears to collect a cap of dirt when the animal is living in soil or leaf mold. The first defense reaction is always flight down the tunnel. If *Rhineura* is caught in a blind tunnel or surprised while digging a new one, the tail tip is pressed downward and the rugose, dirt-covered surface effectively blocks the passage. This reaction could often be observed in the laboratory.

THE PATTERN OF ADAPTATION IN THE TROGONOPHINAE

There is a certain superficial resemblance between the general habitus of the Trogonophinae and that of the Rhineurinae. The resemblance is limited, however, extending only to the horizontally spatulate shape of the snout and, of course, to those characters shared by all amphisbaenids. Closer comparison demonstrates striking differences between the two groups. The Trogonophinae differ primarily by (1) the possession of a changed arrangement of the nuchal muscle groups and lack of any comparable ligamentous attachments of the *M. capitivertebralis* and

similar muscles, (2) a modification of the head joint and shortening of the vertebrae of the anterior thoracic region, (3) the absence of a nuchal or any other post-cephalic fold, (4) the presence of central enlarged shields on the chin, (5) the absence of enlarged pectoral shields, and (6) the absence of a retro-articular process. There are also a number of profound differences in the shape and arrangement of the cephalic bones.

No live trogonophines were available to me. Previous field observations are available only for the species *Trogonophis wiegmanni*

(see Loveridge, 1941, pp. 362-363 for citations; also Saint-Girons, 1953 and Varaldi, 1953). With few exceptions such observations provide no indication of major behavioral differences from those described for *Rhineura floridana*. Because of this lack, deductions regarding the trogonophine functional pattern must be restricted to a consideration of the structural differences from the rhineurine forms. This type of extrapolation is at best an unsatisfactory procedure, and the limitations of the method must be kept in mind in the evaluation of results.

LOCOMOTION

Four of the six structural differences indicate a certain lack of motility of the head joint and anterior column. The muscle attachments also fail to suggest any particular dorsoventral freedom of motion. The absence of any disproportionately large dorsal muscle mass, similar to that found in *Rhineura*, may be confirmed by some incidental observations. The vast majority of the specimens of *Rhineura*, examined for another study, have been found to be preserved with the head retracted and bent upward to the most dorsal position. The retraction of the head is due to the morbid contraction of the heavy dorsal muscles (*M. capitivertebralis*), and tests indicate that such contraction will not occur when specimens are anesthetized or relaxed prior to preservation. Series of the highly modified amphisbaenine genus *Ancylocranium* showed a similar bending, though here the head was swung to the left and right sides in equal numbers of specimens. The reasons for this contraction are not clear, but they offer an excellent indicator for the existence of unbalanced muscle masses.

No similar phenomenon was observed on any acrodont specimen, though several individuals of *Diplometopon* did have the neck thrown into a single S-loop, with the first bend occurring immediately behind the head. The nature of the muscular insertions, evenly distributed as they are, indicates that these do serve not to lift or rotate the head above the axis of the trunk, but rather to maintain it in position upon the head joint.

The peculiarities of the anterior column in *Pachycalamus*, *Diplometopon*, and *Aga-*

modon are reminiscent of those of ceratopsians (Romer, 1956, p. 237), certain rodents (Ray, 1958), and cetaceans. A preliminary study of the articulating surfaces and the relation of neural spines and hypapophyses indicates that there is a reduction in the motility of the anteriormost portion of the column. Any pronounced dorsoventral or lateral bending of the column must thus take place behind this zone.

While the anterior column is stiffened in this manner, its enlarged neural spines provide for attachment of tendons of the dorsal muscle group. These thus remain capable of bending the entire assemblage of head and cervical and anterior thoracic vertebrae. Such bending may take place either laterally or dorsoventrally. That it cannot be concentrated into a limited zone is, however, indicated by the absence of modification in pectoral or corresponding lateral shields.

The presence of enlarged shields along the margin, and particularly along the center, of the lower jaw offers some evidence for the fact that these areas are exposed to pressure or wear, which implies a digging movement with the rostral tip above the ventral axis, i.e., in the position in which it is maintained in the preserved animal.

The absence of any modified nuchal or post-cephalic sulci finally suggests lack of facilitation for the behavior associated with these in *Rhineura*, in which they permit the quick ramming stroke, carried out by head and column with the posterior integument stationary.

The absence of cephalonuchal motility, coupled with the peculiarly shaped skulls of these animals, then poses the problem of alternate means of locomotion. The only proposal that appears to offer an adequate explanation indicates that locomotion takes place entirely by ramming action.

A word of caution may not be out of place at this point. It is customary to refer to the major locomotory or other behavioral pattern of an animal as the "standard" one and to consider the stress distribution within its members in the light of the "standard" imposed forces, which implies a dangerous oversimplification.

Few if any animals restrict themselves to a unique structure usage pattern. Thus muscle

pairs often are activated in an unbalanced fashion, completely upsetting any normal stress pattern. The compression members of such a system might well fail were they capable only of withstanding the "normal" balanced condition. It may be true that the unbalanced condition occurs only rarely, but it is likely to be extremely important to the animal when it takes place.

There is, for instance, a high probability of its occurrence as the result of a predator-induced upset of environmental conditions. Failure of the structural element at such a time would involve immediate negative selection for the oversimplification by eliminating the individual from the breeding population. This would correspond to selective advantage for a more conservative structure capable of withstanding the more rarely encountered, high-magnitude forces imposed in unusual directions. The net effect lies in the retention of a more generalized pattern for a specialized habit. The item does not appear to have been sufficiently accentuated in the consideration of various problems, that of the trabeculae of long bones being a case in point. Generalization of the morphological pattern, on the other hand, adds a further source of error to an analysis such as the present. The behavioral pattern would appear to be more limited than the structural one, and it seems unfortunate that it is the latter and not the former that is preserved in alcohol.

FUNCTIONAL ANALYSIS OF THE PROBLEMS OF RAMMING

The forces required to drive a regular cone into a uniform substrate are discussed and graphically illustrated (fig. 25) above. In 1898, Karl Peter (p. 49), in the course of a perceptive analysis of the caecilian skull, discussed the relative resistances of various surfaces of rotation. While his values were taken from an old artillery textbook and were calculated for air, it is interesting to note that the resistance to the passage of a paraboloid is given as 86.5 per cent of that of a regular cone, while values of 118 per cent and 215 per cent, respectively, are given for an ogive and a hemisphere. Peter also commented on the fact that the tips of rootlets, theoretically exposed to the same forces as the head of a burrowing vertebrate, either were of para-

bolic cross section or were covered by a parabolic cap of mineral particles.

Even a brief consideration suffices to show that the actual problem is somewhat more complicated. Graphic demonstration of this fact is yielded by the diverse shapes of the head in typhlopids, uropeltids, caecilians, and trogonophines. These indicate that it may not be possible to derive a single shape of maximal efficiency (= minimum work per unit of linear penetration) for all conditions. The shape must rather be influenced by factors such as the absolute size of the head, the speed and nature of the digging stroke, the particle size, shape, and nature, and possibly also the moisture content, of the substrate, because capillary and film forces will be of considerable importance at the level of magnitude here considered (Collis-George, 1959).

A straight ramming action through a heterogeneous substrate implies a certain measure of rigidity in the ramming head. Larger solid objects, such as pebbles in sand, produce unbalanced forces tending to deflect or bend the tip away from the line of motion. The action of such unbalancing forces becomes more effective and consequently more damaging with an increase of the ratio of length to diameter (l/r), i.e., with the transition from a short to a long column. The same increase also promotes mid-column lateral deflection, or buckling. The unbalanced force is dependent only on the magnitude of the force applied at the head joint and thus is independent of the diameter of the section at which it is imposed. This fact indicates the requirement of a blunter snout for larger animals, as these must impose higher forces to effect over-all penetration.

A number of factors might promote selection of a tip with differing horizontal and vertical cross sections. Beyond considerations requiring rapid expansion in one direction or another for the protection of various cephalic structures, there remain considerations relating to concepts such as cutting action, which must be evaluated for each specific substrate.

There are two ways in which the forces required for moving the animal may be transmitted to the column. First, there is the feathered muscle arrangement of the M. vertebrocutaneus and costocutaneus that act

between skin and axial skeleton. Second, it is possible to have the forces exerted directly onto the column by pressing a loop of the body against a bend in the tunnel. In this case the muscle action is indirect and serves only to shorten (decrease the radius of) a certain bend, forcing the column against the wall. Both systems may, of course, be employed simultaneously. Because of the additive nature of contraction by a series of muscle slips, the total force exerted in the first scheme is directly proportional to that length of column over which muscular contraction takes place, which indicates that a longitudinal increase of the ramming column is advantageous from the propulsion viewpoint, while the reverse would be true for the rules of columnar loading.

The advanced trogonophines seem to have met the problem by a reduction in the length of the skull and anterior vertebrae, in other words, of those sections of the axial skeleton that offer least attachment to the propulsion apparatus. The region in question has, furthermore, been stiffened, thus increasing the effective l/r ratio.

PATTERN OF CRANIAL MODIFICATIONS WITHIN THE TROGONOPHINAE

The skulls of these four genera graphically reflect the conflict of and interaction between two sets of requirements. Thus each skull must serve as a penetrating tip for the ramming action, yet must retain its prior functions as a capsule for the seat of sensory, nervous, and other activity. Almost all the trends and specializations considered in the descriptive section form a functional reflection of the resulting changes.

The ramming action requires a shortening of the skull as well as the maintenance of a certain curvature or shape by its boundary (or the dermal cover overlying it). The sensory aspect requires that the semicircular canals be of large size and spread laterally across a maximum distance¹ and that the

extracolumella can still touch the substrate. The nervous aspect demands integrity of the cranial capsule against deformation. Among other requirements are the protecting and the positioning of the mandibles and their articulations.

These are the basic and immediately apparent requirements, but far from the only ones. However, they may be used here to demonstrate the manner in which the conflict of requirements is mirrored in the skull. Because of this conflict a change in a single requirement, or rather the relaxation of the selective limit on a single requirement, may by disturbing the equilibrium release various changes only indirectly related to the initial step. It thus appears that the primary influence on the trogonophine skull has been exerted by the need for shortening and that the various other changes form direct and indirect reflections of this fact.

The simplest way of reducing the distance between the rostral tip and the condyle and of still maintaining the actual effective length is by bending or angulation. It is thus not particularly surprising that this method is the one demonstrated by the trogonophine skull. Some slight bending or ventral deflection of the tooth row is to be noted in almost all² amphisbaenid skulls. It appears to have been developed for the protection of the mouth during ramming movements, and the present case might then represent a change in function and consequent further development of an existing condition.

While a bending or angling of the skull increases its functional length as a brain case, it simultaneously magnifies the support problem. Forces are no longer transmitted along the longitudinal axis of the skull, but at an angle to this, and the stress pattern becomes complicated by the appearance of shear and tension components.

It is a gross oversimplification to treat the skull elements as plates and to consider only a two-dimensional aspect, but such simplification may usefully be employed in the comparison of sutures and articulations for the transmission of tension and compression

¹ The sensitivity for the detection of movements (assuming equivalent effectiveness of the neural mechanism) increases with the distance between the lateral extremities of the semicircular canals. This fact helps to explain the presence of the horizontal canals at the lateral extremities of the temporal lobes in *Diplometopon* and *Agamodon*.

² Only *Blanus* among the many species the skulls of which are illustrated by Vanzolini (MS) is shown with a straight (=parallel to the long axis of the body) tooth row.

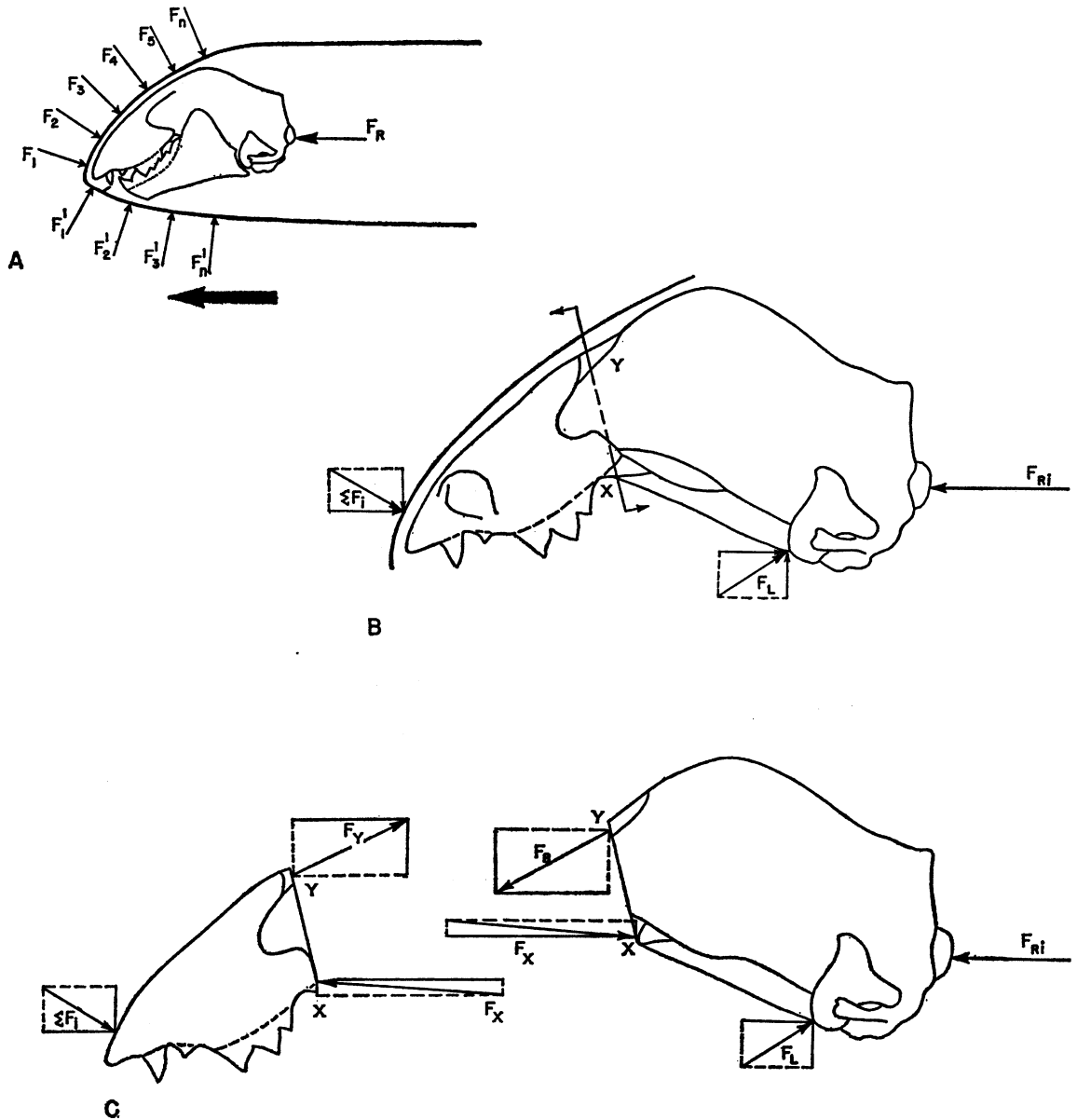


FIG. 29. Static diagrams to show forces imposed on the skull during ramming in *Diplometopon zarudnyi*. Conventions as in figure 27 except where indicated. A. Forces acting on the skull and integument during the ramming stroke. B. Forces acting on the skull. Only the ΣF_i group is here considered. The dorsad forces initially applied to the lower jaw, which may actually be transmitted to the skull in a more complicated manner, are here indicated as acting only on the articular facet of the quadrate. Line X-Y shows the line along which section of forces is made in C. C. Skull loaded as in B, but divided along X-Y. The forces required to maintain each half in equilibrium permit an estimate of the stresses along the line of section. The diagram suggests that the region at X is in tension, while the palatal shelf at Y is under compression.

forces. For purposes of tensile connection it is of course the over-all area of the contact surfaces, and for purposes of compression connection only the cross-sectional area, at right angles to the imposed force, that are of importance. These simple principles may best be demonstrated in a consideration of the superficial stress pattern over some regions of the skull of *Diplometopon* (fig. 12). The force patterns for two conditions are shown in figures 29 and 30.

The ramming force, F_R , is considered to be applied to the condylar articulation. It will be opposed by the reaction forces F_1 , F_2 , F_3 , \dots , F_n . If we restrict the analysis to the forces acting on the extreme tip (assumed to be F_i), we find that the horizontal component of this force is transmitted to the palatal shelf, at X, while the vertical (ventrad) component sets up tensile stresses at Y, in fact along the entire facial plane. The location of compressive stresses at X and of tensile stresses at Y can be demonstrated by our treating only a section of the skull and finding the forces necessary to keep it in equilibrium.

The stress pattern may almost be read from the structure of the skull without recourse to diagrams. The sutures at B are tension sutures with long interdigitations of maxilla, frontal, and parietal, and the entire series of facial articulations is of this type. The actual connection occurs by the numbers of connective tissue fibers (also see above comments on Kritzinger), frictional connections, and interlocking keys (dilation of the fingertips).

The ventral view of the skull demonstrates the compression joints. The tip of the premaxilla wedges between the maxillae, thus passing the compressive force caudad and preventing slippage or structural failure when the ramming stroke is not exactly parallel to the long axis of the body. A portion of the force is transmitted across the palatine, ectopterygoid, and pterygoid to the basiptyergoid processes. All the sutures involved are relatively smooth and show none of the interdigitations common to the dorsal surface.

The second diagram (fig. 30) indicates that the stress pattern set up in the snout during biting is the reverse of that during the ram-

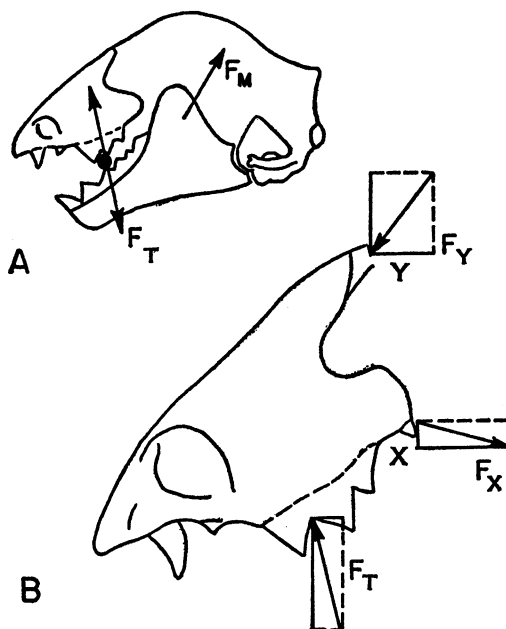


FIG. 30. Diagrams (as in fig. 29) to show forces imposed on the skull during the bite in *Diplometopon zarudnyi*. A. Manner in which forces are imposed on the upper jaw during bite. B. Forces at the plane X-Y. Note that there has been a reversal of the force pattern, with compression at Y and tension of the palatal shelf at X. Conventions as in figure 29.

ming cycle. The initial force is imposed dorsad against the teeth during the bite, which places the facial sutures into compression and exerts a tension along the palatal shelf. Apparently the stresses involved are of a lower magnitude than those of the ramming cycle, as the latter and not the former seem to have been most influential in shaping the architecture of the skull.

A modification of the tension articulation, which also allows the carrying of compression forces, is demonstrated by the broad overlap of the parietal over the occipitals. This consists of parallel plates with short connecting fibers. The fiber position may change (fig. 31) with a change in the direction of the applied force, or there may be double or multiple systems of fibers capable of withstanding forces in a variety of directions. The forces applied along the plates will also tend to press these plates together.

The need for a lateral spread or rather for a retention of the diametric, with a reduction

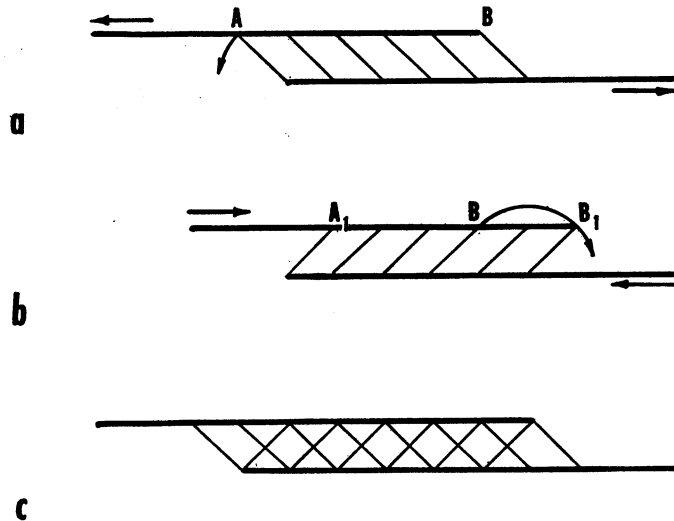


FIG. 31. Schematic drawing of bone articulation by parallel plates with connecting fibers; lower plate assumed fixed. A. System in tension. Note that the upper plate tends to approach the lower. B. System in compression. Note change in fiber direction as well as approach of upper to lower plate after swinging along arc B-B₁. C. System with twin sets of connecting fibers. This can be stressed in either direction without particular lateral displacement of the free plate.

of the longitudinal dimension of the skull, has been one of the most significant items in changing the aspect of the shortened trogonophine skull. This retention of the diameter appears to have at least two causes. First, there is the above-mentioned requirement for retention or even increase of both size and distance between extremities of the semi-circular canals. Second, the posterior aspect must provide for attachment of the several sets of muscles that serve to retain the skull in position upon the vertebral column. The (unilateral) stability of such a system will again be proportional to the distance between the point of its attachment to the skull (application of tensile force) and the central axis of the system of skull-vertebrae (along which act the compressive forces of the column).

This retained or increased lateral dimension has brought with it an effectively more obtuse angle between rostral tip and lateral extremities. More important, however, has been its effect on the articulation of the mandibles and the position of the extracolumella.

The outward shift of the temporal lobes has moved the quadrates into an exposed position, partly out of the "flow shadow" of the maxillae. There is some slight compensation for this by the medial swing of the ventral tips of the quadrates. The articulations of the mandibles are further protected by the lateral projections of the maxillae, the flaring lateroposterior wings of which extend to cover more than half of each articulating surface. The need for such anterior shielding may well help to explain the peculiar shape of the snout.

The exposed position of the quadrates requires that they be capable of bearing and transmitting the compressive forces exerted by the substrate. Such capability is effected by the close adherence between the quadrates and the occipital lobes and by the recessing of the posterosuperior heads of the former. A comparison of the four skulls indicates remarkable constancy of these portions of the otherwise variable quadrates. The ventral tips of the quadrates are supported postero-medially by the flaring plates of the pterygoids. These can prevent inward and back-

ward deflection during ramming because of their medial bracing against the basipterygoid processes. The close junction between pterygoids and quadrates also resists forward movement of the palatal shelf during the bite.

The structural analysis indicates quite clearly that the skull of an adult specimen of *Diplometopon* (as well as that of the other genera here discussed) is effectively akinetic. Extensive movements of palatal and other elements (as suggested by Versluys, 1912, and Kritzing, 1946) are, as discussed above, incompatible with the forces that must be exerted during the burrowing movements.

The modifications of the stapes and extracolumella have been pointed to as one of the most interesting of the various specializations encountered among the trogonophines. Comparison of the lateral views with the diagram given in figure 12 indicates that such stapelial modification may also have resulted from the shortening and angulation of the skull. The effectiveness of such a microphonic device would depend on the transmission of the vibrations from tissue pads to inner ear. In *Amphisbaena* and *Trogonophis* the extracolumella lies along the side of the lower jaw, which is to say, in parallel with the major direction of motion. In *Pachycalamus*, *Diplometopon*, and *Agamodon*, in which the direction of motion undergoes a gradual change,

there is a simultaneous change in the size and direction of the extracolumellar attachment to the skin. It is interesting to speculate whether there is something in the nature of the pickup or transmission that requires the attachment to occur in parallel with the direction of motion or whether the widening of these tissue pads acts for support or stabilization.

Most species of amphisbaenids in which the extracolumella is a simple cartilaginous rod have a rectangular or obtuse angle of articulation between stapes and extracolumella. In *Diplometopon* such an angle cannot be attained without a simultaneous increase in the stapelial length, because the widening of the temporal lobes forces the anterior tip of the extracolumella to swing mediad. The unusual stapelial length may indeed reflect a need to maintain this angle. The stout structure of the stapes is then a secondary result of the requirement for buttressing the stapelial tip which must be exposed laterally beyond the quadrate, and projects into a zone where it is acted upon by the burrowing forces. The buttressed condition of the bone in both *Agamodon* and *Diplometopon* would then be yet another result of the initial requirement for the shortening of the skull. Whether the ossification of the extracolumella resulted as a pressure-induced calci

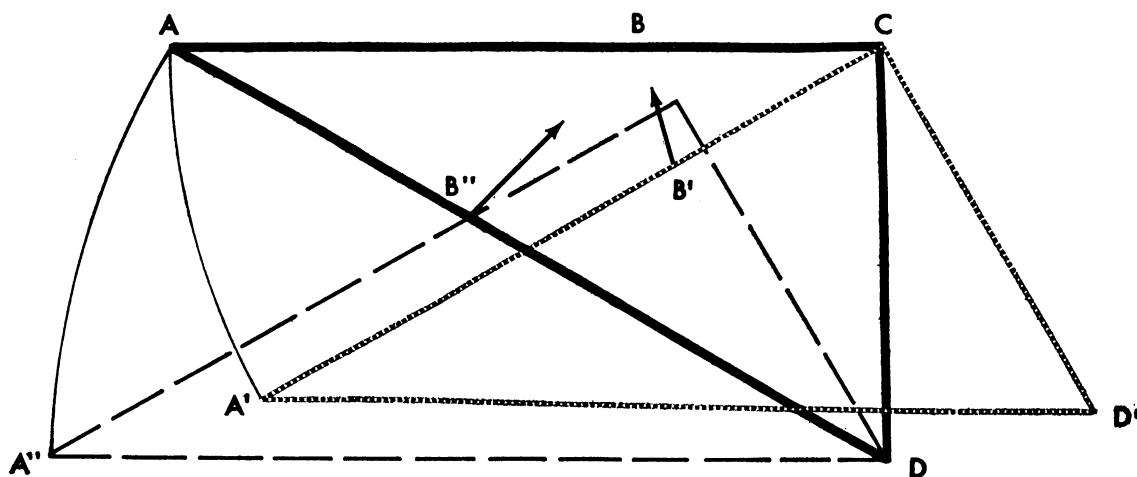


FIG. 32. Schematic diagram to show difference in linear displacement of lower jaw for equivalent (30°) angular rotation around point C lying on the occlusion line A-B (jaw outline shown by dotted line) and around point D lying below the occlusion line (jaw outline shown by dashed line). Note that distance A-A'' is longer than distance A-A'. Note also the direction of forces exerted at points B' and B'' in the closing of the jaw.

fication, or serves some as yet unknown function relating to the auditory mechanism remains an open question. It is certain that the function and variation of the amphisbaenid ear form promising subjects for further investigation.

The final group of modifications deals with those of the lower jaw. Besides the more or less complete absence of a retro-articular process there is the marked increase in the elevation of the tooth line above the level of the glenoid fossa. It is possible to establish a direct correlation of the second of these items with the shortening of the skull.

The reduction in the length of the mandible and of the tooth line brings with it a reduced separation of the anterior tooth tips for an

equivalent angular movement of the dentary. Such reduction in biting distance would be a distinct limiting factor to the prey-capturing capacity of a small reptile. The gape may be increased only by cranial kinesis or by a ventrad shift of the mandibular articulation. As the former method would interfere with the function of the skull as a digging tool, it is not surprising to note the ventrad shift of the glenoid fossa. This shift has two related advantages (fig. 32). First, it produces an increase in the caudad vector exerted onto the object between the teeth. Second, there is an increase in the linear separation of the teeth for a given angular displacement. Both of these items would facilitate the ingestion and mastication of larger food objects.

SUMMARY

1. THE ACRODONT AMPHISBAENIDS have been studied, and detailed descriptions are presented of the integument, skull and mandible, cervical vertebrae, hyoid, and shoulder girdles of four of the six species. Brief comments are made on the degree of lung reduction and nature of dermal innervation.

2. Forms recognized are (forms of which no specimens were available are marked with an asterisk,*):

Trogonophis wiegmanni Kaup
Pachycalamus brevis Günther
Diplometopon zarudnyi Nikolski
Agamodon anguliceps Peters
 **Agamodon compressus* Mocquard
 **Agamodon arabicus* Anderson

3. The subspecies *A. anguliceps immacu-*

latus Calabresi, placed in *A. compressus* by Loveridge (1941), is returned to its original species.

4. Reasons are presented for considering the acrodont forms as a distinct subfamily, the Trogonophinae, clearly separated from other amphisbaenids by a number of structural characters and a special mode of digging.

5. The problems encountered by burrowing species are analyzed on a theoretical basis. The theoretical analysis is tested on the basis of observations on the Florida amphisbaenid species *Rhineura floridana* Baird. The possible burrowing mode of the Trogonophinae is analyzed on the basis of differences from the pattern exhibited by rhineurine species.

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