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THE HEAD SKELETON OF *AMPHISBAENA ALBA* LINNEAUS

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ABSTRACT

The skull of *Amphisbaena alba* Linneaus and its disarticulated components are described in detail and illustrated by photographs and labeled sketches. The cartilaginous components, particularly the adult chondrocranium are characterized in parallel. The bone formerly referred as the orbitosphenoid is considered as a distinct element nonhomologous to the synonymous element in other squamates and hence referred to as a "tabulosphenoid" (sphenoid plate). The element-X (of Zangerl) is considered to represent an epiphysis that facilitates the transmission of muscular forces to the growing skull, rather than being the remnant of an element no longer expressed. Cranial kinesis is discussed as are the general structural patterns associated with the relative distribution of spongy and dense laminar bone.

KEY WORDS: Reptilia, Squamata, Amphisbaenia, *Amphisbaena alba*, osteology, chondrocranium, head anatomy, cranial kinesis

INTRODUCTION

Amphisbaena alba is the largest (longest and stoutest) South American amphisbaenian, reaching more than 750 mm in length (Vanzolini, 1955; Gans, 1986), and has the largest range, extending from Panamá and Trinidad, southward to Bolivia and Paraguay (Vanzolini, 1955; Gans, 1962). Indeed, the species may have the largest range of any amphisbaenian, although the range of *Amphisbaena fuliginosa* is remarkably similar (Vanzolini, 1951*b*). *Amphisbaena alba* appears to be commensal with the leaf-cutter ants, the tunnel systems of which provide it with a unique habitat (Riley et al., 1986).

The skull of *Amphisbaena alba* has been described a number of times as an entity (Cuvier, 1829–1830; Brühl, 1886; Williston, 1918*a* [illustration attributed to Alexander Ruthven], 1925; Gilmore, 1928 [after Williston, 1918*a*, poor proportions]; Vanzolini, 1951*a*; McDowell and Bogert, 1954; Romer, 1956 [after Williston 1918*a*]; Underwood, 1957; Jollie, 1960 [new 3/4 view of side]; Wu et al., 1995) and is sometimes used as a model for all amphisbaenians. These descriptions are based on articulated skulls and commonly only on those of fairly large individuals. However, amphisbaenian skulls have a plywoodlike construction; some individual bony elements overlap substantially, and significant details are lost when only the exposed portions of skulls are described.

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The present characterization of the skull of *Amphisbaena alba* is the first of a series of redescriptions of the skulls of all amphisbaenians. They are intended to serve as the basis for a reanalysis of generic and familial classifications, for which substantial material has accumulated. In addition to a description of the intact skull, this study includes descriptions of each of the cranial bones and their relationships to one another. For the sake of convenience, the descriptive account of each element is followed immediately by a brief defense of the homology and, if necessary, by comments on the literature dealing with the particular element. Beyond providing a baseline for taxonomic comparisons, the study was designed to allow identification of a series of fossil bones from Lagoa Santa (Gans and Montero, in press). The study also led to some strictly morphological conclusions. The large azygous ventral bone formerly referred to as the orbitosphenoid is considered not to be homologous to the synonymous element in other squamates. For reasons presented below it is hence referred to as a "tabulosphenoid" (sphenoid plate).

Materials and Methods

The material of *Amphisbaena alba* used in this study includes five complete and articulated skulls; two articulated, incomplete skulls; three totally disarticulated skulls used for the description of individual cranial elements; three sets of serial sections through the head (deriving from studies with E. G. Wever); and one cleared and stained specimen (Table 1). The disarticulated skulls were obtained by soaking the heads of skinned fresh specimens in water for several weeks until they disintegrated; careful washing thereafter freed the bones. Both photographs and labeled overlays of the identical views are provided.

Whenever possible, the skull and its elements are shown in orthogonal projection (Loeb and Gans, 1986). In this the plate usually shows a central figure which is normally in one of the standard (dorsal, lateral, ventral, medial, etc.) positions, illustrating the element as seen along the major axes or planes of symmetry of the skull; however, more complex elements are shown at other angles as well. The various photographs are placed at right angles to the lines of view (i.e., normal to the surface illustrated).

It is facile to visualize orthogonal projection by considering that the bone has been placed into a transparent box, with the views shown on the plane sides paralleling the surfaces of the element. Once the individual drawings have been completed, some edges are slit, the box is unfolded, and the six or more sides placed flat, maintaining the contact lines between them. Some of the views will likely contain minimal supplementary information and can be omitted. This procedure not only shows processes and sutures in a standard fashion, but allows the comparison of adjacent figures, thus facilitating three-dimensional reconstruction.

The descriptions in this report first deal with the entire articulated skulls and mandibles and thereafter with the individual bones. Discussion of the cranial cartilages and major cranial cavities follows. Each account begins with a paragraph dealing with the general outline of the element, and then discusses its shape and foramina based on the entire bone and its exposure in serial sections. Finally, each contains a brief statement about the identification (homology) of the element and, if appropriate, about anatomical and nomenclatorial comments from the literature. However, as a list of historical treatments of the cranial elements has been

Table 1.—*Morphometric data of the analyzed specimens (in cm). See definitions and acronyms in the Morphometrics section.*

Measurements	CG 3533	CG 3537	UMMZ 149616	AMNH 73233	AMNH 17799	KM 11a	KM 11b	CG 1811	CG 1216	CG 1200	ICN 5733
1. Snout–vent length	55.2	30.9	—	—	41.8*	—	—	—	—	—	55.0
2. Tail length	4.10	2.40	—	—	3.2*	—	—	—	—	—	4.4
3. Skull length	3.18	1.82	2.12	2.79	2.66	—	—	—	—	—	3.02
4. Skull greatest height	0.97	0.48	0.55	0.71	0.75	0.89	0.73	—	—	—	0.93
5. Face length	1.09	0.63	0.78	0.98	1.01	—	—	—	—	—	1.07
6. Face width	1.10	0.55	0.74	0.96	0.99	—	—	—	—	—	1.21
7. Face height	0.60	0.34	0.39	0.50	0.46*	—	—	—	—	—	0.61
8. Maxillary length	0.75	0.43	0.52	0.69	0.69	0.79	—	0.71	0.65	0.69	0.75
9. Occipital width	1.36	0.75	0.87	1.12	1.16	—	1.15	1.32	1.20	1.25	1.29
10. Occipital height	0.75	0.45	0.50	0.62	0.66	0.70	0.64	0.73	0.67	0.73	0.74
11. Occipital condyle width	0.36	0.24	0.27	0.34	0.34	—	0.35	0.35	0.34	0.34	0.35
12. Occipital crest length	0.69	0.32	0.35	0.60	—	0.70	0.55	0.70	0.58	0.70	0.63
13. Parietal width	0.50	0.32	0.38	0.43	0.43	0.50	—	0.45	0.43	0.44	0.49
14. Parietal length	1.49	0.87	0.85	1.15	1.20	1.32	—	1.30	1.25	1.31	1.14
15. Pterygoid width	0.705	0.42	0.54	0.59	0.59	—	—	—	—	—	0.77
16. Parietal + occipital length	2.23	1.22	1.26	1.80	1.78	2.11	—	—	—	—	1.92
17. Crest width	0.12	0.08	0.09	0.12	0.15	0.14	0.12	0.16	0.11	0.13	0.16
18. Frontal segment	0.67	0.40	0.53	0.64	0.62	—	—	—	—	—	0.83
19. Medial segment	1.38	0.76	0.80	1.18	0.80	—	—	—	—	—	1.45
20. Occipital segment	0.49	0.22	0.24	0.33	0.24	—	—	—	—	—	0.63

* Measurement of vertebral column.

published (Gans, 1978), the discussion of literature has been restricted to cases posing potential problems.

Some material derives from loans of several museums, whose curators we acknowledge. The acronyms are as follows: AMNH—American Museum of Natural History, New York, New York, USA (C. J. Cole, R. G. Zweifel); CG—Carl Gans Collection (includes E. G. Wever serial sections); ICN—Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Santafé de Bogota, Colombia (O. V. Castano); KM—Zoologisk Museum, University of Copenhagen, Copenhagen, Denmark (Dr. F. W. Brastrup); UMMZ—University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA (G. Schneider).

The following materials were used to generate the description of the skull. Articulated skulls: CG 3533 (no data), CG 3537 (Capitania Maloca Feia, Marienopolis, Mn. de Villabela, Mato Grosso, Brazil), UMMZ 149616 (Colombia), AMNH 73233 (no data), AMNH 17799 (Trinidad, from New York Aquarium), ICN 5733 (Colombia). Incomplete, articulated skulls: KM 11a (no data), KM 11b (no data). Completely disarticulated skulls (some of the bones are articulated): CG 1811 (Leticia, Colombia). Parietal articulated with tabulosphenoid and frontals, CG 1216 (Leticia, Colombia). Occipital complex articulated with parabasisphenoid and parietal, CG 1200 (Leticia, Colombia). Cleared and stained specimen: CG 3542 (Santo Amaro, Sao Paulo, Brazil). Serially sectioned specimens (frontal sections): CG 1500, 1667, 1668 (dealers, Brazil, Venezuela; cf. Gans and Wever, 1972).

RESULTS

Morphometrics

As most skulls of *Amphisbaena alba* in collections do not provide information about the proportions of the entire specimen, we dissected three specimens (CG 3537, 3553; ICN 5733). For AMNH 17799 the snout–vent length is estimated from the articulated vertebral column. Various measurements of the skull are listed in Table 1 and all but 1, 2, and 10 are illustrated in Figure 1. These are defined as follows:

1. Snout–vent length: Measured from the tip of the snout to the cloacal slit (vent) of the entire specimen.

2. Tail length: Measured from the vent to the caudal tip (this species never displays caudal autotomy).

3. Skull length: Measured from the tip of the snout (premaxilla) to the condyle (exposed posterior to the occipital crest).

4. Skull greatest height: Measured from the ventral point of element-X to point just anterior to the gap between parietal and ascendent process of the supraoccipital.

5. Face length: Measured from the tip of the snout to the posterior end of the maxilla.

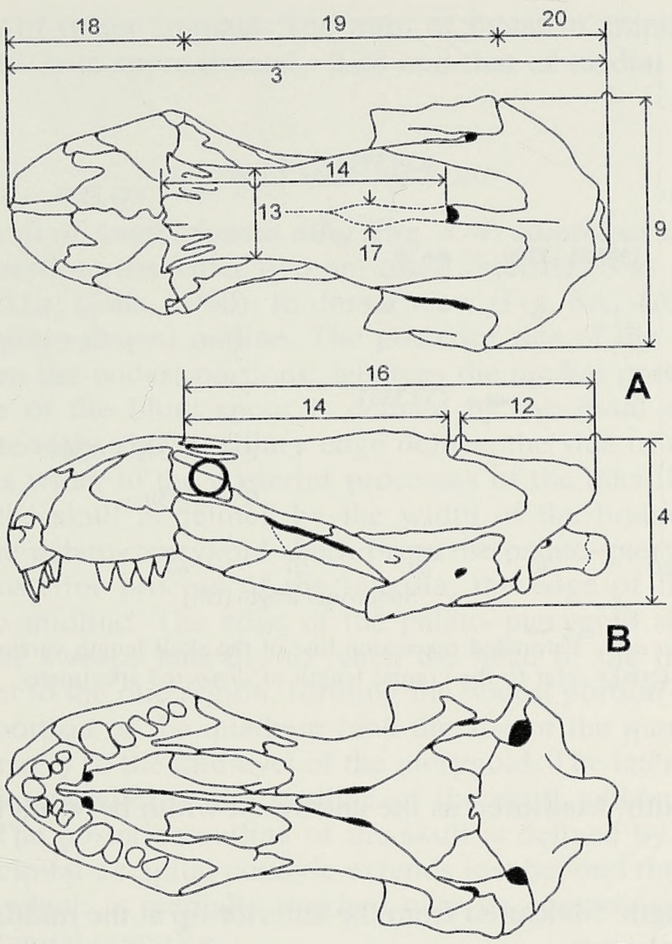

Fig. 1.—*Amphisbaena alba.* Labeled outline of skull showing the measurements in Table 1, items 3 to 20 as defined in text. Measurement 10 cannot be seen in these views. The circle (in view B) shows the approximate position of the eye in the posteriorly open orbit.

6. Face width: Measured just anterior to the maxilla–ectopterygoid joint.

7. Face height: Measured behind the last maxillary tooth, from the top of the frontals to the ventral aspect of the maxilla.

8. Maxilla length: Measured from the posterolateral border of the external nares to the posterior end of the maxilla.

9. Occipital width: Measured between the outer sides of the paroccipital processes.

10. Occipital height: Measured from the anterior end of the occipital ascendent process to the center of the basioccipital plate.

11. Occipital condyle width: Measured horizontally at the widest spot.

12. Ascendent process length: Measured from the anterior end of the occipital ascendent process to the border of the occipital crest.

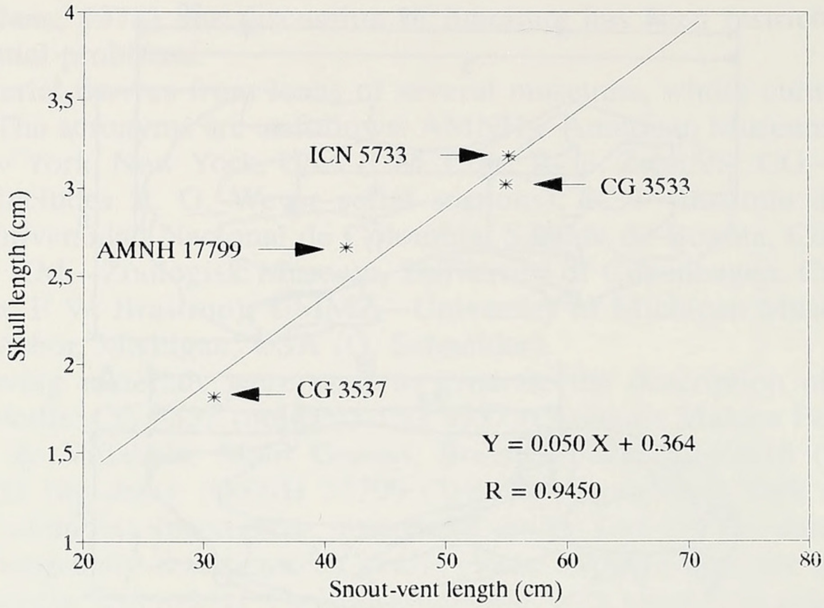

Fig. 2.—*Amphisbaena alba.* Estimated regression line of the skull length versus snout–vent length of intact animals; the asterisks refer to the cranial length of dissected specimens.

13. Parietal width: Measured as the narrowest width between the lateral borders of the parietal.

14. Parietal length: Measured from the anterior tip at the midline to the posterior end of the parietal crest.

15. Pterygoid width: Measured as the narrowest width between the lateral borders of the palato–pterygoid shelves.

16. Parietal + occipital length: Measured at the midline from the anterior tip of the parietal to the posterior end of the occipital crest.

17. Parietal crest width: Measured as the maximum width of the parietal crest.

Measurements 18 to 20 were taken from drawings made with a camera lucida; hence, they are not comparable to direct measurements. The length of the skulls may be subdivided into three portions, namely the facial segment (18), the medial segment (19), and the occipital segment (20). The facial segment extends from the tip of the premaxilla to the maxilla–ectopterygoid joint. The medial segment extends from here to the posterior tips of the quadrates. The occipital segment extends to the posterior end of the occipital condyle.

Although the number of specimens is too low to allow a statistical analysis, the raw data presented here represent a starting point for future studies (Table 1). The lengths of the available skulls (measurement 3) range from 1.82 to 3.18 cm. The width of the occipital complex (measurement 9) ranges from 0.75 to 1.36 cm, and the greatest height of the cranium (measurement 4) from 0.48 to 0.97 cm. The width of the anterior portion of the snout (measurement 6) ranges from 0.55 to 1.10 cm. Figure 2 shows that the skull length varies linearly with the snout–vent length of intact animals. The ratio of facial to cranial length of *Amphisbaena alba* (18/3) is approximately 0.28 and that of medial to cranial length is 0.46.

External View of Skull

The elongate skull of *Amphisbaena alba* (Fig. 3, 4) comprises a facial, a medial, and an occipital portion; the latter two are often referred to as a cranial portion (cf. Vanzolini, 1951*a*; Gans, 1960). In dorsal view (Fig. 3A, 4A), the articulated skull has an hourglass-shaped outline. The posterior tips of the maxillae and the occipital crest form the widest portions; whereas the medial portion is narrowest. The anterior edge of the blunt snout is defined by the nasal and premaxillary curves. More posteriorly, the maxillary edge defines the side of the face, the face gradually becomes wider to the posterior processes of the maxilla. From here the lateral extent of the skull is defined by the width of the braincase, and by the smooth edge of the palato–pterygoid shelf. From the palato–pterygoid suture with the lateralmost posterior process of the maxilla, the edge of the ectopterygoid curves toward the midline. The edge of the palato–pterygoid shelf is narrowest here, but thereafter sweeps laterally to reach the head of the inclined quadrate, which lies adjacent to the otic region, forming the widest portion of the articulated skull. The distal portion of the quadrate (and the site of the mandibular articulation) reaches anteriorly to the midlevel of the pterygoid. The lateralmost extremity of the quadrate lies parallel to the midline of the skull, although curving very slightly mediad. The posterior outline of the skull is defined by the fused occipitals. The wide bicipital occipital condyle extends just beyond the flaring occipital crest (Fig. 4, 5), which is medially notched near its contact with the ascendent process of the occipital complex.

In lateral view (Fig. 3B, 4B), the dorsal surface of the face is slightly concave, the bend beginning at the frontoparietal joint. The ventral surface is formed by the premaxillary plane and lies at an angle of about 35° below the axis of the cranial portion. More posteriorly, along the posteroventral plane of the maxilla, it lies at an angle of only 15°. The dorsal surface of the medial portion is defined by the parietal crest, which starts near the midline of the skull, and shows a widened and dorsally projecting process at the midline; this process serves as the attachment for the mass of epaxial and mandibular adductor muscles. The parietal extends far posteriorly over the compound occipital complex; however, a median notch within the parietal accommodates the ascendent process of the latter. In prepared skeletons, the tip of the ascendent process of the occipital is separated from the posteriormost portion of the medial ridge of the parietal so that a notch is seen in lateral view. Posterior to the notch, the ascendent process of the occipital extends to the level of the posteriorly projecting edge of the dorsal surface; this edge then drops ventrally and anteriorly toward the level of the quadratic articulation. From this level, the occipital condyle extends on a slender neck to form the posteriormost portion of the skull. Ventrally the medial portion of the skull is defined by the projecting palato–pterygoid shelf that angles slightly ventrally from the edge of the maxilla to the condyle of the quadrate (around which it bends). The element-X, the distal extremity of the stapes, and the paroccipital process extend posteroventral to the quadrate. More posteriorly, the skull is delimited by the surface of the ventral plate of the occipital complex.

The dorsal surface of the snout (face) (Fig. 3A, 4A) is formed by the rugose

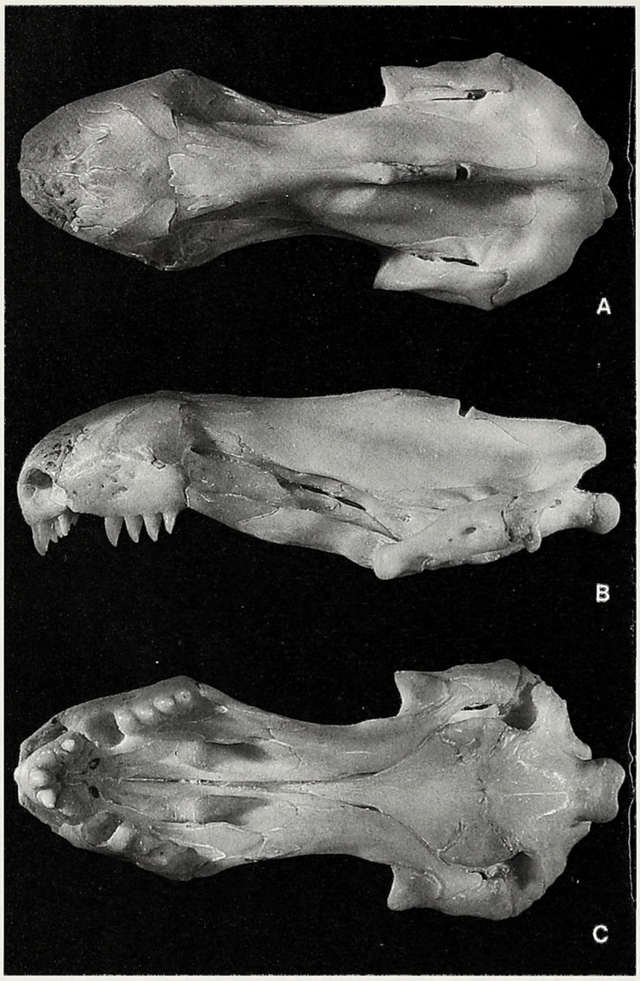

Fig. 3.—*Amphisbaena alba*. Photographs of skull (CG 3533); note that the stapes are missing. Anterior is to the left. The bar shows 0.5 cm to scale. A, dorsal view; B, lateral view; C, ventral view.

nasals, which are separated by a narrow, vertical nasal process of the azygous premaxilla. The nasals roof the external nares, which are ventromedially defined by the premaxilla, and laterally by the maxillae, and lined internally by the septomaxillae. The maxillae form the vertical walls of the snout, reaching the frontals anterodorsally. The premaxillary nasal process reaches the dorsal aspect of the medially interlocking but superficially smooth frontals (which actually extend ventrolaterally more posteriorly, forming a ring around the anterior portion of the cerebral cavity). The maxillae are separated from more posterior frontal contact by the prefrontals, which reach the orbits and partially overlap the frontals medially reducing their dorsal exposure. The maxillae and prefrontals form an important part of the sides of the face, and also of the anterior wall of the orbit. The complex posterior suture of the frontals with the parietals laterally extends as two to four fingerlike processes that form an anteriorly open angle. The parietal defines the medial and dorsal portion of the skull, posterior to prefrontals and frontals; it extends laterally and ventrally from the midline. An anterior projection of the parietal may or may not reach the prefrontal, thus narrowing the posterolateral appearance of the frontals. Authors have been confused by the multiple

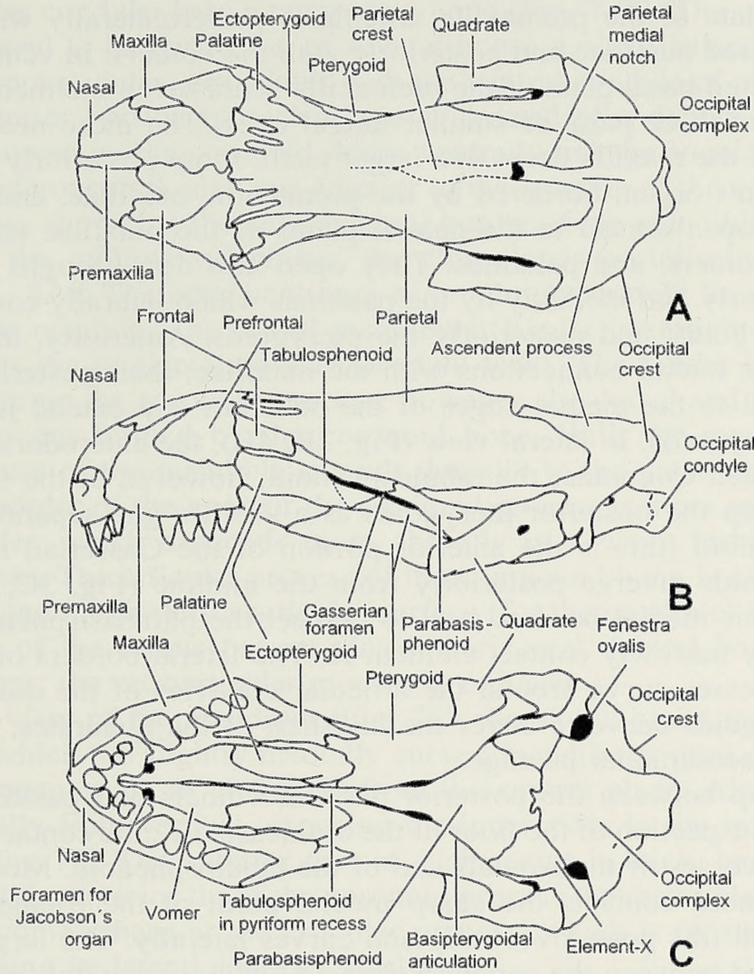

Fig. 4.—*Amphisbaena alba.* Labeled outline of skull shown in Figure 3.

and seemingly independent appearance of frontal exposures, labelling them as distinct elements (May, 1978).

The orbital space is defined anteriorly, but is posteriorly open. All of the elements that intercalate to form the anteromedial portion of the orbit show complex interdigitation so that the patterns of exposure differ among specimens and even bilaterally. The orbital spaces are formed anteriorly by the prefrontals, medially by the ventral processes of the frontals, medioventrally by the tabulosphenoid, and ventrally by the palatine shelf (palatine plus ectopterygoid). The spaces are open posteriorly and dorsally (Fig. 1B). The postorbital spaces ventral to the lateral borders of the parietal and the tabulosphenoid, and dorsal to the palato–pterygoid (and ectopterygoid) shelves, would represent the epipteric cavities; they continue as lateral concavities extending posteriorly to the quadrates and otic region of the occipitals. Posteriorly, the pterygoids are laterally adjacent and suturally joined to the parabasisphenoid; at this level the roof of the concavities is formed by the tabulosphenoid. The wide Gasserian foramen (for the trigeminal ganglion, cf. Vanzolini, 1951*a*) opens between the posterior tip of the tabulosphenoid and the parabasisphenoid. There is no trace of an epipterygoid in this region, a character reported only for *Trogonophis* among amphisbaenians (Gans, 1960).

The basal plate of the premaxilla articulates posterolaterally with the ventral plate of the paired maxillae and posteriorly with the vomers. In ventral view (Fig. 3C, 4C), the tilted basal plate of the premaxilla bears seven inclined teeth, a large median one and three pairs of smaller lateral ones. The more nearly horizontal ventral plate of the maxilla bears five larger teeth. More posteriorly lie the foramina of Jacobson's organ, bordered by the premaxilla, maxillae, and vomers. The internal nares open dorsad to the palatal plates of the maxillae and are defined by maxillae, vomers, and palatines. They open into deep troughs on the palate formed posteriorly and medially by the palatines which laterally contact the maxillae, ectopterygoids, and posteriorly the pterygoids. Anteriorly, the slender vomers have wide lateral connections with the maxillae; their posterior rod-shaped ends lie ventral to the medial edges of the palatines and extend just anterior to contact the pterygoids. In lateral view (Fig. 3B, 4B), the anterodorsal parts of the palatines are seen to contact the tabulosphenoid; however, at the level at which palatines overlap the posterior pterygoids as a shelf, a gap separates them from the tabulosphenoid (this is the anterior portion of the Gasserian foramen). The slender pterygoids diverge posteriorly from the midline (Fig. 3C, 4C). At their midportion, their medial borders start to contact the parabasisphenoid and more posteriorly they narrowly contact element-X. The lateral borders of the posterior pterygoid processes curve around the articular condyles of the quadrates; thereafter the pterygoids curve to cover the midshaft of the quadrates, medially bordering the extracolumellar passage.

A medial gap between the posterior parts of vomers and palatines (pyriform recess) allows inspection of the floor of the braincase, i.e., the contact line between the ventral processes of the frontals and of the tabulosphenoid. More posteriorly, the tabulosphenoid contacts the sharp medial point of the triangular parabasisphenoid, which tilts posteroventrally and curves laterally. The large elements-X are each wedged between the parabasisphenoid and basioccipital from which they are separated by triradiate cartilaginous plates (Fig. 55, 56). The wide, platelike basioccipital (fused into the occipital complex) forms the posterior floor of the cranium. Its posterior border is rounded and bent dorsally, forming the posterior end of the braincase. The lateral otic areas bear the openings of the fenestra ovalis, providing the seat to the stapedial footplate. The columella of the stapes lies across the ventral edge of the quadrate; the cartilaginous extracolumella, in an intact specimen, projects anteriorly along the ventral face of the quadrate to parallel the infralabial scales and end in an infralabial pad further anteriorly (Wever and Gans, 1973).

In posterior view (Fig. 5, 6), most of the area is occupied by the posterior aspect of the occipital complex; hence the fossae and foramina thus exposed can be characterized by reference to the account of this bone in the discussion of individual bony elements below. The tip of the occipital condyle is visible dorsally. Lateroventrally, there is exposure of the extreme ventral portion of the quadrate and ventral to it the posterolateral head of the pterygoid which extends around the former. As the facial portion of the skull bends ventrally, the palatal tip appears ventral to the generally concave basiventral edge.

Mandible

The mandible consists of two rami connected anteriorly and medially by a solid symphysis and each extending posteriorly as a coronoid process and terminating in a mandibular condyle, here a compound bone (Fig. 7, 8). The compound bone (that is presumed to be the fusion of several bones, i.e., articular, splenial, prearticular, and supra-angular) articulates with the ventral condyle of one of the quadrates. The anterior portion of each ramus is formed of a dentary, bearing eight teeth, and followed by the coronoid. More ventrally lies the angular, which wraps around the posteroventral edge just anterior to the condyle of the compound bone.

Lateral views show that the anteroventral border of the mandible gently curves downward at the midline symphysis, the chin slopes posteriorly to the ventral edge (Fig. 7A, 8A). The edge continues as an almost straight line to the edge of the mandibular condyle. The dorsal mandibular border is straight and its medial aspect supports the implantation sites of eight teeth. The border then ascends in a smooth curve up the coronoid process; however, the dorsal and posterior edges of the process are formed by the coronoid bone. With the mouth closed, the coronoid process of the mandible extends dorsally to the palato–pterygoid shelf. The anterior border of the apex of the coronoid process is more rounded than the posterior border, which descends more abruptly in a wavy fashion toward the articular process. The articular process of the compound bone is expanded dorsad and ventrally and the posterior articular surface (for the quadrate) is concave. The posterior part of the ramus has an almost horizontal ventral border below the articular process; the retroarticular process is reduced.

The dorsal view of the mandible (Fig. 7C) shows the broad mandibular symphysis, from which the slightly medially curved mandibular rami diverge to form a posteriorly open angle of about 15° from the central plane. Also, the rami are inclined laterally from vertical, exposing the inner sides in the truly dorsal view shown in Figure 7C. The anterior part of each ramus is thick, becoming thinner posteriorly. At the anterior tip of the coronoid process the mandibles start a medial curve that becomes sharp at the articular process, which is twisted and inclined mediad, exposing its lateral side in dorsal view.

In labial (lateral) view (Fig. 7A, 8A), each dentary forms more than half of its mandibular ramus. Anteriorly the dentaries are slender and show multiple labial (mental) foramina on the anterior half; posteriorly the dentaries become wider; dorsally and ventrally, they embrace the coronoid processes of the mandible. The coronoid processes are formed mainly by the laterally ascending compound bones; however, the coronoid forms a dorsal cap which extends medioventrally to the level of Meckel's canal. The lateral exposure of the compound bone has two foramina, one anterior near the joint with the dentary, and posteriorly another one (posterior mandibular foramen) that penetrates it from side to side anterior to the articular condyle. The mandibular condyle, formed by the compound bone, is bent medially and ventrally. The ventral borders of the coronoid process of the mandible are formed by a ventral process of the dentary and a small labial exposure of the angular.

In lingual (medial) view (Fig. 7B, 8B), each dentary has a Meckel's canal running along the midface from the medial symphysis to a mandibular central foramen of the medial face of the mandible limited by the dentary, angular, and coronoid. The posterior part of Meckel's canal is bordered dorsomedially by the coronoid and ventromedially by the angular, both bones overlapping the dentary. The labial surface of the coronoid process is formed mainly by the coronoid bone. Anteriorly the ventral borders are formed by the angulars; posteriorly they twist toward the labial face. A long, thin exposure of the compound bone lies between the angulars and coronoids; these exposures are widened posteriorly along the

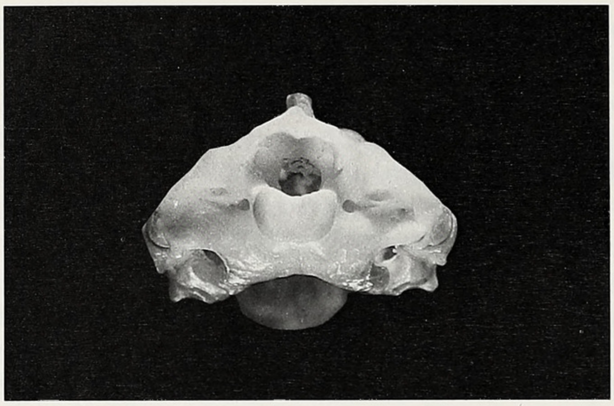

Fig. 5.—*Amphisbaena alba.* Posterior photographic view of skull (CG 3533).

articular process. The labial opening of the posterior mandibular foramen is partially bordered by the posterior end of the coronoid.

The several bony elements of the mandible form a longitudinal tunnel (Meckel's canal) that extends from the posterior mandibular foramen to the anterior part of the dentary. Posteriorly, the tunnel opens at the posterior mandibular foramen; at the middle of its length it opens at the mandibular central foramen and anteriorly it branches to end in several minor foramina on the labial side of the dentary. Some other small foramina of the compound bone and angular also terminate in this tunnel.

Descriptions of Individual Bony Elements

Premaxilla.—The U-shaped basal plate of the unpaired premaxilla terminates in a lateral process on each side (Fig. 9, 10). A medial and vertical nasal process (Jollie, 1960) arises from its middle; its dorsal edge curves smoothly and dorso-posteriorly. The nasal process passes posteriorly between and over the nasals and just reaches the frontals. The lateral aspects of the basal plate articulate with the maxillae, the posteromedial aspects with the vomers, septomaxillae, and nasal septum. Ventrally, the basal plate bears seven "subpleurodont" teeth (Gans, 1957), based in a single U-shaped dental groove with a higher labial than medial wall (Fig. 9C, 10C). The dry teeth tend to split along their axis of symmetry. The labial face of each tooth is in contact with the labial wall; the medial or postero-medial face is free and has a hollow pit, the nutritive foramen, at its base (Fig. 9C, 10C) along which bone reabsorption appears to take place in association with tooth replacement. Some empty "sockets" show a foramen at the bottom. The azygous tooth is the largest, the first paired teeth are more slender but almost as tall as the median one; the next two pairs are shorter. The first three teeth are aligned normal to the curved anterior edge of the premaxilla and the second and third pairs of teeth lie posteriorly in the dental groove at a more acute angle to the medial plane.

The top of each side of the basal plate forms the floor of the external nares. The more posterior lateral processes are covered by the maxillae. The joint surfaces with the maxillae are almost one-third as long as the horizontal edge of the premaxilla; the areas in contact are increased by rugose and longitudinal folding. Ventrally, a vertical wall borders the inner side of the U-shaped lateral processes that contact the vomers and septomaxillae.

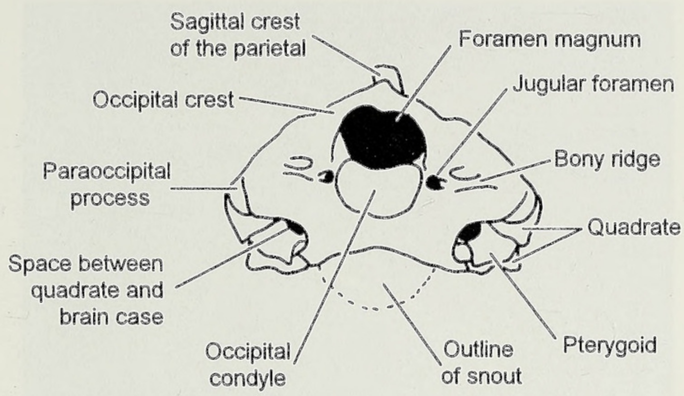

Fig. 6.—*Amphisbaena alba.* Labeled outline of posterior view of the skull shown in Figure 5.

Each side of the base of the nasal process bears a wide longitudinal canal. Its anterior end opens at the side of the vertical blade (Fig. 9A, 10A); anteriorly, the thickened nasal process protects the openings (Fig. 9D, 10D). The posterior end of this canal (see Bellairs and Kamal, 1981) opens directly posteriorly at the articulating surface of the premaxilla and septomaxilla (in which the canal continues), being separated from that of the opposite side by a thin vertical blade (Fig. 9C, 10C). The serial sections show that a narrow vertical canal extends ventrally just before the posterior end. That canal pierces the basal plate and subdivides, terminating at the nutritive foramen at the base of each tooth; a horizontal canal parallel to the dental groove interconnects the vertical canals.

The vertical portion of the nasal process is wide and forms the anterior extent of the snout. After bending horizontally, the posterior extension of the process becomes compressed into a blade, the surface extension of which separates the nasals which meet ventral to it. The rodlike termination of the nasal process lies at the anterior edge of the frontals.

The premaxilla is identified by general homology to the median tooth-bearing bone(s) of other reptiles (Romer, 1956; Fiorini, 1962). See Smith et al. (1953) about comments on the relation and innervation of the azygous median tooth with the egg-tooth.

Maxilla.—In cross section of the head, each of the paired maxillae (Fig. 11, 12) is roughly L-shaped, although the two surfaces join in a curve rather than an angle (Fig. 11E, 12E). The vertical lateral plate forms the lateral surface of the skull and its base gives rise to the teeth at the site at which it bends horizontally to form the palatal plate. Anteriorly, each maxilla contacts the premaxilla; medially the septomaxilla, vomer, and palatine; posteriorly the ectopterygoid; and dorsally the nasal, frontal, and prefrontal.

Anteriorly the lateral plate rises in a dorsovertical line. Posteriorly the lateral plate terminates vertically just posterior to the last tooth. The anterior portion of the dorsal border extends furthest dorsad; a triangular posteromedially directed frontal process (Kritzinger, 1946) arises from its anterior fifth and reaches past the nasal to extend between the frontal and prefrontal which overlaps it. More posteriorly, the dorsal border of the lateral plate terminates roughly in parallel to the ventral edge.

The posteriorly extending frontal process bends toward the midline (Fig. 11A–E, 12A–E). Only the anterior part of the process is visible in an intact skull

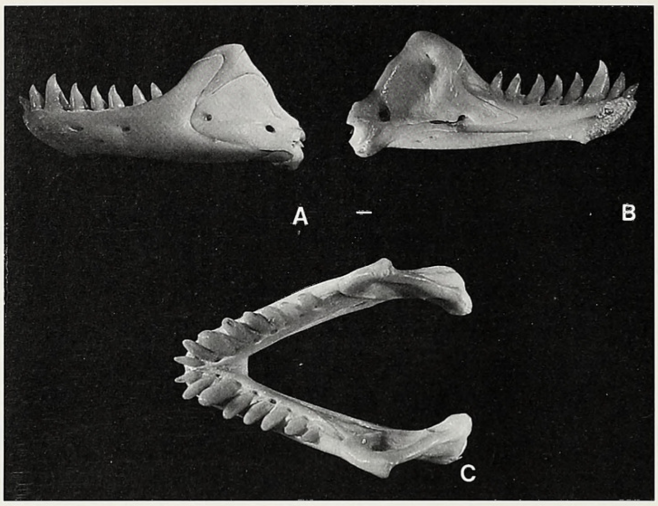

Fig. 7.—*Amphisbaena alba*. Photographs of isolated left mandibular ramus (CG 3533). The bar shows 1 mm to scale. A, lateral view; B, medial view; C, dorsal view of articulated mandible.

because the prefrontal overlaps a triangular portion along the posteroventral edge of the lateral surface.

One or two foramina open at the anteroventral corner of the vertical lateral plate. Here its surface folds inwards to form the side of the external nares. Two to four smaller foramina extend in a row from here to the center of the lateral plate, where one or two large foramina open. The posterodorsal corner of the vertical plate extends dorsally and posteriorly to overlap the maxillo–prefrontal junction; the prefrontal here abuts the medial surface.

The palatal plate of each maxilla extends medially from its ventral edge as a horizontal palatal process lying at an inner angle of about 90° anteriorly but becoming obtuse posteriorly (Fig. 11E, 12E); here it articulates with the ectopterygoid, which forms a continuation of the shelf. Ventrally, the palatal plate bears five posteriorly and medially curved subpleurodont teeth, the surfaces of which are smooth and not ridged (Fig. 11C, 12C); the labial faces of the teeth are curved but the medial ones are straight. The first maxillary tooth is the largest, the posterior ones smaller and subequal. Whereas all of the posterior teeth are smaller than the first, there is also a general trend to anterior to posterior reductions. However, the pattern is disjunct and several generations of tooth replacements may sometimes be involved in a tooth row. The medial wall of the dental groove is wide; from here the palatal process of the maxilla extends toward the midline, forming (with the vomer) a structure analogous to a secondary palate (Fig. 13, 14). A peglike premaxillary process departs just dorsal to the anteriormost maxillary tooth, from the ventral edge of the anterior end of the palatal process of the maxilla. This process overlaps the premaxilla dorsally and is overlapped, in turn, by the septomaxilla (therefore this process is masked in the articulated skull); its ventral articulating surface is folded and rugose as is the premaxillary counterpart. Posteriorly, the palatal plate expands medially and the anteromedial process of the ectopterygoid lies in a ventral groove; however, a tiny lateral process of the maxilla overlaps the ventral surface of the ectopterygoid.

The dorsal face of the palatal plate of the maxilla has two distinct areas of

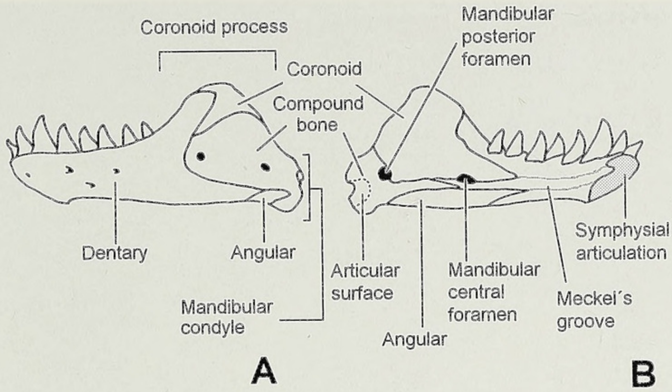

Fig. 8.—*Amphisbaena alba*. Labeled outline of mandible shown in Figure 7. A, lateral view; B, medial view.

different thickness; a maxillary step marks the boundary between these (Fig. 11A, 11D, 12A, 12D). The anterior and thicker area is overlapped dorsally and medially by the septomaxilla and forms the lateral part of the floor of the nares (Fig. 13A, 14A). Anteriorly, the medial edge of this portion forms the bony ventrolateral wall of the capsule of the organ of Jacobson (Fig. 13B, 14B).

The posterior area of the palatal plate of the maxilla forms part of the ventral floor of the nasal passage (Fig. 13A, 14A). The lateral wing of the vomer contacts the maxilla along part of the step that runs along a lateral and posterior diagonal; the joint between vomer and maxilla allows a connection between the opening of Jacobson's organ and the internal choanal opening through which passes the lacrimal duct. A large foramen opens at the inner angle formed by the vertical wall of the step (Fig. 11E, 12E); its canal passes from the dorsal surface of the posterior area of the palatal process to the lateral side of the vertical lateral plate. Here also it meets the posterior end of a canal that runs anteriorly to the lateral side of the nares (deep to the implantation site of the first tooth). A groove along the inner angle of the maxilla extends from the middle to the posterior end of this bone (Fig. 11D, 12D). The lacrimal duct lies in the groove.

The maxilla is identified as being homologous to the paired lateral tooth-bearing cranial bones of other reptiles (Romer, 1956).

Septomaxilla.—The paired septomaxillae (Fig. 15, 16) are exposed only on the inside of the nares. Each septomaxilla forms the roof of an organ of Jacobson and lines the floor of an anterior nasal passage (Fig. 13, 14). The complexly shaped bone lies dorsal to a vomer (Fig. 13B, 14B) and to the palatine process of the maxilla; whereas its posterior aspect contacts the wing of the vomer, the lateral border of the septomaxilla overlaps the palatal plate of the maxilla. The flattened dorsal surface is slightly concave.

The medial flat face of the septomaxilla contacts the medial cartilage of the nasal septum. However, the anteroventral corners of the paired bones pass ventral to the nasal septum and contact the opposite septomaxilla. The high anterior end contacts the premaxilla; posteriorly the medial face is ventrally arched (Fig. 15C, 16C) so that only its anterior and posterior ends make ventral contact with the vomer. At the midlevel of the septomaxilla there is a gap between the ventral concavity of the medial face and the underlying vomer (Fig. 13B, 14B). In medial view, the vertical flat face reaches less than half the height of the nasal cavity; a

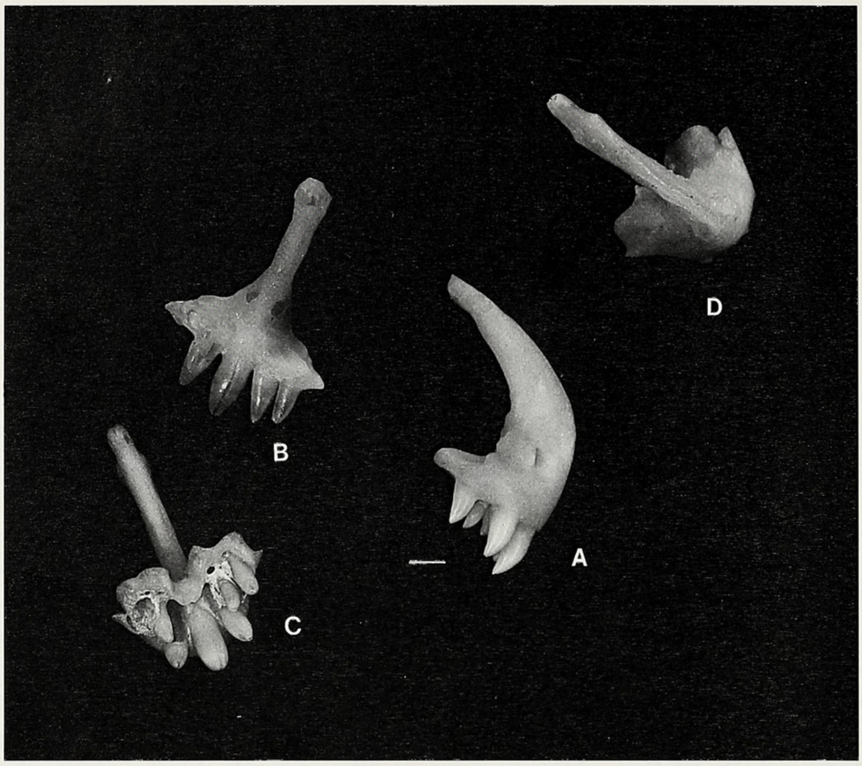

Fig. 9.—*Amphisbaena alba.* Photographs of premaxilla (CG 1811). The bar shows 1 mm to scale. A, lateral view (top of figure is dorsal, right is anterior); B, posterodorsal view; C, posteroventral view; D, dorsal view.

cartilaginous sheet (the nasal septum) rises between the medial borders of the septomaxillae, extending dorsally to the nasals. This medial sheet provides medial closure of the nasal capsules and partial separation of Jacobson's organs.

The straight medial border of the flattened septomaxilla is higher than the lateral one, so that the dorsal surface of the bone is inclined ventrolaterally. The anterior border continues laterally as a slender lateral process (Fig. 15A, 16A). Posteriorly, the thin lateral septomaxillary border expands over the maxilla and the wide U-shaped posterior border overlaps the vomer.

The anterior face of the septomaxilla is thicker at the medial side and becomes thinner laterally. Its medial region makes full contact with the premaxilla. The lateral anterior border overlaps the premaxillary process of the maxilla. At the anterolateral edge, a slim lateral process extends over the anterior palatine plate of the maxilla reaching to the border of the external nares; here the process bends dorsally to follow the shape of the nares. Near the midline, the septomaxilla is penetrated by a longitudinal passage (Fig. 15B, 16B); anteriorly, the larger medial opening faces the posterior foramen of the longitudinal canal of the premaxilla and a lateral opening faces anteriorly to reach the external nares dorsal to the premaxillary plate. In *Monopeltis,* the passage carries the medial nasal branch (of the olfactory nerve) and a small artery (Kritzinger, 1946).

In medial view of the septomaxilla (Fig. 13B, 14B), the thin anteromedial corner matches the inner concavity of the nasal process; more posteriorly the medial border is straight. The dorsal face is saddle-shaped, having a convex longitudinal axis and a concave transversal one (Fig. 15A, 16A). Anteriorly and

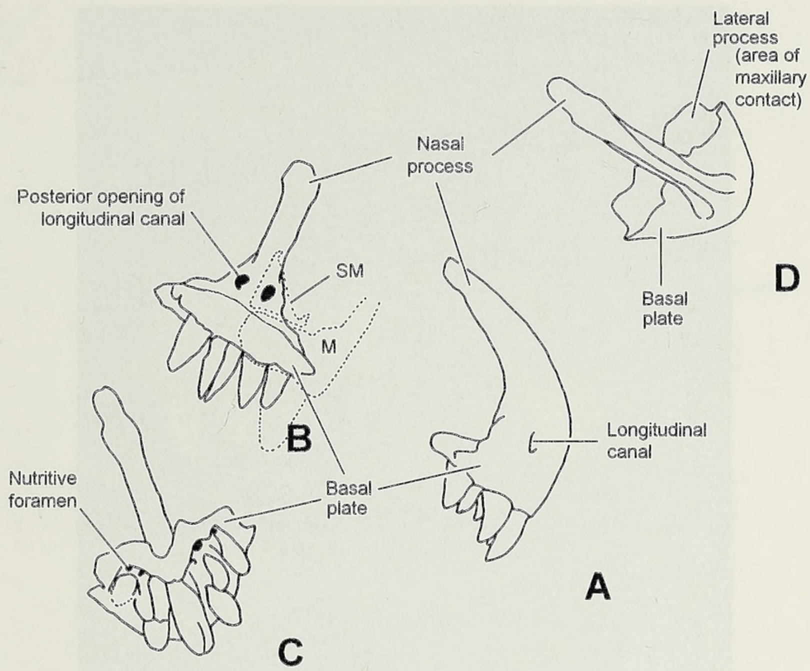

Fig. 10.—*Amphisbaena alba.* Labeled outline of premaxilla shown in Figure 9.

medially it is defined by slightly elevated borders; the posterior border is bent ventrally and contacts the vomer. The canal that pierces the septomaxilla opens posteriorly near the end of the dorsal middle border.

In ventral view (Fig. 14A, 15A) the concavity of the septomaxilla forms an inverted cup that roofs Jacobson's organ. The anterior and medial sides of the cup are bordered by a high ridge. The lateral flat border contacts the dorsal face of the palatine process of the maxilla and the thin U-shaped posterior border overlaps the anterior border of the vomerine wing; it thus encloses the posterior aspect of the organ of Jacobson. Some specimens show an elliptical foramen displaced to the midline at the dorsal edge of the cup; this foramen represents a medial opening of the longitudinal passage.

The septomaxilla is identified as the paired element that forms the base of each naris and roof of the vomeronasal system.

Vomer.—The complex, very elongate paired vomer has an elongate medial portion that parallels the midline of the palatal roof of the mouth (Fig. 17, 18) and from which arises a lateral wing. Anteriorly, the vomer lies ventral to the septomaxilla (Fig. 13B, 14B) and a slender anterior process of its medial portion contacts the premaxilla. More posteriorly there is a lateral wing, the edge of which abuts, and extends partially dorsal to, the palatal plate of the maxilla. The very slender posterior process of the medial portion extends ventral to the medial border of the palatine, ending just anterior to the contact of the latter with the pterygoid. The two vomers contact one another at the midline for the anterior third of their length; a medial gap separates them posteriorly (this is the anterior part of the pyriform recess). The anterior medial portion forms a vertical flat wall that rises dorsally from the straight medial edge; more posteriorly, the ventral edge of this wall inclines laterally, rotating to expose its surface in a ventral view. An-

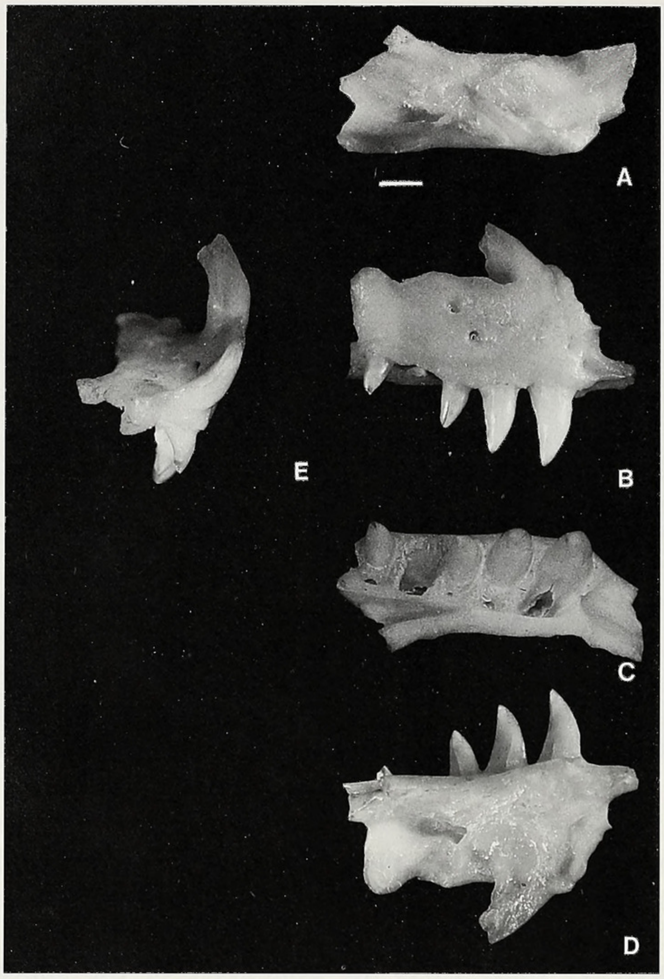

Fig. 11.—*Amphisbaena alba*. Photographs of right maxilla (CG 1811), anterior to the right. The bar shows 1 mm to scale. A, dorsal view; B, lateral view; C, ventral view; D, medial view; E, posterior view.

teriorly, this medial face is high and flat; it becomes gradually lower posteriorly with the posterior process terminating in a point (Fig. 17B, 18B).

The slender anterior process of the vomer contacts the posterior concavity of the premaxilla. At its middle, a triangular lateral expansion of the process forms part of the anterior border of the palatal opening of Jacobson's organ. The expansion is pierced by a foramen that extends from the medial face, to open on the anterolateral one. Here the foramen faces anteriorly and ventrally; in intact skulls, the foramen lies just anterior to the opening of Jacobson's organ. The anterior process is ventrally inclined from the plane of the rest of the vomer; it forms an angle at its base (Fig. 17B, 18B). This inclination reflects the inclination of the premaxillary basal plate relative to the rest of the skull (Fig. 13B, 14B).

The anterior border of the lateral wing of the vomer forms the posterior border of the bony frame for Jacobson's organ. Dorsally, the middle of the anterior border of the wing rises as a dorsal anterior ridge that converges posteriorly onto the medial wall (Fig. 17A, 18A), delimiting the posterior floor of the cavity of Jacobson's organ; the floor terminates posteriorly forming a narrow groove, whereas the adjacent and concave septomaxilla shapes the dorsal closure (Fig. 13B, 14B).

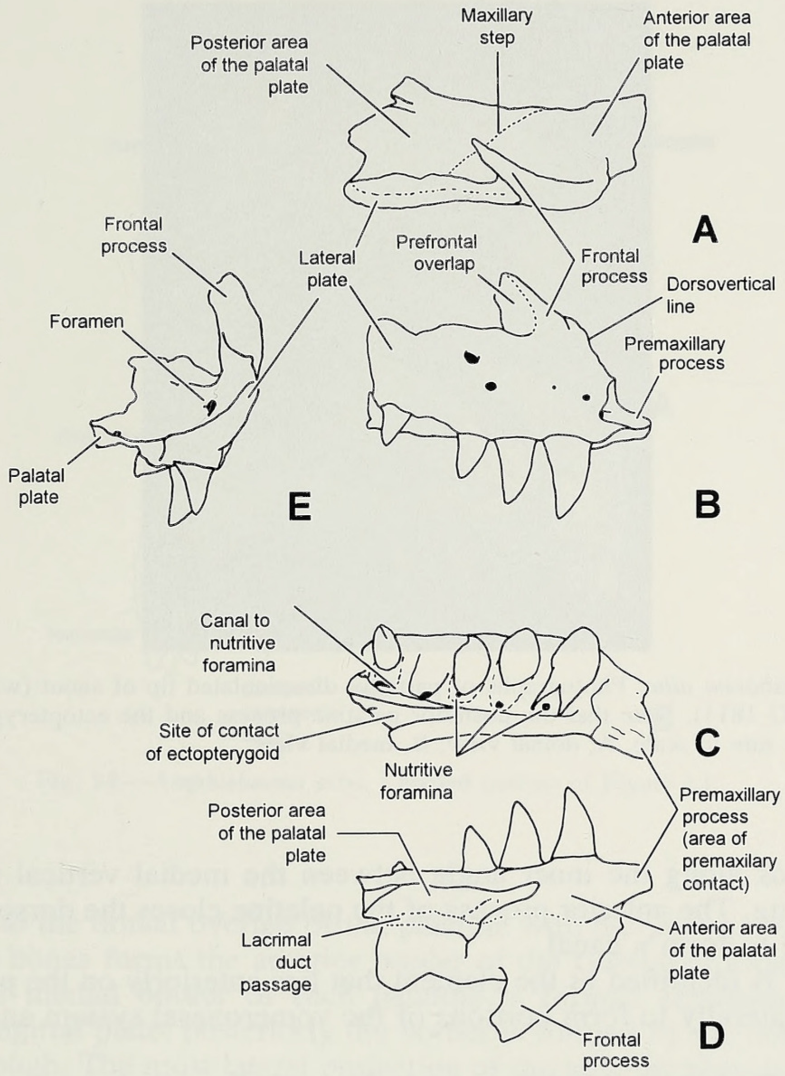

Fig. 12.—*Amphisbaena alba.* Labeled outline of maxilla shown in Figure 11.

At the center of the vomerine floor opens a canal which extends to the tip of the anterior process of the palatine (not illustrated). The smooth posterodorsal surface of the vomerine wings forms the floor of the nasal passage. At the base of the posterior vomerine process (the parasagittal plate), an anterior process of the palatine overlaps the vomer.

In dorsal view, the surface of the lateral wing shows an anterior ridge that diverges posteriorly from the midline and is paralleled by the median border of the maxillary shelf (Fig. 17A, 18A), thus forming an intermediate channel for the lacrimal duct (see Maxilla). Posteriorly, the dorsal surface of the lateral wings is smooth. The lateral border lies dorsad to the posterior surface of the palatal process of the maxilla, without touching it; the gap between them shapes the internal choana. Posteriorly, the thin vomerine margin is in ventral contact with the anterior border of the palatine.

Anteriorly, the vomers form a tunnel along the sagittal plane that leads to foramina piercing the medial vertical plates just anterior to their divergence. The foramina emerge at the tips of the anterior process of the palatine. A posterodorsal

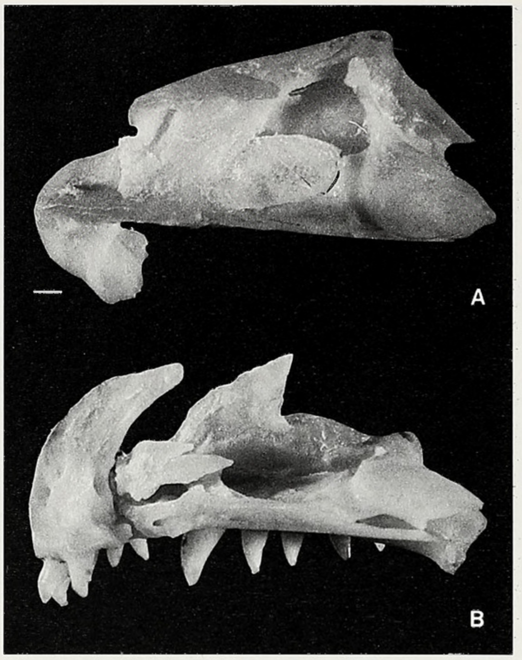

Fig. 13.—*Amphisbaena alba*. Photographs of partially disarticulated tip of snout (without the nasals and frontals) (CG 1811). Note that the posterior palatine process and the ectopterygoid are broken. The bar shows 1 mm to scale. A, dorsal view; B, medial view.

groove extends along the inner angle between the medial vertical plate and the horizontal wing. The anterior process of the palatine closes the dorsolateral aspect of the groove to form a canal.

The vomer is identified as the element that lies anteriorly on the palatal surface and extends laterally to form portions of the vomeronasal system and the internal choanae.

Palatine.—Each paired palatine roofs the posterior portion of a deep and inverted, posteriorly flattened palatal trough (Fig. 19, 20). The ventral edges of the palatines thus lie on the surface of the buccal palate, although the two medial edges of the bones are separated from each other by a narrow pyriform recess. Anterolaterally, each palatine contacts a vomer; laterally (posterior to the internal choana) each lies dorsal to the maxilla and the ectopterygoid, posteriorly each overlaps the pterygoid and dorsally each contacts the frontal, the (azygous) tabulosphenoid, and the prefrontal.

The center of the palatine forms a high vault, the palatal trough, that continues the choana posteriorly. The anteriormost portion of the trough is clearly highest (deepest), the palatine becoming shallower and flattening posteriorly at its articulation with the pterygoid. In dorsal view (Fig. 19A, 20A), the roof is triangular. The anterior high border forms the posteroventral closure of the nasal passage (Fig. 13, 14); the medial straight border is vertical but the lateral border extends laterally shaping the ventral wall of the orbital space as the anterior portion of the palato—pterygoid shelf (Fig. 3B, 4B). Anteriorly, the flattened dorsal surface of the bottom of the trough (the roof of the palatine) just contacts the frontal; more posteriorly it is in broader contact with the tabulosphenoid (Fig. 19A, 20A). Whereas these bones are adjacent, rather than forming an articulation, sections show ligamentous connections between them. The tabulosphenoid contact termi-

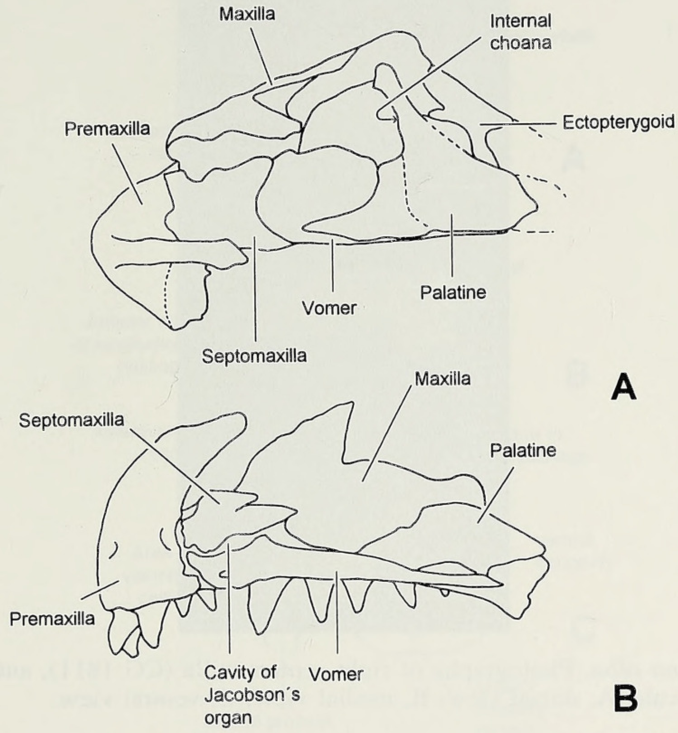

Fig. 14.—*Amphisbaena alba.* Labeled outline of Figure 13.

nates anterior to the dorsal overlap of the palatine with the pterygoid and the gap between these bones forms the anterior border of the Gasserian foramen.

The straight medial border of each palatine is formed anteriorly by a high concave parasagittal plate; posteriorly the border is formed by the medial edge of the choanal trough. The most lateral projection of the palatine plate is a triangular lateral process, the anterodorsal edge of which forms the posterior edge of the internal choana; the lateral projection then bends posteroventrally and recurves toward the midline, defining the internal choana. The posterior edge of the choana overlaps the dorsal surface of the maxilla and, posteriorly, of the ectopterygoid (Fig. 19C; also 3C, 4C). Anteriorly, the medial edge of the projection lies parallel to the medial border of the palatine (on the other edge of the trough). The lateral border is widest anteriorly; more posteriorly, it approaches the midline, narrowing the bone. The thin and flat posterior edge of the palatine overlaps the dorsal edge of the pterygoid.

Although the palatines do not show foramina, four horizontal canals pass through the sutures of each palatine with adjacent elements. Anteromedially, the dorsal contact of the palatine roof with both tabulosphenoid and frontals is interrupted by a canal that runs alongside the lateral process of the frontal from the inner side of the orbit to the medial nasal septum. Anterolaterally, the suture of the dorsal face of the palatine with the ectopterygoid is perforated by another canal extending from the ventrolateral side of the orbit to the groove along the inner angle of the maxilla. Posterodorsally, the posterior end of the suture between the tabulosphenoid and palatine shows a third canal that runs from the lateral gap between the parietal and the palato–pterygoid shelf to the medial gap between palatines. The fourth canal lies posterolaterally and can be double; it is shaped

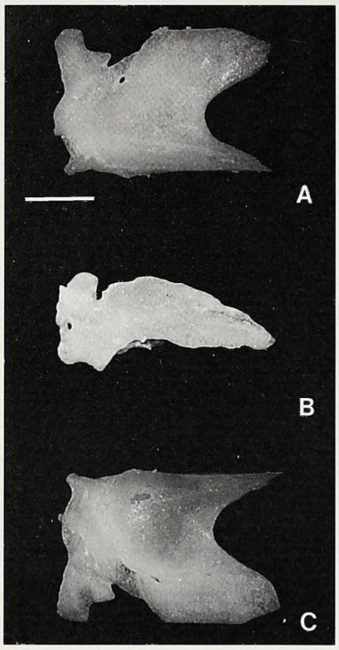

Fig. 15.—*Amphisbaena alba*. Photographs of right septomaxilla (CG 1811), anterior to the left. The bar shows 1 mm to scale. A, dorsal view; B, medial view; C, ventral view.

through the junction of palatine, pterygoid, and ectopterygoid, connecting the dorsal and ventral surfaces of the palato–pterygoid shelf; in smaller skulls (shorter than 1.8 cm) this gap is relatively wider. Could this be a reduced infraorbital fenestra that is otherwise common in other squamates (Jollie, 1960)?

The palatal trough provides posterior continuation of the air passage to the mouth. Moreover, in unskinned specimens the ventral aspect of each palatal trough is closed by a triangular projection of connective tissue that extends laterally from the medioventral border of the palatine. The free border of the tissue touches the lateral triangular process of the palatine. Thusly, it forms a closed canal, more posteriorly displacing the internal choana toward the posterior end of the palatine. This neochoanate condition (in the sense of Lakjer, 1927) of *Amphisbaena alba* is similar to that of *Monopeltis* (Kritzinger, 1946); the amphisbaenian secondary palate would be analogous to those of scincids (Greer, 1970) and some gymnophthalmids (Gans, 1978; Presch, 1976).

The palatine is here identified as the element that lies anteriorly on the palatal surface, that forms the frame of the palatal trough, and that extends posteriorly onto the pterygoid surface.

Ectopterygoid.—The paired triangular ectopterygoid (Fig. 21, 22) connects anteriorly to the maxilla and posteriorly to the pterygoid (Fig. 3B, 3C, 4B, 4C); ventrally it has a triangular (triradiate) exposure on the palato–pterygoid shelf and dorsally it reaches the lateral fold of the palatine (Fig. 3B, 4B). Each ectopterygoid is doubly forked. Anteriorly it has lateral and medial processes (Fig. 21A, and 22A), and posteriorly it has dorsal and ventral ones (Fig. 21D, 22D).

In a dorsal view, the ectopterygoid is Y-shaped (Fig. 21A, 22A); the widely separating anterior arms of the Y enclose the posterior aspect of the maxilla. The short and blunt anterolateral process contacts the posterior tip of the maxilla at the level of the back of the last maxillary tooth. This laterally compressed process

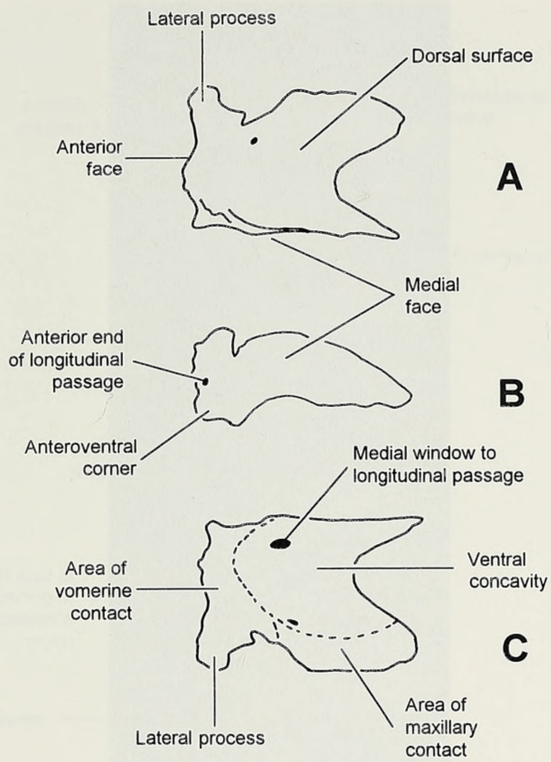

Fig. 16.—*Amphisbaena alba.* Labelled outline of septomaxilla shown in Figure 15.

extends posteriorly as a dorsal blade to reach the posterodorsal process (Fig. 21D, 22D), and forms the side of the palato–pterygoid shelf. The slender anteromedial process is longer than the anterolateral one and rests in a ventral groove of the palatal process of the maxilla.

The midline of the concave dorsal surface of the body of the ectopterygoid bears a faint ridge that just fits the lateral border of the palatine. The joint with the palatine runs posteriorly from the middle point between the anterior processes. It parallels the lateral line of the ectopterygoid; thus, the mediodorsal area of the ectopterygoid is covered by the palatine, whereas the lateral one is free.

The posterodorsal and posteroventral processes of the ectopterygoid interlock with the lateral anterior process of the pterygoid; the posterodorsal process attaches to the medial face of the lateral dorsal ridge of the pterygoid and the posteroventral process attaches to the ventral face of the pterygoid. Both processes are compressed. The base of the posteroventral process lies anterior to the posterodorsal one; in lateral view, they are parallel (Fig. 21D, 22D). In ventral view, the posteroventral process is slightly medial in relation to the posterodorsal one (Fig. 21C, 22C). The posteroventral process is more slender and shorter than the posterodorsal one. A small foramen perforates the base of the posteroventral process.

The ectopterygoid is identified as the element that completes the lateral edge of the palatal surface between the maxilla and the palato–pterygoid shelf. Lakjer (1927) incorrectly labeled this bone as a jugal, because a jugal usually forms the ventral and posterior margins of the orbit; a true jugal may be present in some amphisbaenian fossils of the family Hyporhinidae (Estes, 1983).

Pterygoid.—Each flat Y-shaped pterygoid (Fig. 23, 24) extends from anterior

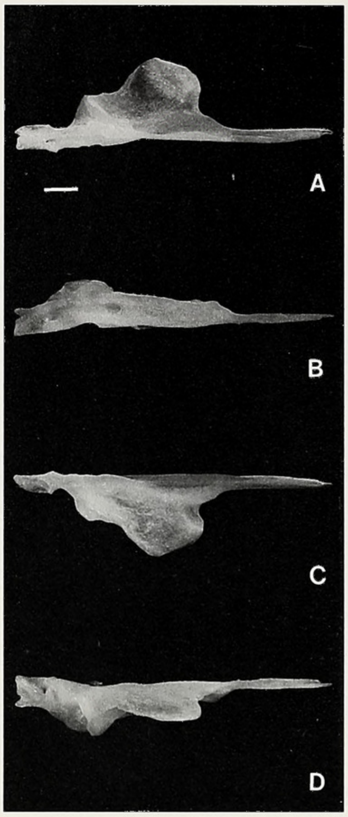

Fig. 17.—*Amphisbaena alba.* Photographs of right vomer (CG 1811), anterior to the left. The bar shows 1 mm to scale. A, dorsal view; B, medial view; C, ventral view; D, lateral view (angle of this view is slightly off horizontal).

contact with the palatine and ectopterygoid to pass ventrolaterally at the level of the cranial base where its lips rise and curve around the medial face of the ventral extent of the quadrate. The pterygoid abuts on the parabasisphenoid, but there is no clearly marked basipterygoid articulation (see below).

The main plate of the pterygoid is strongly dorsally inclined toward the midline (Fig. 3C, 4C), forming the posterior part of the palato–pterygoid shelf. The anterolateral process articulates with the ectopterygoid, the anteromedial process contacts the palatine, and its posterior process extends to reach and curve about the distal head of the quadrate. Medially the pterygoid parallels the lateral edges of the parabasisphenoid. The paired pterygoid is subtriangular in ventral view from the articulation with the palatine to the posterior apex where the bone curves around the quadrate. The lateral portion of the pterygoid is triangular in cross section, rising into a lateral dorsal ridge. This portion is anteriorly open, forming a deep pocket (not illustrated) which articulates with the posterodorsal process of the ectopterygoid. Medially, the bone is extended by a wide, thin flange that anteriorly articulates with the palatine and then abuts or parallels the edge of the parabasisphenoid.

The concavity of the anterior border of the pterygoid, between the anteromedial and anterolateral processes, is displaced to the midline; thus, the border of the base of the medial process is shorter than those of the longer lateral one. Most of the anterior border and the entire medial process are dorsally covered by the

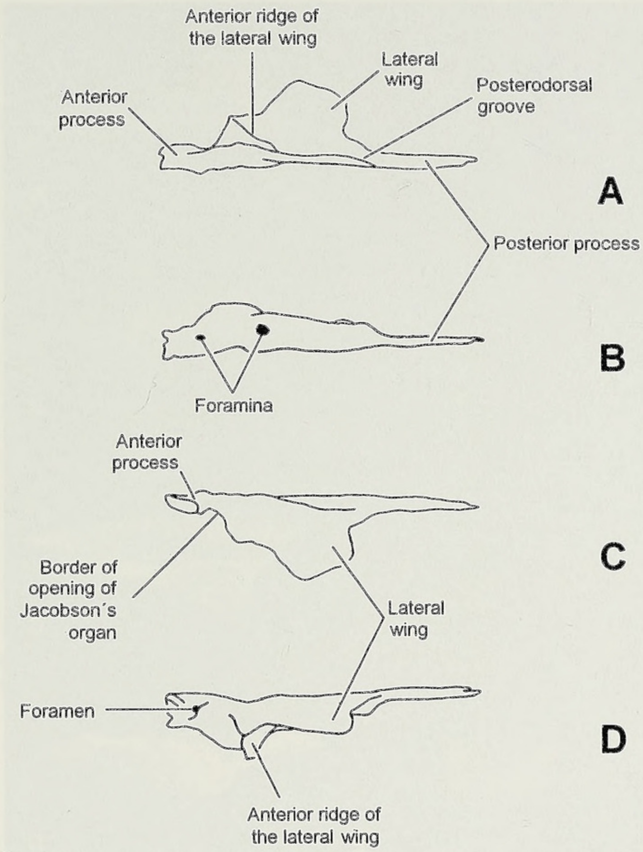

Fig. 18.—*Amphisbaena alba.* Labelled outline of vomer shown in Figure 17.

palatine that extends posteriorly at the midline. The articular surface bears short, shallow anteroposterior ridges.

Anteriorly, the medial border of the pterygoid lies ventral to and lacks contact with the tabulosphenoid and the parabasisphenoid, thus forming a longitudinal gap; more posteriorly it makes a loose medial contact with the parabasisphenoid (basipterygoid articulation) and may contact the edge of element-X. The portion of the pterygoid just opposite to the basipterygoid articulation can show (in section) a scattering of cartilaginous cells (Fig. 55B, 56B); these are not involved in production of a cartilaginous pad. The posterior portion of the medial border is free where it bridges the gap that separates the anterior part of the quadrate from the braincase (the posterior extension of the postorbital space).

In ventral view, the slim anterolateral process is covered by the posteroventral process of the ectopterygoid. At the lateral border, the pterygoid is a curved solid structure that is triangular in cross section; its ventral surface forms the base of the medial extension of the bone (the pterygoidal plate) that reaches to contact the parabasisphenoid. In dorsal view (Fig. 23A, 24A), one sees that the laterodorsal ridge and main plate of the pterygoid are separated by a narrow groove anteriorly; posteriorly, the groove ends in a pocket, into which fits the posterodorsal process of the ectopterygoid. Posteriorly to the anterolateral groove, the medial face of the lateral plate is continuous with the main one, shaping a step as a railing marks the ventrolateral border of the postorbital space. At the posterior end, the pterygoid is twisted laterally and sends a process around the medial and

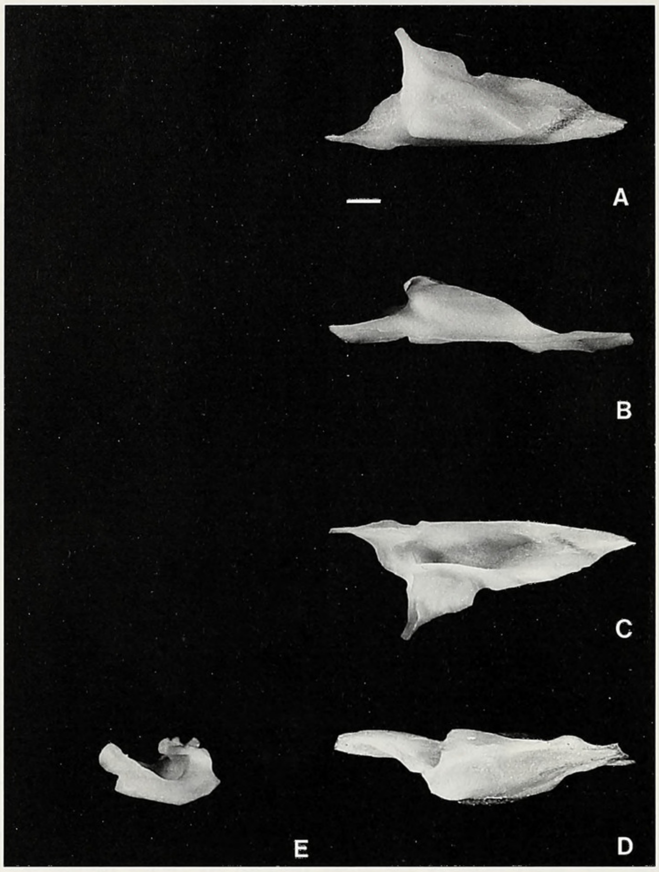

Fig. 19.—*Amphisbaena alba*. Photographs of right palatine (CG 1200), anterior to the left. The bar shows 1 mm to scale. A, dorsal view; B, medial view; C, ventral view; D, lateral view; E, anterior view.

posterior sides of the distal articular head of the quadrate (see also Fig. 55B, 56B). Here, the pterygoid shows a dorsolateral groove which fits the contour of the distal head of the quadrate. The posterior process of the pterygoid overlaps the medial and posterior borders of the ventral exposure of the anterior head of the quadrate. The articulated posterior process, ventral to the midbody of the quadrate, borders the extracolumellar path. The center of the posterior process shows spongy bone surrounded by a lamellar shell (Fig. 55, 56).

This large bone is identified as the pterygoid by its size, position, and anterior contact with the palatines and posterior articulation with the ventral shaft of the quadrate.

Nasal.—Each thick nasal (Fig. 25, 26) forms a subtriangular roofing over a naris, its typically rugose dorsal surface being incurved both in the anteroposterior and transverse planes. During skinning one can see that parallel ligamentous slips leave the foramina and connect the nasal to the thickened anterior integument. The anteromedial corner curves ventrally. The anterior side of the triangle forms a smooth curve marking the concave anterior narial edge. The lateral corner is truncated near its contact with the maxilla; it may slightly overlap the maxilla or embrace the maxillary anterodorsal edge. More posteriorly, the border angles more medially and forms a similar junction with the maxillary frontal process. The posterior side is concave and forms a complex series of articular shelves that

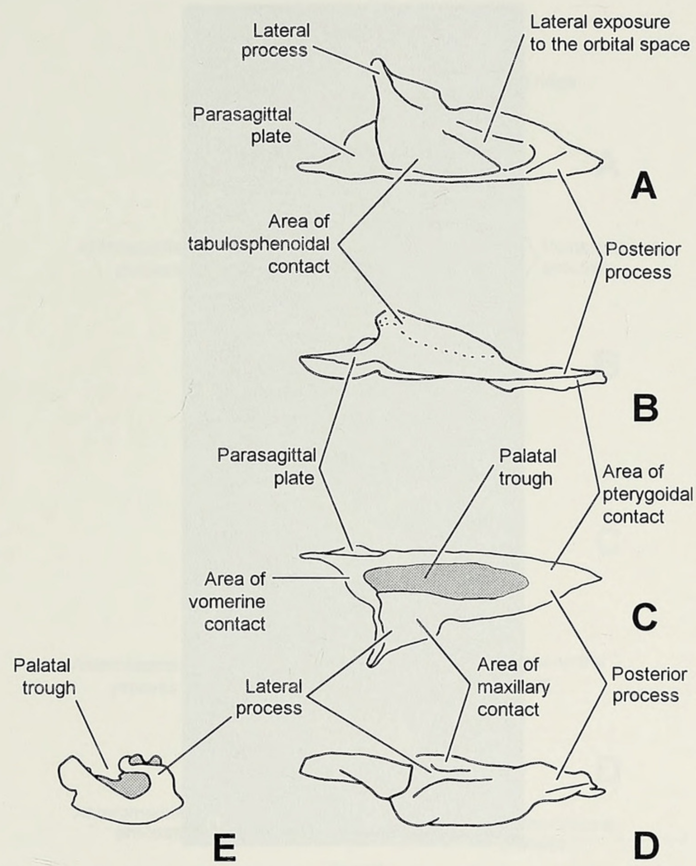

Fig. 20.—*Amphisbaena alba.* Labeled outline of palatine shown in Figure 19.

embrace the edge of the frontal. The medial border projects ventrally a concave bony medial sheet that embraces the nasal process of the premaxilla. The ventral portion of the medial sheet contacts that of the opposite nasal ventral to the nasal process of the premaxilla.

In ventral view, the internal surface of the nasal is concave and smooth (Fig. 25C, 26C); it defines the roof of the nasal passage. The medial border of each nasal is anteriorly curved where it fits around one side of the nasal process and descends parallel to this to form the dorsomedial roof of the nares. Ventrally, the thin, concave medial sheet contacts that of the opposite nasal near the midline. It is continuous with the cartilaginous nasal septum. Although the length of the ventral and dorsal borders of the medial sheet are similar, the ventral one is shifted posteriorly and its end is bent ventrally more markedly than the dorsal one. The concave anterior end of the medial sheet is wider than the posterior one, thus fitting the ventral widening of the premaxillary process and anteriorly having a ventral point of contact with the septomaxilla.

Posteriorly, at the middle of the joint with the frontals, the nasal has a narrow wedgelike frontal process. Between the frontal process and the posteromedial corner of the nasal, a thin, rugose (frontal) plate ventrally underlies the frontal. Lateral to the frontal process, the posterior border of the nasal bears two foramina that face into a notch of the frontal (not illustrated). Inside the bone, these foramina divide and connect to the numerous foramina that open onto the dorsal surface. The dorsal foraminal pattern has a centrifugal disposition from the center of the

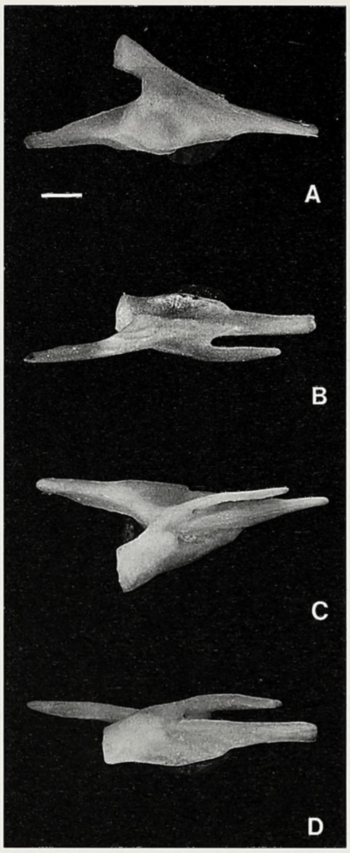

Fig. 21.—*Amphisbaena alba.* Photographs of right ectopterygoid (CG 1811), anterior to the left. The bar shows 1 mm to scale. A, dorsal view; B, medial view; C, ventral view; D, lateral view.

nasal (where the foramina pass perpendicular to the surface) toward the borders (where they lie more tangential to the surface and are continued by open grooves) (Fig. 25A, 26A).

The bone is identified as the roofing element of the naris and by its association with the premaxilla and maxilla.

Prefrontal.—The paired subtriangular prefrontal (Fig. 27, 28) forms the posterior part of the roof and posterolateral closure of the nasal passage. Laterally it extends the cheek dorsally above the maxilla, and forms the anterior wall of the orbit. The bone is not penetrated by any foramina; however, the lacrimal duct reaches the posterior face, lying either in a V-shaped groove or in an incomplete canal. The prefrontal is bordered anteriorly and ventrolaterally by the maxilla; dorsomedially it contacts the frontal and posteroventrally the palatine. The parietal sends anterior processes that sometimes contact the prefrontal.

In dorsal view, the lateral border of the prefrontal articulates ventrally with the lateral plate of the maxilla (Fig. 27A, 28A). The straight medial border articulates with the frontal process of the maxilla (the prefrontal lies external to the posterior part of this process) and the dorsal plate of the frontal; the posteromedial process of the prefrontal bends medially and lies in a groove of the frontal which usually does not reach the anterior process of the parietal (in AMNH 73233 the anterior process of the parietal contacts the prefrontal on one side; also see Jollie, 1960). Laterally, the posterior border bends ventrally. It contacts the ventral process of the frontal and the dorsal surface of the palatine. A concave, smooth surface faces

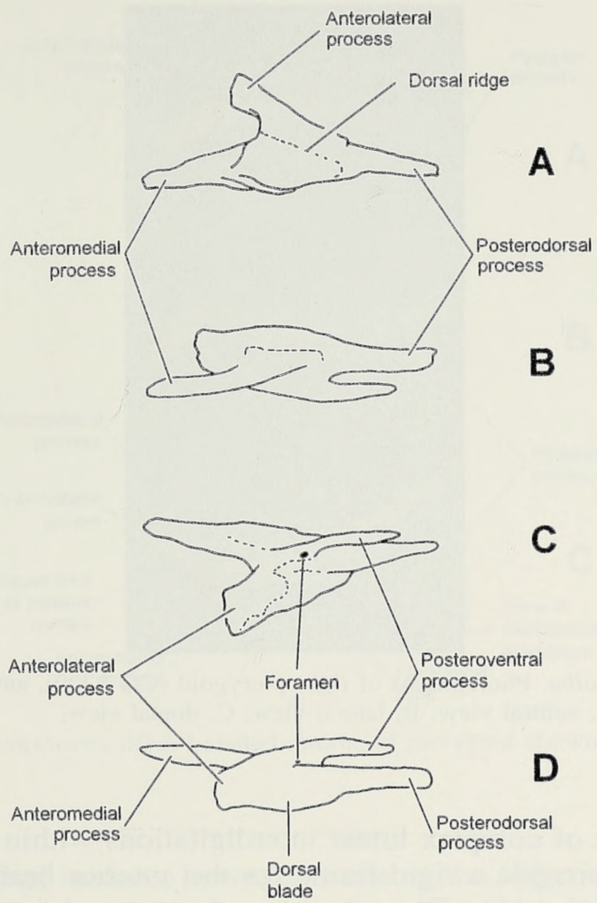

Fig. 22.—*Amphisbaena alba.* Labeled outline of ectopterygoid shown in Figure 21.

posteriorly to form the anterior wall of the open orbit (Fig. 1B, 27A, 28A). The bifurcate ventrolateral extent contacts the inner side of the lateral maxillary wall; the gap formed by the bifurcation (for the passage of the lacrimal duct) is laterally closed by the maxilla.

The prefrontal is identified as the element dorsal to the posterior aspect of the maxilla and in articulation with the frontal. However, as the lacrimal duct is closely associated with this bone, Kesteven (1957) proposed that it was the lacrimal, a bone penetrated by the duct which only lies adjacent to it in *Amphisbaena.* However, the lacrimal has frequently been lost in squamates; the prefrontal has not.

Frontal.—Each paired frontal (Fig. 29, 30) has a thick dorsal horizontal plate that articulates with that of the opposite side. Along the middle of its extent, the plate gives rise to a ventrolateral process that passes ventrad around the anterior end of the cerebral chamber and that ventrally contacts the frontal of the opposite side; the two frontals thus form a frontal ring (frontal fenestra) around the anterior end of the cerebral chamber (Fig. 31C, 32C). The horizontal dorsal plate of the frontal articulates anteriorly with the premaxilla, nasal, maxilla, and prefrontal, and posteriorly with the parietal. The lateral process has lateral contact with the prefrontal and ventral contact with the palatine and tabulosphenoid. All portions of the frontal are relatively thick; serial sections show that the centers of both the dorsal and lateral plates show scattered lacunae, suggesting spongy bone. The

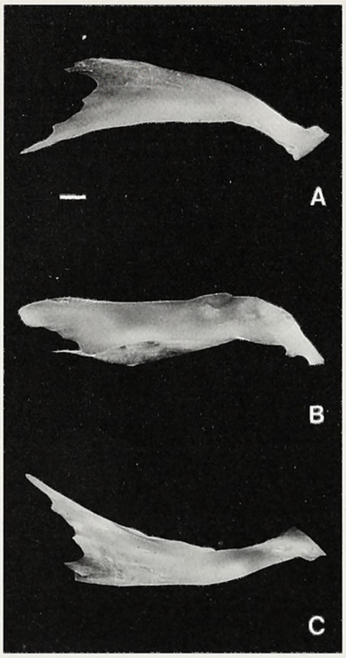

Fig. 23.—*Amphisbaena alba.* Photographs of right pterygoid (CG 1200), anterior to the left. The bar shows 1 mm to scale. A, ventral view; B, lateral view; C, dorsal view.

articulations consist of complex linear interdigitations within the articulating surfaces; these bones provide a rigid frame for the anterior braincase, connecting it firmly to the facial elements. The exposure of sutures along the external surface of the skull gives a poor indication of this complexity of internal sutures.

In situ, the anterior half of the dorsal plate of the frontal is ventrally inclined (Fig. 29B, 30B) beginning the profile of the snout. The truncated anteromedial corner fits the nasal process of the premaxilla. The anterior border joins with the nasal. A deep notch at the middle of the anterior frontal border is entered by the frontal process of the nasal (Fig. 29A, 30A). More laterally, one or two smaller notches sometimes mark the joint with the nasal. Anteriorly, the lateral border of the frontal contacts the frontal process of the maxilla. More posteriorly, the frontal has a deep, medially curved groove that embraces the posteromedial process of the prefrontal.

The medial border of the dorsal plate is thick. The median suture of the two frontals is marked along the cranial surface; however, the bone shows two or three layers. Whereas each layer articulates with that of the opposite side, the articulating curves, although matching those of the opposite side, are not congruent between layers (Fig. 29A, 30A). The asymmetrical arched folds and grooves of the medial surfaces fit those of the opposite side. They lock the dorsal interfrontal joint and prevent anteroposterior sliding along the midline.

Posteriorly, each frontal sends an articular plate ventral to the anterior edge of the parietal. The posterior border of this plate widens laterally. A thin, ventral projection of the adjacent (ventral) surface of the parietal keeps the simple medial edges of the articular plates from medial contact. More laterally, the articular plate of each frontal has a complicated suture with the overlying parietal. These lateral portions of the articular plates bear finger-shaped dorsal flutings and ridges that are oriented posteriorly and medially (Fig. 29A, 30A). Most of the ridges are

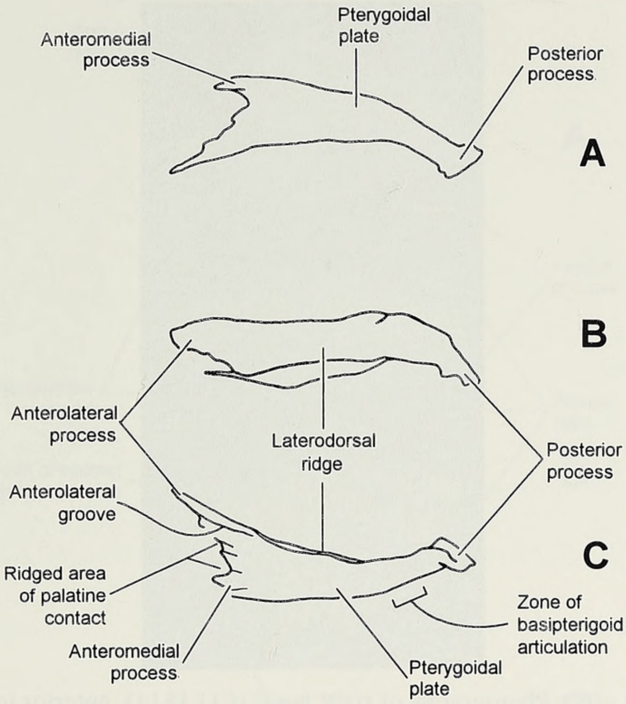

Fig. 24.—*Amphisbaena alba.* Labeled outline of pterygoid shown in Figure 23.

covered by the parietal surface; however, some of the larger ridges extend to and perforate the parietal to reach its dorsal surface (Fig. 31A, 32A).

At the level of the posterior end of the prefrontal, each frontal forms a lateral process; ventral to this, the ventral process then bends medially to form the floor of the anterior braincase. The sides of the ventral process of the frontal extend posteriorly to form a triangular exposure, dorsally with the anteroventral surface of the parietal and ventrally with the anterior curve of the tabulosphenoid (Fig. 2B, 2C, 3B, 3C, 31B, 32).

The ventral process of the frontals makes an elongated ring, the "frontal fenestra" (in CG 1811, reaching approximately 2.2 mm horizontally and only 1.5 mm vertically) (Fig. 31C, 32C). This fenestra is anteriorly closed by sheets of connective tissues pierced by nerves deriving from the anterior brain.

The thick, ventral end of each frontal has a grooved medial articular surface. Anteriorly, one or two processes interweave with those of the opposite side forming a lock-and-key junction that fixes the frontals relative to each other in a pattern similar to that of the dorsal interfrontal articulation. The anteroventral face of the ventral process contacts the palatine; posteriorly, this process contacts the azygous tabulosphenoid, of which two anterolateral processes embrace the interfrontal medial suture (Fig. 29, 30, 31C, 32C). The interdigitations of the wide contact surface with the tabulosphenoid are much shallower than those of the dorsal junction with the parietal.

Anteriorly, the lateral side of the ventral process gives rise to a vertical plate, the lateral process that extends ventrally below the frontal floor. This plate forms part of the posteroventral closure of the nasal cavity (Fig. 29D, 30D, 33, 34). The frontal is in contact with the palatine and tabulosphenoid at the ventral junction of the vertical plate with the frontal lateral wall. This is the site of the aforemen-

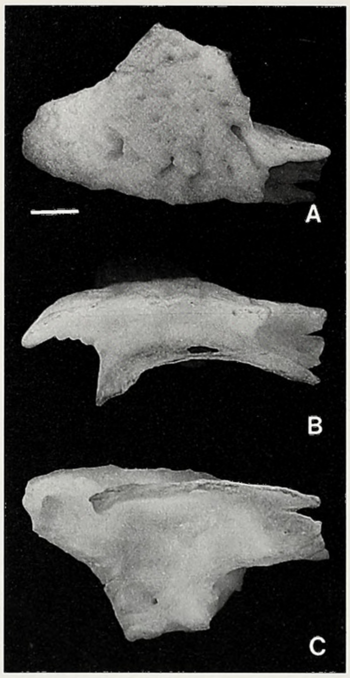

Fig. 25.—*Amphisbaena alba.* Photographs of right nasal (CG 1811), anterior to the left. The bar shows 1 mm to scale. A, dorsal view; B, medial view; C, ventral view.

tioned (see palatine) gap connecting the medial side of the orbit with the nasal capsules.

These unique bones are referred to as the frontals because in amphisbaenians they surround the olfactory passage anterior to the forebrain. Unlike those of most other reptiles, they preclude the formation of an interorbital septum. Bellairs (1949) specifically concluded that this aspect of amphisbaenian frontals is unique. However a similar ventral closure of the frontals is seen in other lizards, such as some Geckkonidae (Jollie, 1960).

Parietal.—The azygous medial parietal (Fig. 33, 34; also 3, 4, 31, 32) provides most of the roof and sides of the braincase. Anteriorly, the parietal forms an overlapping articulation with the frontals and posteriorly with the supraoccipital area of the occipital complex. A triangular, dorsal planar area includes the zone of frontal articulation (Fig. 31A, 32A). Its apex joins smoothly to a long medial crest that rises as it extends posteriorly and then widens to a dorsal boss after which the parietal splits to form a deep medial notch. Two wide and slightly convex lateral plates extend ventrally, thus shaping the lateral sides of the braincase; they contact the frontals, the tabulosphenoid, and the anterolateral processes of the occipital complex.

The development of the anterior part of the sagittal crest is variable depending on the size of the skull; on smaller skulls it may be only a slightly raised ridge. On larger skulls, it is represented by a higher and thickened blade. Posterior to the middle of the parietal length, the sagittal crest rises more sharply in a concave outline to a site at which it is broader and forms a flat dorsal facet (Fig. 31A, 32A); more posteriorly, a deep medial notch in the parietal forms around the continuation of the crest, seen as an ascendent process arising from the dorsal plate of the occipital region. The medial edges of the parietal, adjacent to the

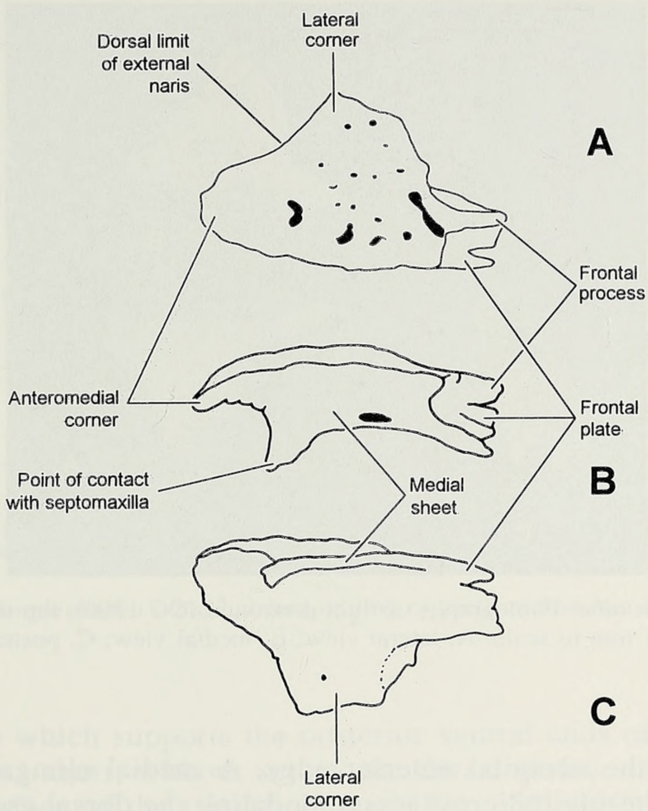

Fig. 26.—*Amphisbaena alba.* Labeled outline of nasal shown in Figure 25.

process, become thinner posteriorly. The posterior end of the sagittal crest of the parietal bears a concave articular facet. There is a vertical cartilaginous rod (the processus ascendens tecti synotici, Gaupp, in Kritzinger, 1946) between the facet and the ascendent process of the supraoccipital area.

Anteroventrally, the parietal articulates with the frontals at a complex, deeply notched, surface suture. The wide ventral articular surface of the anterior portion of the parietal shows long grooves that match the frontal ridges (Fig. 33A, 34). A tiny longitudinal blade at the sagittal line keeps the posterior ends of the frontals from contact. The parietal, and hence the cranium, is narrowest near the posteriormost extent of the frontal. More laterally the parietal edge inclines posteroventrally and forms a simple junction with the ventral process of the frontal.

The sharp ventrolateral borders of the parietals laterally overlap the vertical paired dorsal processes of the azygous tabulosphenoid. The inner (medial) surface of the ventrolateral borders of the parietal show elongate ridges that match those of the tabulosphenoid (Fig. 33B). Posteriorly, as the vertical dorsal processes of the tabulosphenoid are shallower, the parietal border becomes flat.

The parietal reaches its greatest width at the site of the flat lateral facets; here it is in dorsolateral contact with the dorsal anterolateral processes of the occipital complex. The inner surface of the parietal bears scalelike posterior projections (Fig. 33B) that fit into grooves on the anterior tips of the occipital. Posteriorly, the posterior plate of the parietal widely overlaps the dorsal plate of the occipital complex. The ventral face of the overlapping area is gently and longitudinally grooved; anteriorly, and laterally from the midline, it shows a short flap that

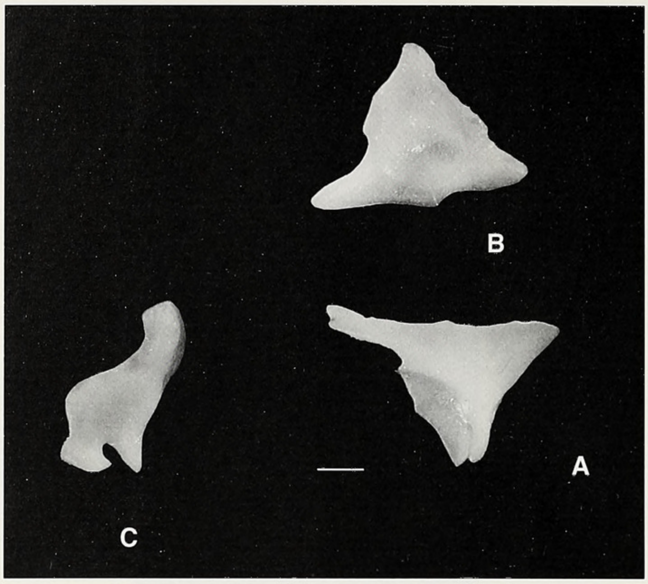

Fig. 27.—*Amphisbaena alba.* Photographs of right prefrontal (CG 1200), top is dorsal, anterior to the right. The bar shows 1 mm to scale. A, lateral view; B, medial view; C, posterior view.

embraces part of the occipital anterior edge. A medial elongated notch extends posteriorly from the sagittal crest accommodating the dorsal ascendent process of the supraoccipital area that posteriorly prolongs the sagittal crest. The lateral borders of the medial notch turn slightly dorsad, covering the base of the lateral faces of the occipital process.

The smooth inner surface of the parietal roofs and forms the sidewalls of most of the cranial cavity. Its dorsomedial line shows a shallow groove that marks the base of the sagittal crest.

The parietal is identified as the very large element roofing the braincase anterior to the occipital region. Although paired in many squamates, it is azygous in amphisbaenians.

Tabulosphenoid (ex Orbitosphenoid).—The unpaired tabulosphenoid (Fig. 35, 36) forms an elongated section of the floor of the anterior braincase between the frontals and the parabasisphenoid. The concave lateral borders of the tabulosphenoid articulate dorsally with the parietal, their closure shapes the sides of the braincase. Anteriorly, the most external portion of the tabulosphenoid extends dorsally to the palatines. Posteriorly, its posterior border medially overlaps the parabasisphenoid; more laterally it forms the anterior border of the Gasserian foramen.

The center of the tabulosphenoid is thick; however, each of the edges tends to be thinned, its medial surfaces being extended laterally and anteriorly and its peripheral surfaces being extended posteriorly. The curved grooves on the surface thus interlock with those on the adjacent elements.

The processes on the anterior edge of the tabulosphenoid lie ventral and external to those of the frontals, and are thinner than the body of the tabulosphenoid. The V- or U-shaped split between the anterior processes embraces the sides of the posterior part of the ventral interfrontal suture (Fig. 31C, 32C). In dorsal view, the anterolateral processes show shallow grooves that diverge posteriorly (Fig. 35A, 36A); the dorsal surfaces of the anterolateral processes are delimited pos-

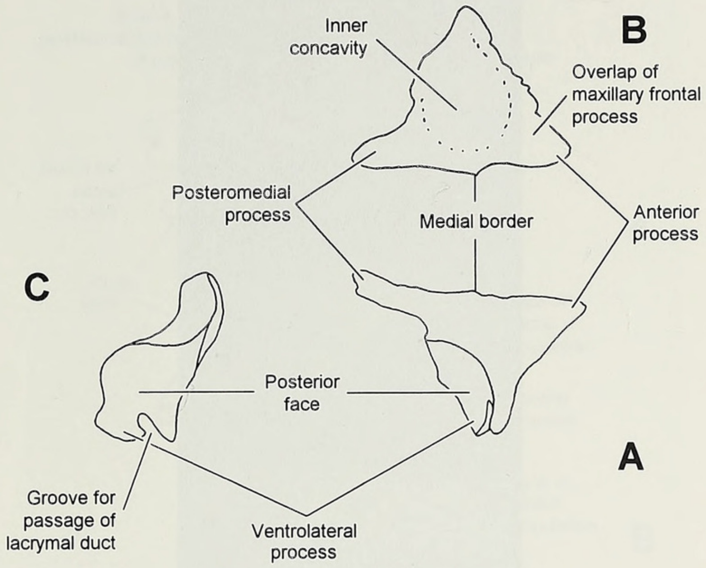

Fig. 28.—*Amphisbaena alba*. Labeled outline of prefrontal shown in Figure 27.

teriorly by a step which supports the posterior ventral ends of the frontals. Ventrally, each process abuts, without suture, the dorsal surface of a palatine.

The ventral surface of the tabulosphenoid (Fig. 35C, 36C) bears a slight and round medial keel, extending posteriorly from the anterior zone between the palatines to the level of the anterior tip of the parabasisphenoid. Here, the medial keel of the tabulosphenoid divides and the halves diverge posteriorly, forming a triangular medial groove, in which rests the rostrum of the parabasisphenoid. The posterior ends of the ridges are grooved, matching the ridges of the parabasisphenoid. The bottom of the medial groove may show a narrow posterior slit, or a scar, that could be evidence of a medial fusion of the posterior part of the tabulosphenoid (cf. Bellairs and Gans, 1983).

Each lateral portion of the posterior border of the tabulosphenoid contacts the most anterior point of the anterolateral processes of the occipital complex. Medial to this, the posterior border forms a small concave section of the most anterior border of each Gasserian foramen. The medial portion of the posterior border of the tabulosphenoid, between the posterior projections of the ventral ridges, is variable in shape and in its relationship with the parabasisphenoid. The center may be V-shaped and rest upon the dorsal surface of the anterior rostrum of the parabasisphenoid, or in other specimens it may be straighter and articulate with a step of the dorsal face of the parabasisphenoid.

In dorsal view, the vertical dorsolateral processes rise a little inward of the lateral borders and run posteriorly parallel to them. They are highest in their anterior third; posteriorly they descend gradually almost to nothing. The internal (medial) faces of the dorsal processes are straight and vertical, but the external (lateral) processes are inclined to the lateral border until they meet with the ventral face, and jointly form the sharp lateral border of the bone. The lateral faces of the dorsolateral processes contact the ventrolateral sides of the parietal; anteriorly, they show ridges that match the grooves on this bone. Posteriorly, the vertical blades of the tabulosphenoid are lower and the lateral borders just support the borders of the parietal.

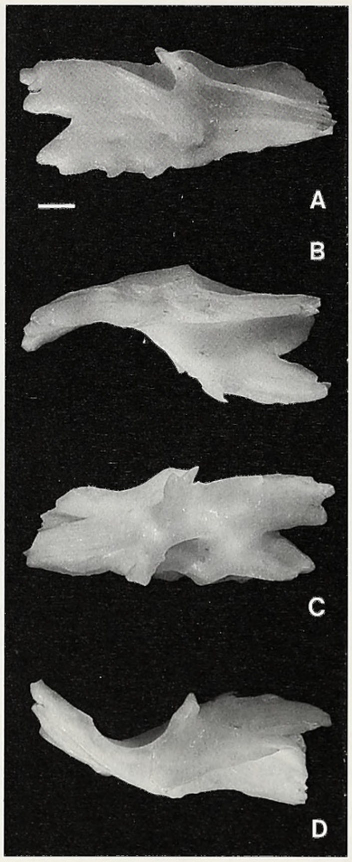

Fig. 29.—*Amphisbaena alba.* Photographs of right frontal (CG 1200), anterior to the left. The bar shows 1 mm to scale. A, dorsal view; B, medial view; C, ventral view; D, lateral view (this view is slightly tilted relative to view B so that their outlines differ).

The dorsal medial surface of the tabulosphenoid is smooth and concave (Fig. 35A, 36A). The posterior ventral groove for the parabasisphenoid does not modify the inner floor of the cranial cavity. On either side, midway between midline and lateral margin, open the ducts for the optic nerves (Kritzinger, 1946). These run anterolaterally and end beside the base of the ventral ridges at the tip of the articulation with the parabasisphenoid.

In lizards, the orbitosphenoid generally is a small, paired cartilage replacement bone. However, the analysis of embryonic material of the amphisbaenian genus *Leposternon* suggests that the elements of this region are paired membranous ossifications combined with the remnants of cartilages that fuse to produce the adult condition (Bellairs and Gans, 1983); clearly, this embryonic pattern suggests that we are dealing with the occurrence of a different, perhaps a compound bone. Hence, we depart from Bellairs and Gans (1983) and modify the name to tabulosphenoid (platelike sphenoid), to emphasize the distinction and to encourage examination of more and particularly embryonic material of possibly related outgroup forms.

Parabasisphenoid.—The azygous parabasisphenoid (Fig. 37, 38) is a wide, spearhead-shaped plate, with a thickened, roughly rectangular medial portion the dorsal surface of which forms the floor of the braincase. The ventral surface of the portion extends thin flanges that form the posterior part of the palate. Anter-

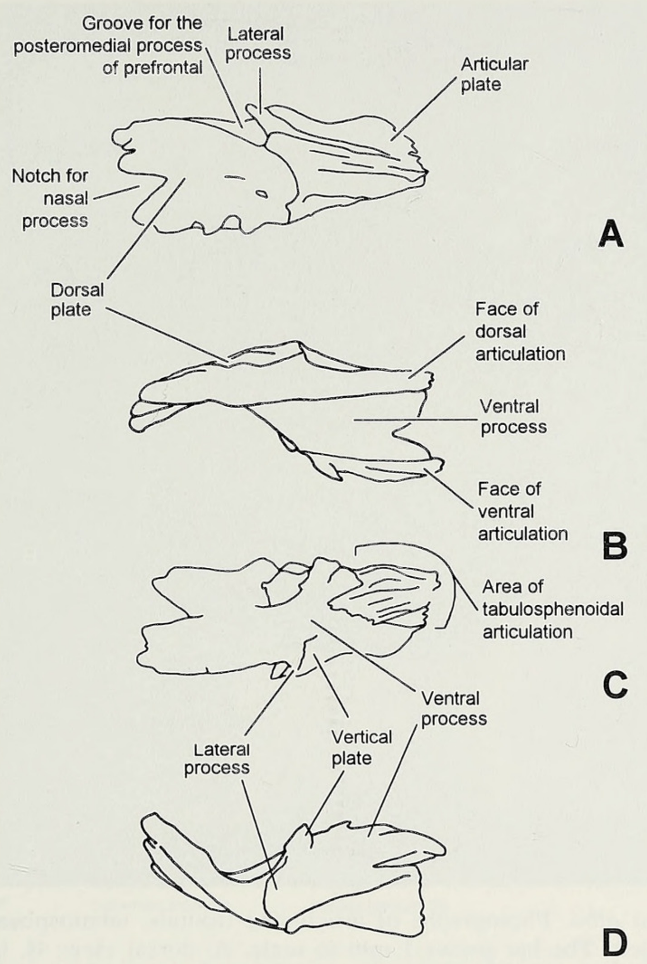

Fig. 30.—*Amphisbaena alba.* Labeled outline of frontal shown in Figure 29.

odorsally, a blunt connection with some wedged projections inserts into the tabulosphenoid, and anteroventrally a sharp rostrum rests in a ventral groove of this bone. Posteriorly, the parabasisphenoid is ventrally inclined and articulates with the basioccipital area of the occipital complex. The parabasisphenoid is in lateral contact with a pterygoid on each side. Laterally the posterior border contacts an element-X on each side. Medially, the parabasisphenoid–basioccipital suture forms an irregular interdigitation either on the dorsal or ventral level of the bone.

The lateral edges of the parabasisphenoid angle outward evenly from their anterior rostrum up to the site at which the braincase starts; thereafter, the lateral edges of the parabasisphenoid flare more widely. A lateral concavity defines the volume between dorsal and ventral surface (Fig. 37B, 38B).

The medial axis of the ventral face of the parabasisphenoid is straight (Fig. 37B, 38B). Posterior to the middle of the parabasisphenoid length, the posterior borders of the ventral face extend into wide lateral plates (basipterygoid processes, Jollie, 1960; basipterygoid shoulders or angles, Vanzolini, 1951*a*) that are inclined ventrally; the plates laterally contact the medial borders of the pterygoids. These plates each bear a cartilaginous nodule shown mainly in the sections (Fig. 55B,

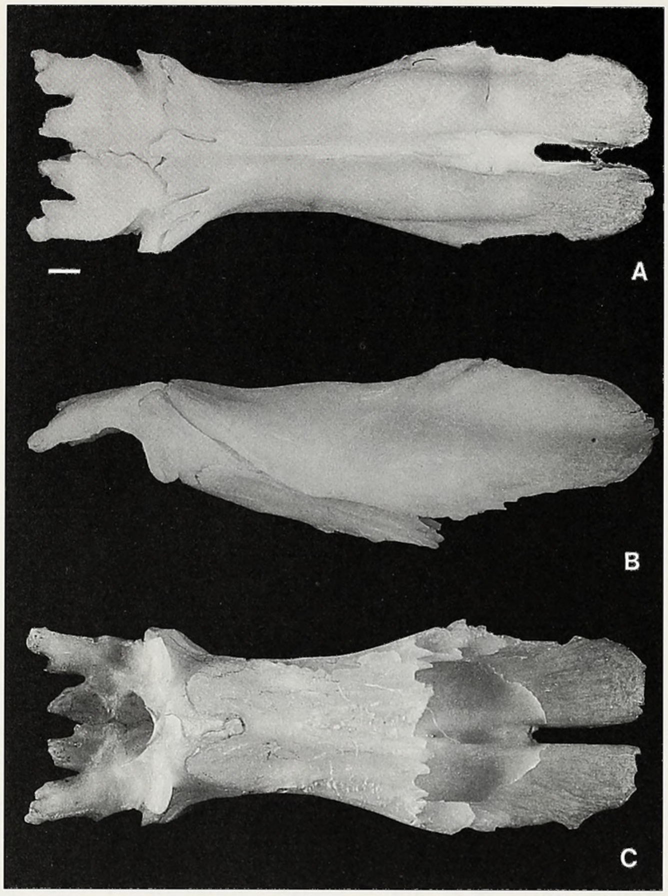

Fig. 31.—*Amphisbaena alba.* Photographs of articulated frontals, tabulosphenoid, and parietal (CG 1811), anterior to the left. The bar shows 1 mm to scale. A, dorsal view; B, lateral view; C, ventral view.

56B). Posteriorly the lateral plates are joined with the elements-X by a synchondrotic joint.

Each concave lateral face of the parabasisphenoid forms a groove that is open to the gaps left between palato–pterygoid shelves ventrally, and parietal and lateral sphenoid areas of the occipital complex dorsally. A large foramen enters the lateral side of the parabasisphenoid, near the midlength of the brain cavity (the anterior end of the parabasal canals; Jollie, 1960).

The thin dorsal surface of the anterior rostrum of the parabasisphenoid that contacts the tabulosphenoid seems to be formed mainly by the projection of the dense ventral layer of bone. At the posterior end of this contact surface there is either a smooth slope to the posterior and thicker area of the parabasisphenoid, or a more or less transversal and dentate step bordering the posterior edge of the tabulosphenoid. More posteriorly the concave dorsal face forms a shallow medial "basin" (best seen in histological section and representing the sella turcica) that is rounded posteriorly and elongated anteriorly. Its posteriorly displaced bottom is the thinnest region of the bone. There is no special depression for the hypophysis. The high and thick dorsolateral borders of the basin form the ventral borders of the Gasserian foramina. Anteriorly, the lateral dorsal borders project as small tabulosphenoid processes, dorsal to the anterior tip of the bone, that fit into grooves on the posterior ridges of the tabulosphenoid.

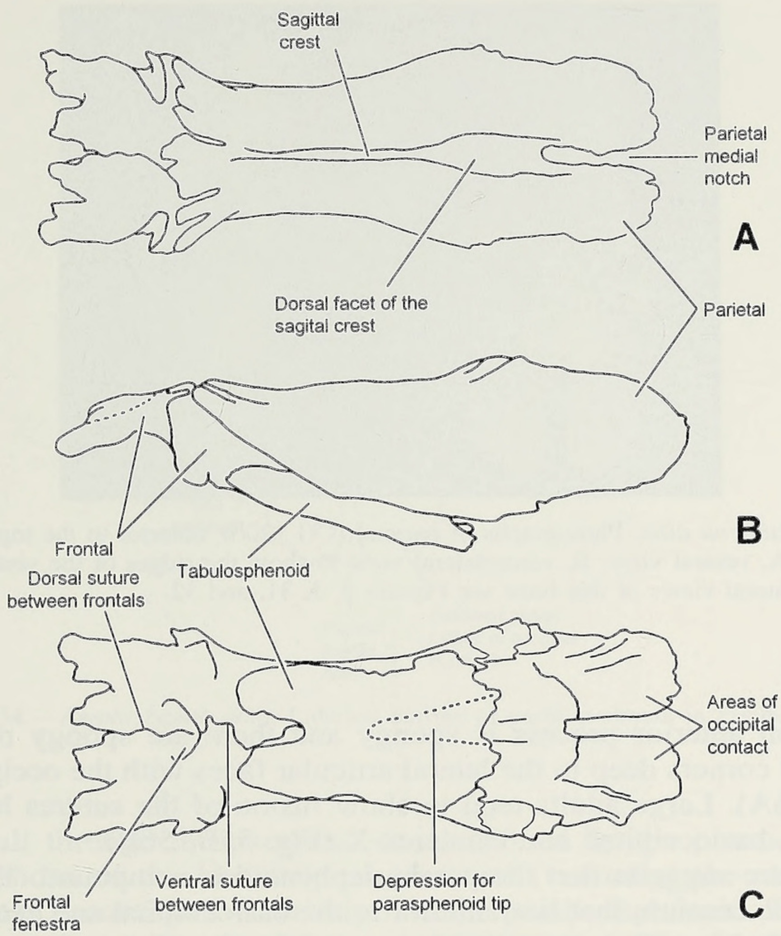

Fig. 32.—*Amphisbaena alba*. Labeled outline of anterior braincase shown in Figure 31.

The thick posterolateral borders of the parabasisphenoid form flat contact faces for chondral articulation with the element-X of each side. A parabasal (Jollie, 1960) or Vidian (after Rieppel, 1993; Fig. 36C, 38C) canal opens at the base of the ventrolateral plate, just between the facets of articulation with element-X and the basioccipital area. Through this canal passes the internal carotid artery and the palatine branch of the facial nerve; anteriorly it opens on the lateral side of the parabasisphenoid. At its middle, the canal branches off to a canal that opens at the dorsal basin, carrying the internal carotid. The ventral side of the anterior foramen of each parabasal canal may bear a narrow and short fissure or a tiny scar marking the base of the ventrolateral plate; some specimens lack this scar (CG 1216, CG 1811, CG 3534, AMNH 73233, KM 11).

Medially between the elements-X of the two sides, the posterior border of the parabasisphenoid contacts the basioccipital area. Three areas of contact can be distinguished (Fig. 37D, 38D): at the midline there is a narrow zone, concave in the basioccipital area, with a thin articulation of dense connective tissue; more laterally the gap with the basioccipital is wider and each lateral area of the parabasisphenoid articulation shows rugose, or porous, convex surfaces that are faced with corresponding articulation faces of the basioccipital area. These lateral articular faces are covered with one leg of the triradiate cartilaginous plate (Fig. 55A, 56A). The frontal sectional slides show that the parabasisphenoid bone at the base

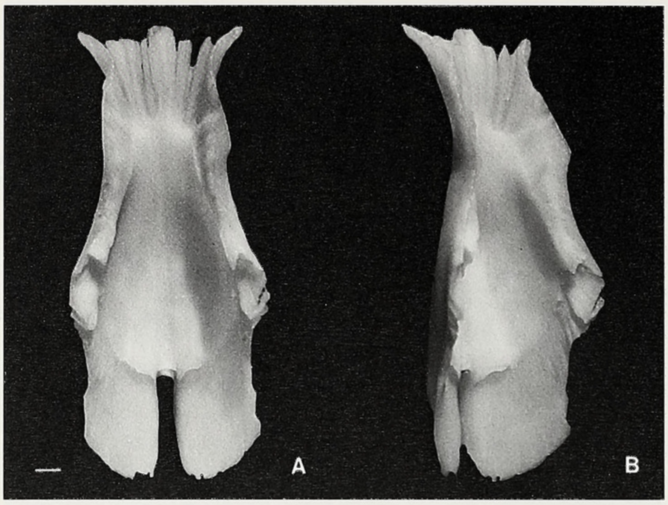

Fig. 33.—*Amphisbaena alba*. Photographs of parietal (CG 1200), anterior to the top. The bar shows 1 mm to scale. A, ventral view; B, ventrolateral view to show the ridges of the ventrolateral border. For dorsal and lateral views of this bone see Figures 2, 3, 31, and 32.

of the rostrum anterior process is spongy and there are spongy regions in the posterolateral corners deep to the lateral articular faces with the occipital complex (Fig. 55A, 56A). Large adults tend to show fusion of the sutures between parabasisphenoid, basioccipital, and elements-X (Fig. 55B, 56B).

The literature suggests that the parabasisphenoid is compound. The portion of the floor of the cranium that lies anterior to the basioccipital and extends laterally and ventrally to contact the pterygoids is considered to derive from the basisphenoid. The triangular anteroventral portion that contacts the tabulosphenoid is considered to be a fused anterior parasphenoid. This interpretation follows Zangerl (1944) and Jollie (1960). Kesteven (1957) stated that reptiles lack a parasphenoid, and that the amphisbaenian parabasisphenoid represents only the basisphenoid. Moreover, Zangerl (1944) discussed the possibility that juveniles of *Leposternon* may have two sutures, an anterior one between the basisphenoid and parasphenoid and a posterior one between the basioccipital and basisphenoid. Regardless of the situation in other species, our specimens of *Amphisbaena alba* show only the posterior one. Zangerl also mentioned separation of a presphenoid in the extreme anterior tip of the parabasisphenoid; no such separation appears in our material.

Element-X.—The elements-X (Fig. 39, 40) are small, massive bones (defined by the triradiate cartilaginous plates), each fitting into a lateral socket between the parabasisphenoid and the basioccipital and prootic areas of the occipital complex (Fig. 55, 56). In large specimens, the elements-X tend to fuse as the plates close.

In ventral view, each element-X has a subtriangular shape. The apex faces the midline and the rounded lateral side (Fig. 39C, 40C) faces to the fenestra ovalis; the anterior side forms a synchondrosis with the parabasisphenoid and the posterior side with the lateral expansion of the basioccipital plate. The anterior and posterior faces are flat; whereas the anterior area of articulation has an oval outline, the shape of the posterior one is subtriangular.

A thickening at the center of the dorsal face (Fig. 39B, 40B) embraces the end of the prootic process. The internal carotid artery passes ventral to the stapes to

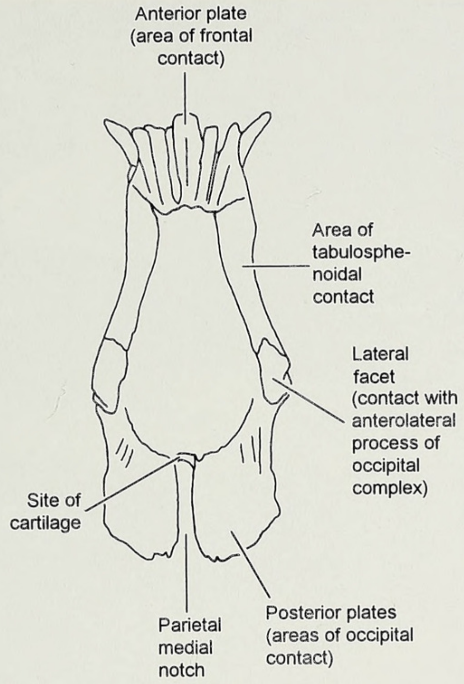

Fig. 34.—*Amphisbaena alba*. Labeled outline of parietal shown in Figure 33A.

enter the skull through the parabasal canal defined by the prootic process, the lateral expansions of the basioccipital area and (ventrally) the element-X. The parabasal canal is continued anteriorly into the parabasisphenoid. The element-X is entirely spongy and its articulations are cartilaginous (Fig. 55, 56).

The nature of the element-X as an element of the amphisbaenian skull has been discussed in the previous literature but there is no agreement among authors. Zangerl (1944) cites Williston (1917) as having labeled the elements as "paroccipitals," but our copy of the paper lacked such a figure; however, in Williston (1918*a*) the element is coded "pc." Williston, 1918*a*, only included the view of the skull to illustrate the vertebrae of the head joint and does not identify the abbreviation; however, in the next paper in the journal (Williston, 1918*b*) and in his summary book (1925) the abbreviation "pc" is coded as prootic. Diverse alternative interpretations can be found: Lakjer (1927) and Jollie (1960) called them sphenoccipital epiphyses; Zangerl (1944) found no certain homologies to any reptilian bone, calling them "elements X"; Vanzolini (1951*a*) suggested homology to the basitemporal of birds and crocodilians; and Kesteven (1957) considered them as reduced prootics. Gans (1960, 1978) considered these elements as bony epiphyses suitable for muscular attachment, a position supported by our histological evidence. Hence we accept the position of Lakjer (1927) and Jollie (1960). However, the double synchondroses generate uncertainty as to whether the epiphyses pertain to the basioccipital or the parabasisphenoid. For this reason the term element-X remains suitable.

Stapes.—The paired stapes (Fig. 41, 42) have a subcircular, thick footplate that fits into each fenestra ovalis of the occipital complex; both faces of each footplate are quite concave. Its distal face gives origin to a bladelike stapedial columella (Fig. 41A, 42A) that projects ventrolaterally toward the quadrate. The anterior edge of the columella forms an articulation for the cartilaginous extracolumella

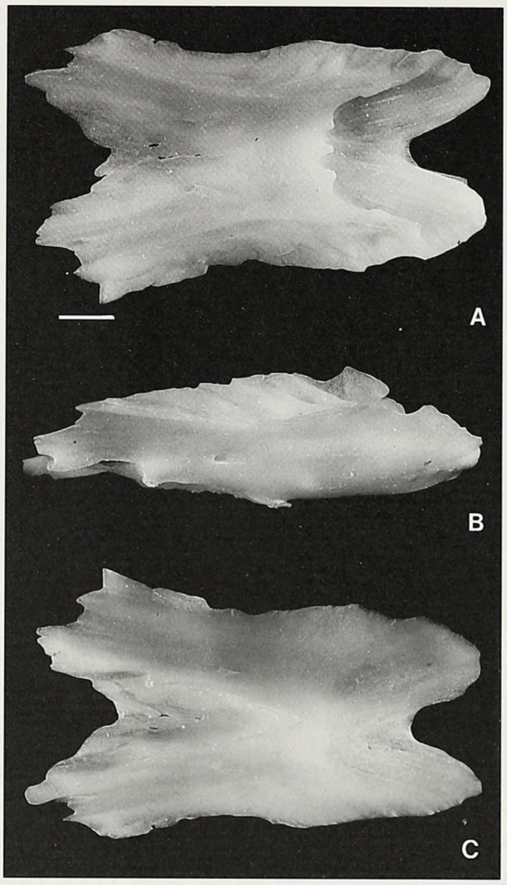

Fig. 35.—*Amphisbaena alba.* Photographs of tabulosphenoid (CG 1200), anterior to the right. The bar shows 1 mm to scale. A, dorsal view; B, lateral view; C, ventral view.

just before its distal end. The footplate, but not the columella, is formed of spongy bone.

The footplate fits exactly into the fenestra ovalis as a plug; the outline of the proximal (inner) face of the footplate follows the almost circular shape of the transverse section of the auditory tube. A step or ridge of the otic capsule (seen only internally) passes half around the auditory tube; on the lateral side, it supports the border of the proximal stapedial face. At the opening of the auditory tube the inclined anterior border of the footplate is thicker than the posterior one (Fig. 41A, 42A). The distal face extends anteriorly, overlapping the anterior border of the tube, covering part of the facial canal of the occipital complex.

The compressed columella (Fig. 41B, 42B) ascends perpendicularly from the center or from the anterolateral side of the distal face of the stapedial footplate, as a projection of the border. Both faces of the base of the columella show tiny foramina. The posterior border of the columella shows an S-curvature, with the distal tip rounded; the anterior border of the columella rises almost straight. Its distal end bears an anteriorly oriented articular face that connects with the extracolumella.

The stapes are recognized as being the bones that close the fenestra ovalis and distally contact the cartilaginous extracolumellae (Wever, 1978).

Quadrate.—The quadrate (Fig. 43, 44) is a paired, complexly shaped long bone that links the side of the cranium (paroccipital process) to the posterior end of

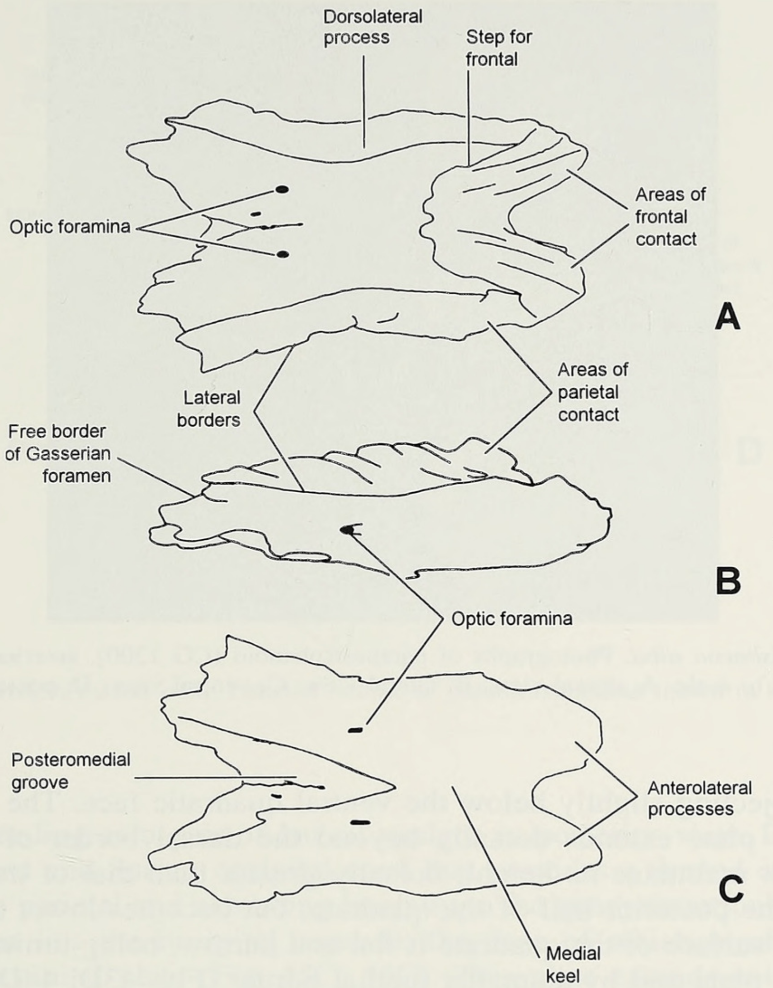

Fig. 36.—*Amphisbaena alba.* Labeled outline of tabulosphenoid shown in Figure 35.

the mandibular ramus (articular process of the compound bone). Anteriorly, its longitudinal axis slightly approaches the sagittal plane (at an angle less than 10°) and is vertically inclined at an angle of approximately 30°. The posterior continuation of the postorbital space, which is continued to the otic region, separates the medial face of the quadrate from the braincase. Anteriorly (distally), the medial and ventral sides are embraced by the posterior end of the pterygoid; posteriorly it contacts the columellar tip and the extracolumella swings around its ventral exposure.

The quadratic proximal articulation with the paroccipital process is subcircular in shape, and its surface is strongly concave (Fig. 43E, 44E). The distal articular head of the quadrate is slightly wider and higher than the shaft of the bone and the articular surface is saddle-shaped; its convexity is vertical and its concavity horizontal. The ventral side of the articular head protrudes, leaving a marked posterior ridge (Fig. 43B, 44B) that is embraced by the posterior process of the pterygoid. The lateral sides of the distal end are flat and vertical (Fig. 43A, 44A).

A lateral plate emerging tangentially from the shaft shapes a wide and flat lateral face of the quadrate, the center of which has a hollow concavity, the bottom of which is pierced by a lateral foramen (Fig. 43A, 44A). The lateral plate extends

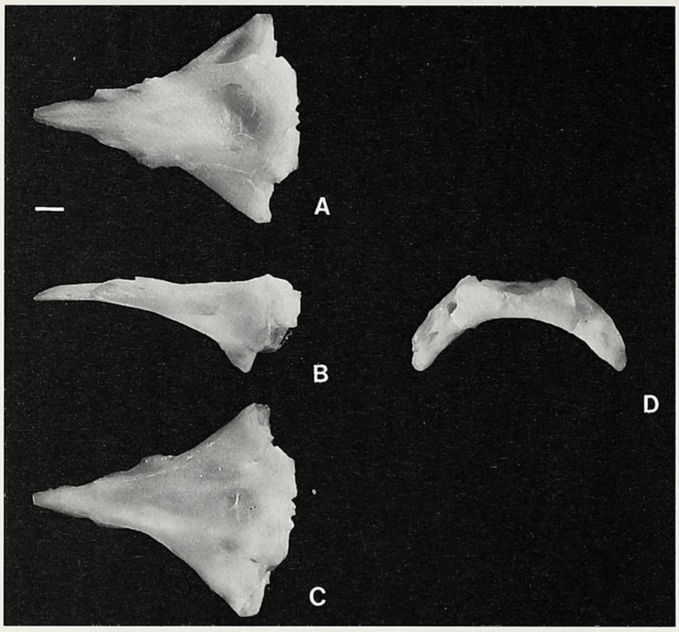

Fig. 37.—*Amphisbaena alba.* Photographs of parabasisphenoid (CG 1200), anterior to the left. The bar shows 1 mm to scale. A, dorsal view; B, lateral view; C, ventral view; D, posterior view.

ventrally, projecting slightly below the ventral quadratic face. The posterior part of the lateral plate extends dorsally beyond the dorsal border of the proximal articulation; it maintains its height, dorsally greater than that of the body of the bone, along the posterior half of the quadrate, but becomes lower anteriorly.

The dorsal surface of the quadrate is flat and narrow, being limited at the sides by the lateral plate and by a smaller medial border (Fig. 43D, 44D) that extends from the anterior half of the quadrate (where the opposite lateral plate becomes lower). These two projections form an intermediate concave dorsal canal along the quadrate. A distinct dorsal foramen pierces the base of the lateral plate; its canal ends at the center of the lateral plate (lateral foramen).

The ventral view of the quadrate (Fig. 43B, 44B) shows a narrow, flat corridor along which runs the extracolumella. This corridor passes anteriorly from the ventral posterior end of the quadrate and spirals laterally to end at the lateral face of the distal end.

The medial side of the distal head and the posteroventral border of the quadrate shaft contact the posterior process of the pterygoid; its expanded head rests next to the ventral extracolumellar corridor. One or two tiny foramina appear just dorsal to the attachment of the pterygoid. Both proximal and distal heads of the quadrate are formed of spongy bone. However, the shaft and the projecting plates represent dense laminar ossification (Fig. 55, 56).

The quadrates are identified as the bones that provide articulation of the mandible to the braincase.

Occipital Complex.—The occipital complex (Fig. 5, 6, 45, 46) represents the posteriormost aspect of the skull. Several cranial elements appear to have fused, making the structure most complex, geometrically and developmentally. Several of its elements remain as anteriorly reaching processes, making the occipital complex easiest to describe from back to front. It consists primarily of the fused four-element (supraoccipital, exoccipitals, basioccipital) ring framing the foramen mag-

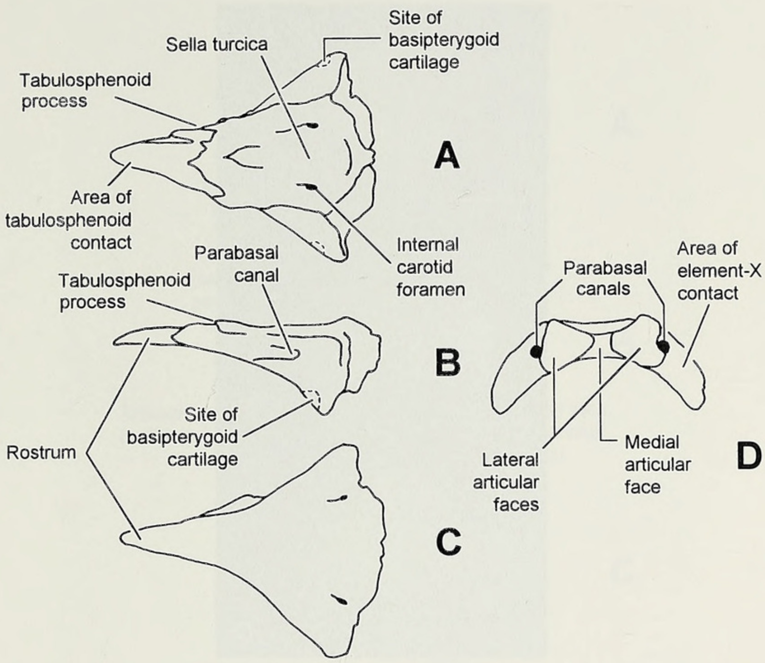

Fig. 38.—*Amphisbaena alba.* Labeled outline of parabasisphenoid shown in Figure 37.

num, and extending as a pair of lateral wedges in posterior view. Dorsally there is a pronounced and flaring occipital crest that provides a domed roof anteriorly underlying the parietal and extending laterally to the quadrate articulation. Ventral to the foramen lies the occipital condyle, the base of which reaches anteriorly into the basioccipital plate (Fig. 45C, 46C). This plate extends anteriorly to the contact zone with the parabasisphenoid and laterally to the cup-shaped articulation with the elements-X. Somewhat anterior to the foramen magnum, the occipital complex broadens and sends lateral branches to the paroccipital processes. The thick zone between the dorsal and basioccipital plates is complicated by fusion of the multiple elements that comprise the internal portions of the otic apparatus. The auditory canal emerges through the ventrolaterally placed fenestra ovalis which holds the stapedial footplates.

The occipital condyle is double knobbed (bicipital) and formed of spongy bone. The articular surfaces are smooth (and seen in section to be covered with hyaline cartilage), whereas the rest of the surface is rougher. In posterior view, the condyle has the shape of a kidney resting on its side. As the anterior part of the bicipital occipital condyle is narrower than the posterior head, it shapes a "neck." The bicipital knobs project further dorsally than ventrally; they are more widely separated by the midventral border of the foramen magnum (Fig. 5, 6). The atlantal vertebra surrounds the condyle like a ring; its dorsal projection reaches the inner face of the dorsal roof of the foramen magnum which constrains its opening. The condylar articulation is unique in having a meniscus.

The foramen magnum opens in the center of the posterior face of the occipital complex immediately dorsal to the occipital condyle (Fig. 5, 6). The posterior face is delimited dorsally by the occipital crest, laterally by the paroccipital processes, and ventrally by the ventral plate of the occipital. Lateral to the foramen magnum, the surface of the posterior face is concave. Lateral to the base of the

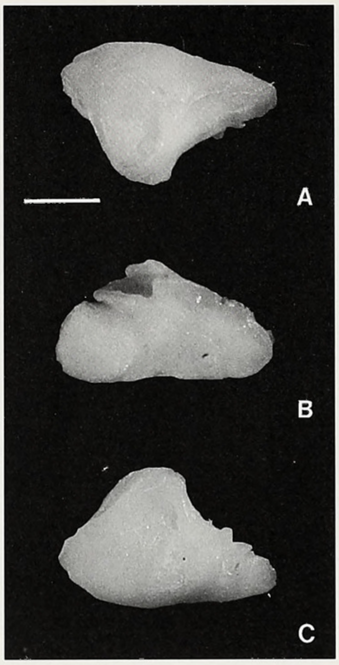

Fig. 39.—*Amphisbaena alba.* Photographs of right element-X (CG 1200), anterior to the left. The bar shows 1 mm to scale. A, dorsal view; B, medial view; C, ventral view.

occipital condyle appear two large jugular foramina; they open into a chamber from which five foramina radiate. The largest foramen passes to the cranial cavity; the internal opening lies just posterior to the otic capsule. Two of the four smaller foramina enter from the ventral surface, one enters medially, and the last one dorsally. Two bony ridges extend laterally along the posterior face from the level of the jugular foramen to the posterior part of the paroccipital process.

The posterior border of the dorsal plate is elevated into a transverse occipital crest that projects beyond the posterior aspect of the cranium and reaches almost to the end of the middle of the occipital condyle. The extent of crest and condyle in dorsal view are affected by slight allometric differences and angulation of the long axis. In dorsal view, the border of the occipital crest is generally medially notched.

The dorsal plate roofs the foramen magnum. There is a wide transverse occipital crest that curves from the quadratic articulations to the midline. The most striking feature of the dorsal plate is the high and thick sagittal ascendent process, which fits into the median notch of the parietal and thus continues the sagittal crest of the parietal posteriorly (Fig. 45A, 46A). In lateral view (Fig. 45B, 46B), the anterior part of the process has a baseline that runs parallel to the dorsal border; however, the posterior end of the baseline rises to meet the dorsal border of the occipital crest. The dorsal plate spreads laterally and anteriorly from the base of the ascendent process forming a doubly crescentic element, the posterior crescent deriving from the occipital crest and the more anterior one from the flared edge between the anterolateral processes. The plate roofs the posterior part of the braincase and the otic capsules. The roof of the otic capsules shows some spongy bone. The anterior part of the dorsal plate thins and its surface shows a pattern of ridging that provides an interlocking articulation with the posterior portion of the overlapping parietal. Two slim anterolateral processes extend the dorsal plate, as their

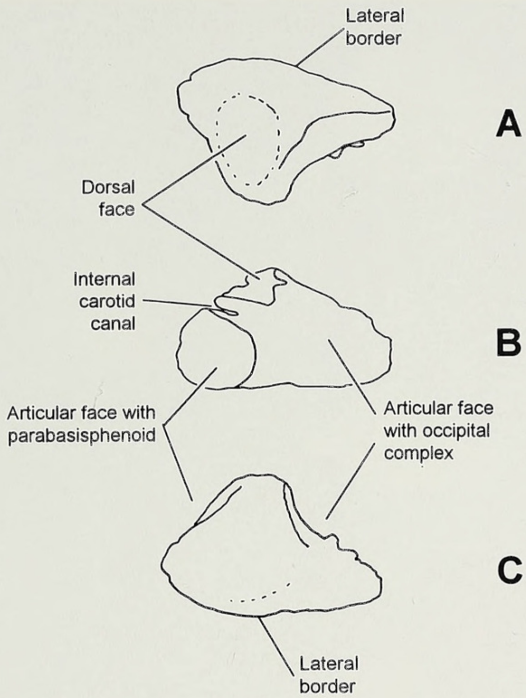

Fig. 40.—*Amphisbaena alba.* Labeled outline of element-X shown in Figure 39.

ventral border forms the dorsal edge of the postorbital gap and the Gasserian foramina. More posteriorly, the lateral border of the dorsal occipital plate is continuous with the paired anteroventrally projecting paroccipital processes.

The basioccipital plate is smaller than the dorsal one (Fig. 45C, 46C); its concave anterior border articulates medially with the parabasisphenoid. Lateral to this, wide, paired ventral anteroventral processes (tuberculum sphenoccipitale; Jollie, 1960) contact the element-X of each side via a thick synchondrosis and bend ventrally, thus shaping a concavity between them. Laterally, a notch on each side of the ventral plate forms the medial border of the auditory canals into which fit the stapes. More posteriorly, the paroccipital process gives rise to a vertical plate. The posterior aspect of the basioccipital plate is inclined dorsally; its posterolateral borders are rounded whereas the flat medial region extends posteriorly to the condylar neck.

The lateral paroccipital processes are short and massive. Anteriorly, each ends in a blunt and hemispheric quadratic articulation that faces lateroventrally, reflecting the inclination of the quadrate (Fig. 45B, 46B). All paroccipital processes are formed of spongy bone as are the adjacent areas of the contacting plates (Fig. 55, 56).

The fenestra ovalis lies medial to the paroccipital process. The medial border of the process is connected to the basioccipital plate by a curved plate. This plate delimits the posterior and medial aspects of the externally open middle-ear cavity; the paroccipital process and the quadrate delimit the cavity laterally. The stapedial footplate fits on a narrow step in the wall of the auditory tube, just internal to the fenestra ovalis, which it then occludes. The step lies mainly on the medial surface of the auditory tube, but also continues slightly around the anterior and

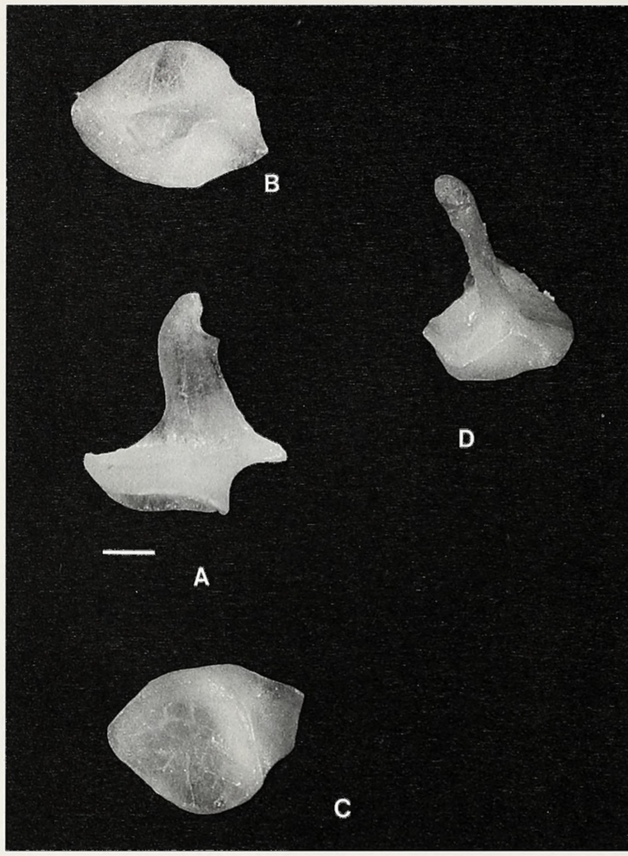

Fig. 41.—*Amphisbaena alba.* Photographs of right stapes (CG 1811); the orthogonally presented pictures are all rotated from the lateral view. The bar shows 1 mm to scale. A, lateral view; B, distal view; C, proximal view; D, anterior view.

posterior area. At the ventral side of the step, a foramen opens from the region dorsal to the posterior face of the auditory canal.

Anterior to the fenestra ovalis arises a wide facial canal, defined at each side between the dorsad base of the anterolateral process and the ventral prootic process. The anterior end of this canal shapes the posterior border of the Gasserian foramen. The facial canal is partially overlapped by the stapedial footplate. Just anterior to each stapes, one (or two) foramina pierce the bone to open at the inner ventrolateral angle of the braincase (not illustrated). Ventral to the facial canal, a prismatic prootic process contacts the element-X. The internal carotid passes through a canal between this prootic process and the anteroventral lateral one.

Internally, the complex forms the smooth posterior aspect of the braincase. Also, its lateral wings house the internal portions of the otic apparatus (Wever and Gans, 1973; Baird, 1978) which are discernible only in section although they may be visualized by treating the bone with essential oils. As the structure is unitary and shows almost no sutures, homology of the components remains a problem. In a frontal view (Fig. 45D, 46D), the inner roof of the braincase is formed by the ventral surface of the dorsal plate. Anteriorly, the dorsal occipital part of the braincase is wide, but posteriorly the roof of the braincase is narrowed by the projection of the otic capsules that are bulky on the sides and fuse dorsally with the dorsal occipital plate. More posteriorly, the braincase expands slightly in the lateral dimension but is constrained again by the foramen magnum. Two

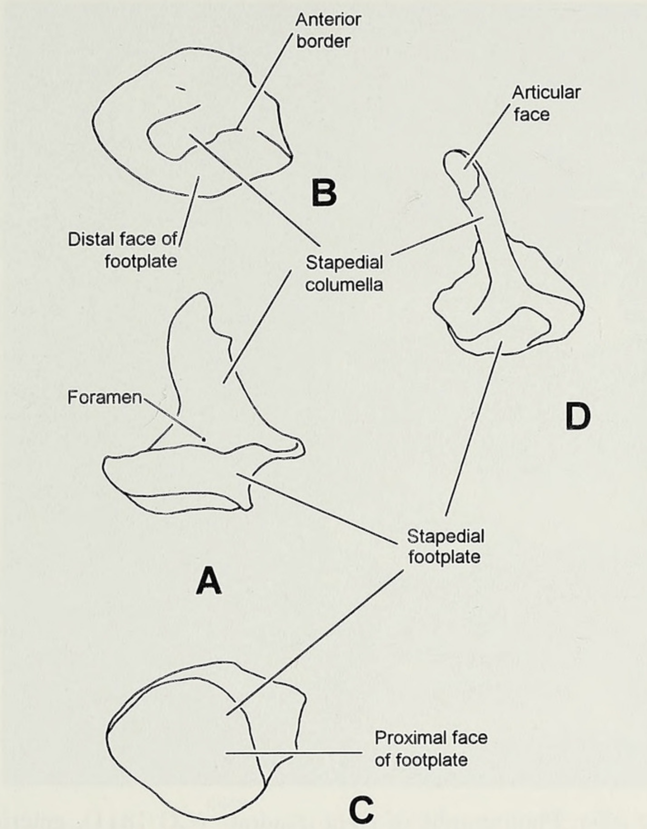

Fig. 42.—*Amphisbaena alba.* Labeled outline of stapes shown in Figure 41.

large, anteriorly facing foramina pierce the inner surface of each otic capsule. One of these opens from the bottom of the otic capsule near the floor of the brain cavity. The other opens more anteriorly and dorsally. The floor of the braincase is concave, shaping a basin supporting the cerebellum. Posteriorly, the base of the occipital condyle forms a rising edge from the basin.

Whereas a comparison with other reptiles makes it reasonably clear that the amphisbaenian occipital complex is compound, it is difficult to decide which elements are included. Certainly it includes the occipitals (cf. Gans, 1960). The anterolateral processes have been described as separate pleurosphenoids by Zangerl (1944), but Rieppel (1993) presumed them to be homologous with the alar processes of the prootic; also, a series of elements of the otic complex are presumably fused within this area. One of the skulls (CG 1216) shows that the anterolateral processes of the occipital complex are bifid. The sutures could be interpreted, with reservation, to represent the boundaries between the supraoccipital and laterosphenoid; if so, these processes are compound. However, until embryos are available for description, this pattern remains to be confirmed.

Dentary.—The dentary (Fig. 47, 48) is the main bone of each mandibular ramus. Anteriorly it is joined with the opposite dentary by means of a complex symphyseal articulation, diverging posteriorly in an angle of 15° from the medial axis (Fig. 7C); posteriorly the dentaries are divided into pointed posterodorsal and posteroventral processes. The dorsal border of each dentary bears eight teeth and posteriorly curves dorsally and then horizontally in a continuation that forms the anterior border of the coronoid processes of the mandible. The ventral border of

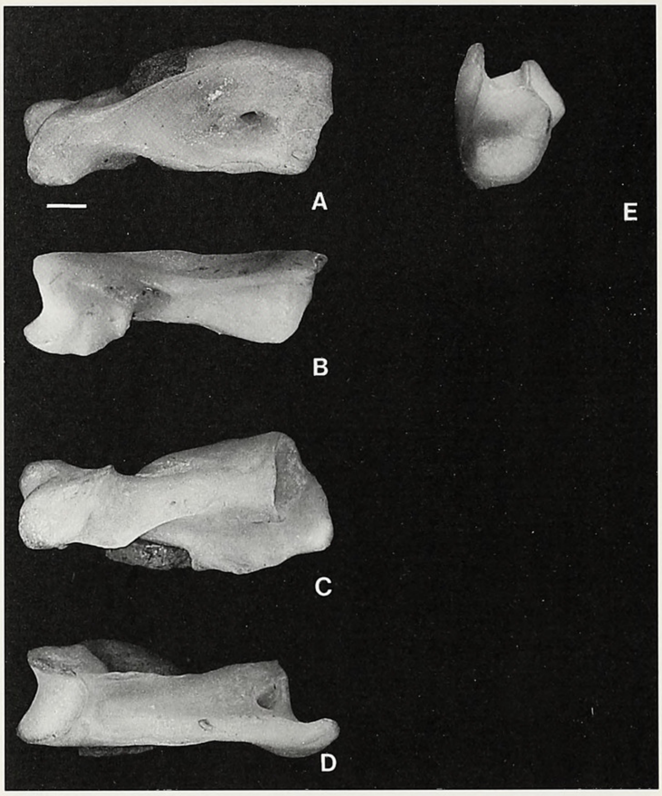

Fig. 43.—*Amphisbaena alba.* Photographs of right quadrate (CG 1811), anterior to the left. The bar shows 1 mm to scale. A, lateral view; B, ventral view; C, medial view; D, dorsal view; E, posterior view (slightly tilted to the right).

the dentary leaves the symphyseal surface in a sharp dorsomedial curve then gradually curves ventrally and horizontally. The angular prevents contact of the dentary with the articular process of the compound bone. The dorsal and ventral processes are separated by a wide, hollow posterior cavity into which fits the dentary point of the compound bone. On the labial side the dentary lies labial to the coronoid, but more ventrally the sliver of the compound bone lies lingual to it. On the lingual side, the posterodorsal process is covered by the coronoid and angular; the ventral process is covered by the angular.

The symphyseal surface is flat, elongated, and separated from that covered by a thin layer of hyaline cartilage. The longest axis of the symphysis is oriented ventrally and posteriorly; the articulation surface expands dorsally and ventrally, so that it is wider than the cross section of the dentary. A notch on the posterior (inner) side is shaped by the extension of Meckel's canal.

In a lateral (labial) view (Fig. 47B, 48B), the dentary shows two longitudinal rows of mental foramina which perforate to the posterior cavity. The dorsal row begins posteriorly with a large foramen at the center of the lateral face, and is prolonged anteriorly by two to four smaller foramina. The ventral row begins more anteriorly and is composed of two to four small foramina in a dorsally angled line that meets the dorsal row anteriorly.

The solid posterodorsal process shapes the anterior border of the coronoid processes of the mandible, reaching almost to its top; here it bends posteriorly, fitting

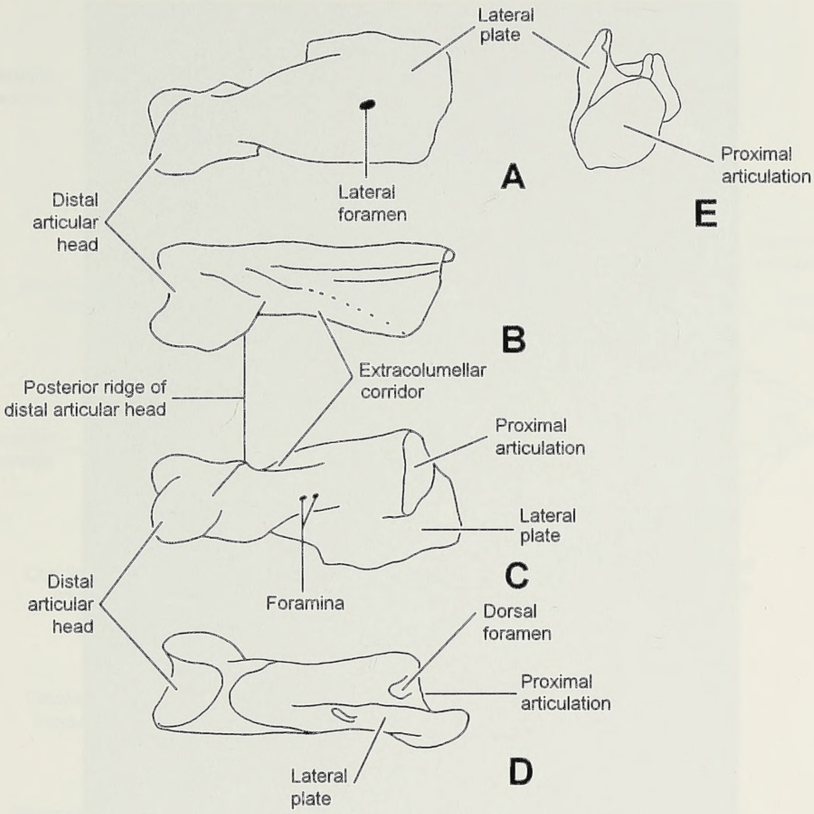

Fig. 44.—*Amphisbaena alba.* Labeled outline of quadrate shown in Figure 43.

into a lateral groove of the coronoid. A flat posterior face of the posterodorsal process contacts the coronoid; at its base begins the posterior cavity of the dentary.

Between the two processes opens a wide and deep posterior cavity into which the compound bone fits. Two thin plates, lateral and medial, shape its lateral walls. The posterior cavity is vertically elongated; anteriorly it narrows into a branching tunnel that runs anteriorly and opens to the foramina of the lateral face of the dentary. The coronoid and angular fit into a triangular depression on the lingual surface of the medial plate.

Meckel's canal is open along the medial face of the dentary. Anteriorly it extends to the mandibular symphysis; posteriorly it reaches the mandibular central labial foramen that is formed between the dentary, compound bone, and coronoid (in the articulated mandible this aperture seems to be shaped only by coronoid and dentary). A rod of cartilage (Meckel's cartilage) runs along the entire canal and extends posteriorly, lying lateral to the angular and penetrating the mandible by its central foramen; the cartilage ends in a sharp point in the anterior part of the longitudinal tunnel of the compound bone. The posterior part of Meckel's canal is bordered dorsally by the coronoid and ventrally by the angular borders; its posterior end is limited by the posterior overlapping sliver of the compound bone.

In dorsal view (Fig. 47C, 48C), the dentary shows a slight inclination toward the medial plane. The dorsal border is labially widened, supporting the bases of the teeth in subpleurodont tooth implantation (Gans, 1957). The conical teeth are inclined anteriorly and laterally; however, the points are curved medially and

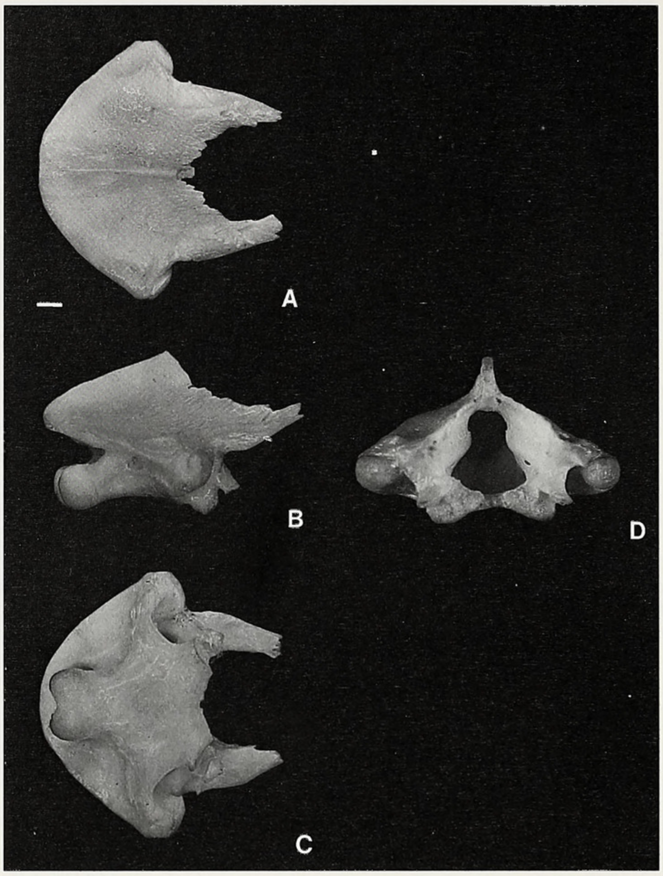

Fig. 45.—*Amphisbaena alba.* Photographs of occipital complex (CG 1811). The dorsal and ventral views are tilted as they are perpendicular to the dorsal and ventral plates respectively, and not to the horizontal plane of the bone; anterior to the right. The bar shows 1 mm to scale. A, dorsal view; B, lateral view; C, ventral view; D, anterior view.

posteriorly. The anterior teeth are further inclined than the posterior ones, which are more straight. The most anterior tooth is relatively small, the second is larger, and the third the largest of the mandibular series, exceeding the height of the other teeth by one-third. Posteriorly, the other teeth become smaller, but the level of their tips is maintained as the dentary base rises posteriorly. On the lingual side, the bases of the teeth show nutritive foramina on the plane of the curvature. Each tooth appears to have a plane of weakness beginning at the basal foramina; several teeth are split along this plane which is coincident with the plane of curvature. The bases of the teeth are ankylosed to their sockets by a ring of cement.

The dentary is recognized as the sole tooth-bearing bone of the mandible.

Compound Bone.—The complex compound bone (Fig. 49, 50) is the most posterior bone of the mandible and bears the mandibular articulation with the quadrate (Fig. 55, 56). Its anterior point (the dentary process) is inserted into the posterior cavity of the dentary. Below this it is in contact with the posterior ventral processes of the dentary and with the angular; dorsomedially the compound bone contacts the coronoid. Its medial (lingual) side is mostly covered by the coronoid and angular. The disarticulated compound bone bears three processes: a posterior

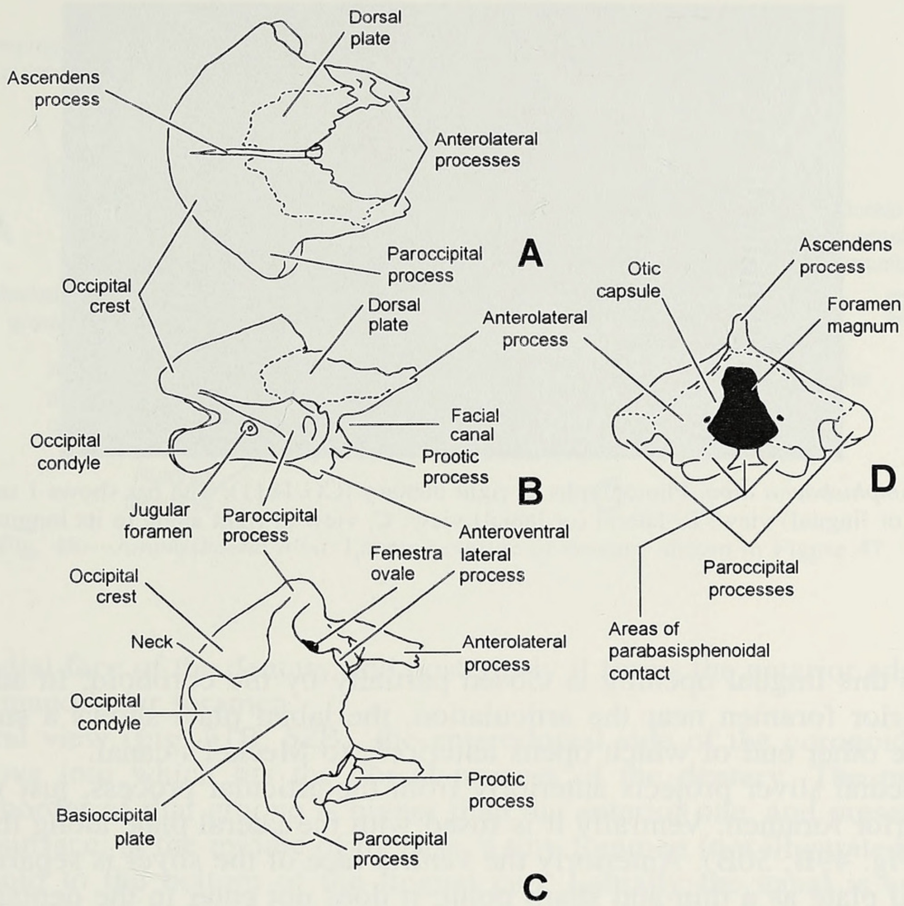

Fig. 46.—*Amphisbaena alba*. Labeled outline of the occipital complex shown in Figure 45.

articular process, a wide triangular lateral plate terminating in a dentary process, and a ventromedial sliver.

The articular process is bent medially, more dorsally than ventrally (i.e., its dorsal borders are closer to the medial plane than the ventral ones). This inclination compensates for the lateral inclination of the articulated mandible (Fig. 7C). The articular and quadrate are equivalently displaced and the entire mandible can close into the V-shaped angle between the maxillae. The posterior articulating head is massive and is ventrally thickened by the base of the ventromedial sliver (Fig. 49B, 50B). The vertical concavity of the articulation surface faces posteriorly and medially, matching the anterior articulation of the quadrate. The articular process is composed of spongy bone (Fig. 55B, 56B), as is an anterior branch extending along the ventral side. The other bony tissues are dense.

The lateral plate of the compound bone comprises most of the lateral side of the posterior mandible (Fig. 49B, 50B). Its concave ventral surface rests upon the ventral process of the dentary (Fig. 49C, 50C). The anterior dentary process extends the labial plate to fit deeply into the posterior cavity of the dentary at the site at which the dorsal border of the lateral plate overlaps the coronoid. Anteriorly to the articular process, the lateral plate is pierced by a posterior mandibular foramen; medially (Fig. 49A, 50A), the aperture opens to the posterior portion of Meckel's canal in the compound bone. The posterior foramen of the lingual side lies dorsal to the posterior base of the ventromedial sliver; in the articulated

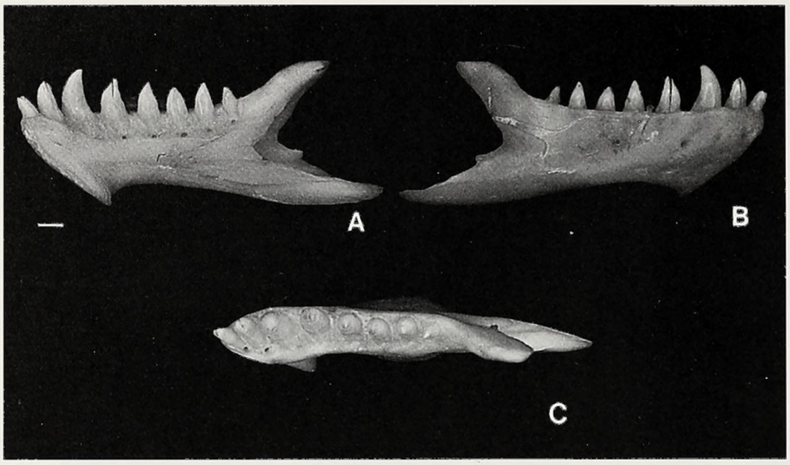

Fig. 47.—*Amphisbaena alba*. Photographs of right dentary (CG 1811). The bar shows 1 mm to scale. A, medial (or lingual) view; B, lateral (or labial) view; C, view at right angle to its longitudinal axis.

mandible this lingual opening is closed partially by the coronoid. In addition to the posterior foramen near the articulation, the labial plate shows a smaller foramen the other end of which opens anteriorly to Meckel's canal.

The medial sliver projects anteriorly from the articular process, just ventral to the posterior foramen. Ventrally it is fused with the lateral plate along the ventral border (Fig. 49B, 50B). Anteriorly the ventral face of the sliver is separated from the lateral plate as a thin and sharp point; it does not enter in the dentary pocket as the lateral plate, but overlaps the medial face of the dentary, covering Meckel's canal posteriorly. The dorsal border of the medial sliver contacts the center of the medial face of the lateral plate (Fig. 49A, 50A), with which has a suture line; the dorsal space left between the sliver and the lateral plate defines a wide longitudinal canal (Meckel's canal) that connects the posterior and central foramina of the medial side of the mandible. The canal of the compound bone is closed lingually by the coronoid and ventrally by the angular.

The compound bone seems to result from fusion of the supra-angular (the labial sliver), the articular (posterior articulation head), the splenial (the labial plate), and the prearticular (the ventral face that joins the supra-angular and splenial). This issue needs further analysis as the bone shows only two dermal ossification centers in embryos of *Amphisbaena darwini* (Montero et al., 1999).

Coronoid.—The flat rectangular coronoid (Fig. 51, 52) shapes the lingual aspect of most of the coronoid process of the mandible. On the lateral face of the mandible it is almost fully covered by the compound bone and dentary. However, it is completely exposed on the medial face of mandible, and anteriorly contacts the dentary, ventrally Meckel's canal (which separates it from the angular), and posteriorly the compound bone. The dentary contact includes a slender anteroventral coronoid process resting upon the medial face of this bone.

The concave medial surface of the coronoid shapes a wide and shallow central cup (Fig. 51A, 52A). The high and broad anterodorsal border of the central cup represents the bottom of the lateral groove that embraces the posterodorsal process of the dentary. The thin ventral border of the coronoid covers the compound bone medially; anteriorly the border contributes to the closure of the central foramina

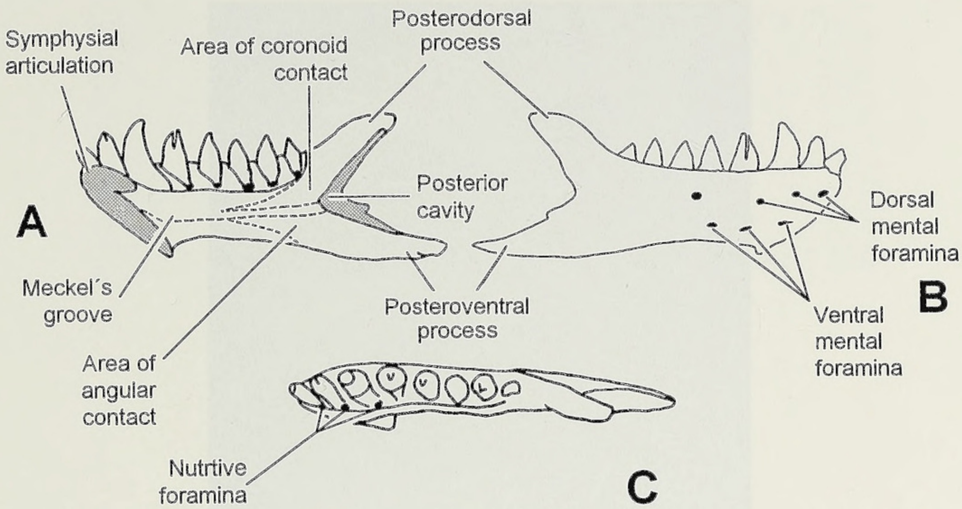

Fig. 48.—*Amphisbaena alba.* Labeled outline of dentary shown in Figure 47.

of the medial face of the dentary and posteriorly it forms the anterior edge of the posterior mandibular foramen.

In lateral view (Fig. 51B, 52B), the anterodorsal side of the coronoid bears a deep groove into which fits the dorsal process of the dentary. The prominent posterior border of that groove is higher than the anterior one, and presents a flat posterior surface; at the middle of its base, a tiny foramen (not illustrated) pierces the coronoid to the bottom of the lingual cup. Labially the canal is continued ventrally by a narrow and deep groove that runs along the posterior border of the lateral groove, ending at the central labial foramina of the mandible.

The anteroventral process of the coronoid is a thin, spear-shaped blade that rests on the labial face of the dentary. The anterodorsal border is straight; the ventral one bears a constriction that is shaped by the dorsal border of the central labial foramina (forming a neck). The ventral border extends straight anteriorly meeting acutely with the dorsal border at the point.

The densely boned coronoid is so identified as it is the main component of the dorsal coronoid process of the mandible.

Angular.—Most of the slender rod-shaped angular (Fig. 53, 54) lies on the medial face of the ventral process of the dentary. Posteriorly the angular twists from the lingual face toward the labial one, passing ventrally along the posterior border of the mandible.

The anterior end of the angular is sharp and acute. At the middle, the angular has a triangular cross section, showing a dorsal border (that anteriorly shapes the ventral border of Meckel's canal, and that posteriorly underlies the compound bone; Fig. 53B, 54B), a lateral face (that rests upon the dentary; Fig. 53C, 54C), and a medial free face (Fig. 53B, 54B). Posteriorly, the medial and lateral faces are obliterated by a ventral face that twists from the lingual to labial side of the mandible (Fig. 53A, 54A). Near the middle of the angular, it is pierced by a foramen from the medial to the dorsal surface; it connects the internal longitudinal canal of the compound bone with the labial surface. As the canal of the angular bifurcates, its labial surface shows two foramina.

The angular is identified with some diffidence as the ventral bony element of the mandibular ramus.

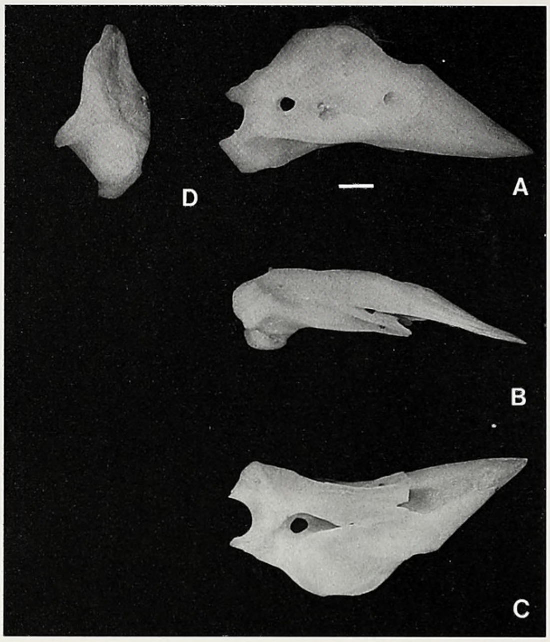

Fig. 49.—*Amphisbaena alba.* Photographs of right compound bone (CG 1811), anterior to the right. The bar shows 1 mm to scale. A, lateral view; B, ventral view; C, medial view; D, posterior view.

Cartilages

Although descriptions of the cranial skeleton commonly emphasize the osseous elements, we here add a short supplemental description of the cartilaginous elements. These are important because of the role of the chondrocranial elements in development, because they have a functional role even in adults, and because cartilages are critical for mechanical function during growth. Consequently, their characterization completes the description of the skeletal structures of the skull. We follow the terminology of Bellairs and Kamal (1981) and Pratt (1948). The following description is based entirely on the serial sections.

The well-developed nasal septum is a narrow (two to five cells wide) plate that lies along at the sagittal plane of the snout, beginning at the level of the premaxilla and nasals anteriorly to terminate posteriorly at a level just anterior to the frontal fenestra. The septum extends dorsoventrally, from the dorsal roof of the snout to the ventral midline between the vomers and palatines. Dorsally, it meets the internasal suture with the premaxillary septum and expands laterally thus forming the parietotectal cartilage which comprises the roof of the nasal capsule.

Anteriorly, the nasal septum sends off anterior branches at the site of contact between the nasals and each branch projects anteroventrally and is continuous with the nasal cupula that surrounds the external nares. The nasal process of the premaxilla separates these branches. The extreme tip of the nasal septum bends ventrally and projects as two posterior rodlike cartilages that are continuous with a cartilaginous concha and an anterodorsal cup inside the cavity of Jacobson's organ.

The nasal capsule is roofed by a poorly developed cartilage that has a large fenestra superior. Laterally, this parietotectal cartilage is continuous with the paranasal cartilage, a cup-shaped lateral plate that forms the lateral wall of the olfactory chamber. The medial cup-shaped projection of the paranasal generates the

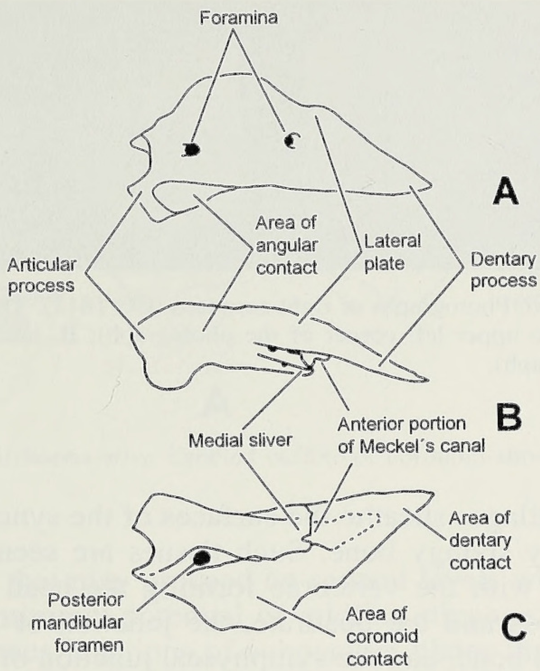

Fig. 50.—*Amphisbaena alba.* Labeled outline of compound bone shown in Figure 49.

hemispherical concha around which lies the very large and anteroposteriorly elongated olfactory chamber. The posterior wall of the olfactory chamber is formed partially by a posterior cartilaginous plate (planum anteorbitale). Medially, the ventral corner of this plate has a rod-shaped paraseptal cartilage that passes anteroventrally, thus running along the medial sides of the vomer to the level of the middle of Jacobson's organ. However, it does not contact the cartilages of Jacobson's organ. Only a sheet of connective tissue separates the brain cavity from the nasal cavities in the frontal fenestra; the cartilaginous planum anteorbitale lies lateral to the frontal fenestra.

Posteriorly, the nasal septum is continued as a thick medial rod, the trabecula communis. This passes between the palatines, just ventral to the frontals; the medial contact of these bones precludes formation of an interorbital septum (Bellairs, 1949), a character unique in amphisbaenians among squamate reptiles. More posteriorly, the trabecula communis passes ventral to the tabulosphenoid. Just anterior to the anterior tip of the parabasisphenoid (that underlies the posterior part of the tabulosphenoid) the trabecula communis splits posterolaterally to form the paired trabeculae. These trabeculae run posteriorly at the sides of the anterior tip of the parabasisphenoid, but terminate just anterior to the posterior border of the tabulosphenoid.

The elements thus far defined are adult remnants of the embryonic chondrocranium. More posteriorly, there are two additional kinds of cartilages, those of the basisphenoid–pterygoid junction, and the epiphyseal ones (Fig. 55, 56).

Sections show that the cartilage of the basisphenoid–pterygoid junction forms a nodule that lies within the former bone at the site at which the shoulders of the pterygoid bend laterally around the latter bone. Whereas the wall of this nodule bulges into the gap between the bones, adult specimens show most of the gap filled by dense connective tissues.

Fig. 51.—*Amphisbaena alba*. Photographs of right coronoid (CG 1811). The bar shows 1 mm to scale. A, medial view (anterior to upper left corner of the photograph); B, lateral view (anterior to upper right corner of the photograph).

The epiphyseal cartilages sheathe the surfaces of the synovial junctions and are generally underlain by spongy bone. Such tissues are seen at the connection of the occipital condyle with the vertebrae forming the head joint, the junction of the paroccipital process and the quadrate, the junction of the quadrate with the mandibular compound bone, and the symphyseal junction of the mandibles (which lacks a synovial cavity). Only the head joint shows cartilaginous or connective tissue menisci.

Cartilage also sheathes the articular surface of the element-X, as seen in sections by the elaborate triradiate synchondrosis (Fig. 55, 56). Together with its spongy internal structure, and the observation of fusion to the parabasisphenoid and the basioccipital plate in the largest adult, this supports the above-mentioned concept that these elements function as epiphyses.

DISCUSSION

Mechanical Framework

The structural pattern of the skull is seen less adequately on the basis of general exposure of the several cranial elements than on three-dimensional reconstruction based on serial sections and consideration of the individual disarticulated bones. The preceding analysis documents that examination only of the surface exposure of the individual cranial elements does not provide sufficient understanding of amphisbaenian skull architecture. Sections and drawings indicate both the nature of inter-element articulations and the pattern of the internal ossifications. Particularly the former is critical as almost all bones form junctions that not only provide abutment with or without minor interconnection but complexly overlap portions of the adjacent bones. This aspect of the cranial architecture of amphisbaenians is characteristic and differs profoundly from that of other squamates.

As noted in earlier papers (cf. Gans, 1974, 1978), the skull is strong and seemingly simple. However, rather than having major cranial elements being composed of single bones that articulate by simple joints involving the edges of plates, the bones overlap and commonly interdigitate; the junctions tend to be three-dimensional and extremely complex. Many of the skeletal elements (premaxilla, tabulosphenoid, parietal, occipital, compound bone) are azygous either due to their intrinsically azygous nature or due to fusion during ontogeny. The anterior portions of the skull are comprised of paired bones; however, these also show a

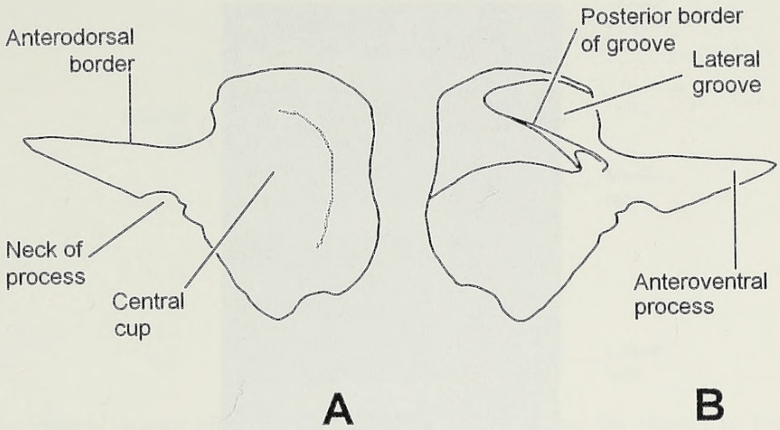

Fig. 52.—*Amphisbaena alba.* Labeled outline of coronoid shown in Figure 51.

complex interlocking that may proceed on several levels within a single junction; interlocking ensures minimal potential of midline slippage.

In some sites one sees junctions of subparallel plates that overlap widely with the contact fields fitted with lands and grooves the axes of which are likely important, as the arrangement thereof (angles between, rather than number of grooves) has low variance. This phenomenon is well demonstrated by the contact zone between parietal and supraoccipital. Simultaneously one sees joints in zones at which the edges of the articulating bones are swollen, and in which the surface of articulation curves and bulges in a three-dimensional array. These curves shift semi-irregularly, with those of the sides being asymmetrical. The surfaces of bony intercalation furthermore may lie near either the deep or superficial surfaces of the bones being joined; they may reach the free surface or be placed within the depth of the bones. The intrinsic irregularity accounts for the differing numbers of projecting fingers on the two sides of the skull (e.g., at the frontal parietal joint).

Unlike the articulation of the elements of the ophidian snout, which provide edge-to-edge or end-to-end contact, the entire elements of the snout of *Amphisbaena alba* tend to be complexly bent. Therefore, one rarely sees simple planar lines that parallel much of the edge between bones (i.e., in the nasomaxillary joint), lines that would mark sites of potential inter-element slippage. Furthermore, this trend is emphasized by the complex bending and projection of the elements. For instance, cranial sections prove to be difficult to interpret, as processes of particular elements may show up multiple times in a sequence, e.g., the frontal–prefrontal–maxilla and the tabulosphenoid–parietal–frontal sequences.

Many of the zones of articulation are narrow and filled with dense, collagenous connective tissue which should preclude significant sliding movements. This is the most common pattern; for instance, it is seen in the frontal–parietal and the medial basisphenoid–basioccipital junctions. In some other cases the crevices are filled with a much wider band of connective tissue; whereas this also may limit slippage, the width of such articulations should be reduced whenever they are loaded in compression. This is seen between the vomer and premaxilla, and in the more lateral part of the basisphenoid–basioccipital junction including its continuation into the edges of the elements-X.

A relatively few articulation zones of adult animals have cartilage (details be-

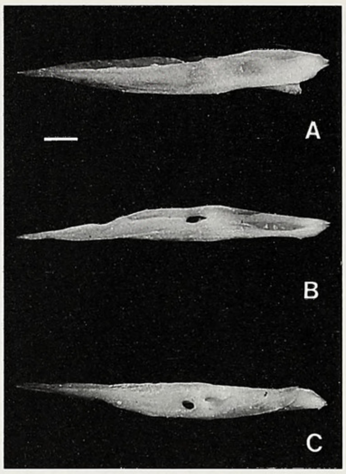

Fig. 53.—*Amphisbaena alba.* Photographs of right angular (CG 1811). Anterior to the left. The bar shows 1 mm to scale. A, ventral view; B, medial view; C, lateral view.

low). This cartilage may be in nodular form as in the zone in which the pterygoid contacts the basisphenoid. Also, several joint surfaces may be lined with a thin layer of hyaline cartilage. Such areas occur whenever the joints involve synovial cavities and probably contribute to the addition of lubricating fluids. Beyond this, the compressibility of the cartilage assures congruence (parallel shape) of the sliding surfaces as the rotating elements move past each other. Consequently, cartilaginous areas facilitate rotational movements in zones being loaded in compression normal to the surface. The three main sets of synovial cavities are that at the head joint between the vertebrae and the occipital condyle, that between the paroccipital process and the quadrate, and that between the quadrate and the articular surface of the mandible.

What is even more critical is that most of the sites involving the application of normal compressive forces are, in all but the largest specimens, underlain by spongy bone. This suggests that throughout the process of growth the combination of synovial cavity, cartilage, and spongy bone represents a complex that permits joints to be loaded during rotation.

An overview of the skull thus indicates that it represents a tubular structure which is approximately six times as long as its narrowest dorsoventral or lateral extent. The anterior elements consist of solid lamellar bones that are interlocked as described above. In several cases these bones show local thickenings with the deep and superficial surfaces providing projecting processes that overlap adjacent elements (e.g., maxilla and prefrontal, nasal with premaxilla anteriorly and with frontal posteriorly). Hence the snout forms a compression-resistant wedge, although its articulation at the frontal level is looser than at other sites.

From the frontal to the occipital levels all elements form a heavily walled tube, with the walls approximately parallel to the long axis. The bones are dense and lamellar and even at their complex sites of interlocking (e.g., dorsoventral between parietal and tabulosphenoid, anteroposterior between frontals and parietal) have almost no sponginess. Such a heavily walled tube has substantial resistance to compressive and torsional loading, as well as to the associated buckling. The noncircular construction of the tube increases its resistance to bending about the

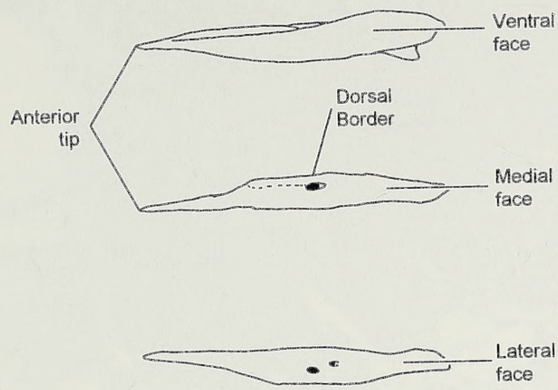

Fig. 54.—*Amphisbaena alba*. Labeled outline of right angular shown in Figure 53.

dorsoventral axis. A supplemental resistance to bending is produced both by the parietal–occipital keel and by the firmly associated pterygoids.

The complex occipito–otic element shows the combination of multiple influences. The central zone serves as a shell for the central nervous system and the lateral elements for the otic complex. In terms of mechanical function the central–medial zone involves a posterior prolongation of the compression-resistant tube. This would allow transmission of straight tunneling forces. The laterally flaring paroccipital processes allow some of the backward-directed compressive forces resulting from a push of mandible against the substratum to be opposed by forces acting on the occipital condyles. The angulations of the bilateral sutures allow resistance to rotational forces whenever torsion is imposed by the trunk and exerted by the snout. As noted in earlier reports (cf. Gans, 1974), the skull is also capable of resisting bending along the nasal–frontal level during bites. It is clear that we are here dealing with a primary chain of sequential compressive elements, as documented by the occurrence of three sequential synovial joints and three sets of cartilage plates.

Cranial Kinesis

Various authors (Versluys, 1898; Kritzinger, 1946; Vanzolini, 1955; Romer, 1956) have referred to cranial kinesis in the amphisbaenians; in some cases, there is reference to the conditions in juvenile skulls. However, other studies (e.g., Gans, 1960) have suggested that adult kinesis is most unlikely, in part because the articulation of the fronto–parietal joint involves two axes. However the possible degrees of freedom are greatest at the naso–frontal junction which, however, is stabilized by the complex prefrontal.

The present observations do not eliminate the possibility of some cranial flexibility in adults, but severely restrict it. The fronto–parietal joint is very solid and the possibility of slippage between parietal and tabulosphenoid is limited by the sturdy anterior, lateral, and posterior articulations. The nasal capsule does not permit significant internal movement nor does it allow much movement on the frontals. The premaxilla, nasals, maxillae, and prefrontals are solidly interlocked with each articulation folded to involve two or more planes. Ventrally, the palatines are overlapped by vomers and frontals. Also, the palato–pterygoid joints overlap significantly; their fluted interdigitation may allow only a most limited anterior–posterior sliding.

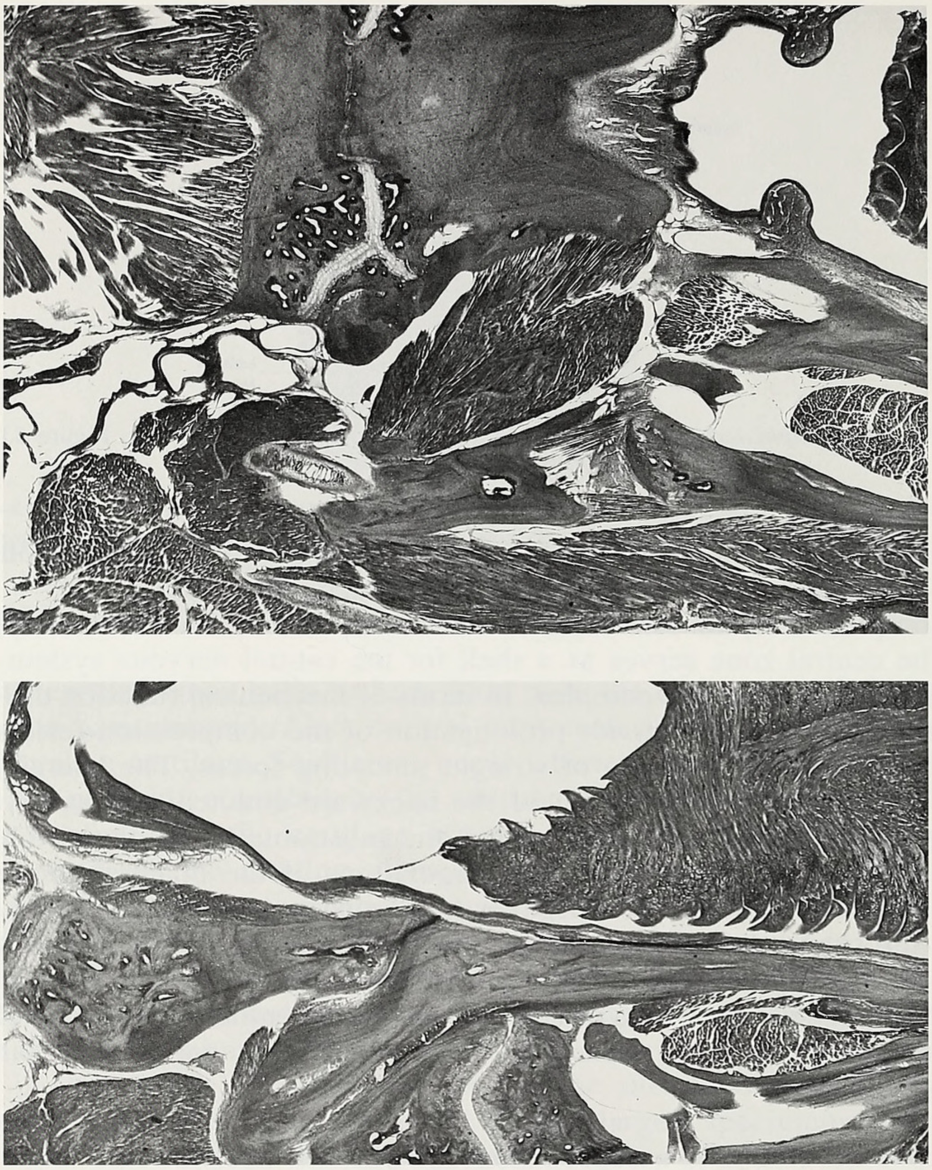

Fig. 55.—*Amphisbaena alba.* Details of horizontal serial sections to show cartilaginous contributions to various joints (E. G. Wever slide set 1667). A, detail of basipterygoid (slide 173); B, detail of tight joint between basioccipital and basisphenoid, as well as more lateral chondrosis, splitting to form the outline of the element-X (slide 194). Use Figure 56 for scale.

The anterior attachment of the vomers is relatively loose and ligamentous, which might allow some minor slippage that could be transmitted to the quadrate by the palato–pterygoid chain. Consequently, the slippage likely would be transmitted to the shaft of the quadrate and some equivalent movement would have to permit rotation of the parabasi–pterygoid joint. This slippage could be lateral instead of anteroposterior; however, examination of the serial sections suggests that flexibility of the connective tissues in the narrow slit would be limited (Fig. 55, 56). The issue is complicated because the vomer is much more slender than the other bones in the chain; flexibility might involve bending and rotation within elements. The bending of the vomer could press on the capsule of Jacobson's

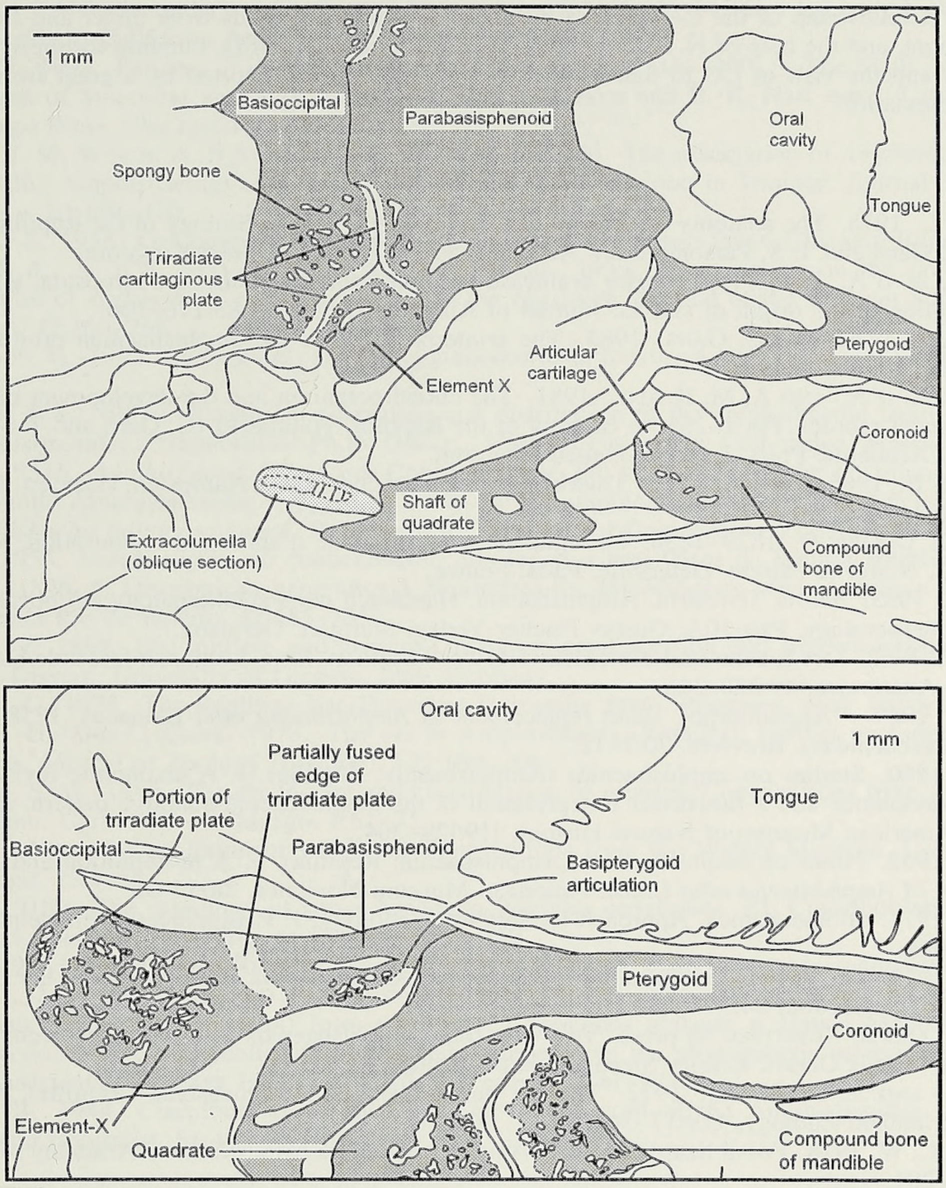

Fig. 56.—*Amphisbaena alba.* Labeled outline of horizontal serial sections shown in Figure 55.

Organ and tend to extrude its contents, as postulated for Monopeltis by Kritzinger (1946).

Rather than considering kinesis to be involved primarily in anteroposterior displacements within parasagittal planes, it may be useful to consider lateral movements. For example, rotation of the head of the quadrate might laterally displace the posterior wing of the pterygoid; however, the symphyseal fusion of the mandibles would limit this and would also limit the facility of the edges of the pterygoid in assisting ingestion and swallowing.

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LITERATURE CITED

BAIRD, I. L. 1978. The anatomy of the reptilian ear. Pp. 193–275, *in* Biology of the Reptilia, Volume 2 (C. Gans and T. S. Parsons, eds.). Academic Press, London, United Kingdom.

BELLAIRS, A. D'A. 1949. The anterior braincase and interorbital septum of Sauropsida, with a consideration of the origin of snakes. Journal of Anatomy (London), 83:116–146.

BELLAIRS, A. D'A., AND C. GANS. 1983. The reinterpretation of the amphisbaenian orbitosphenoid. Nature, 302:243–244.

BELLAIRS, A. D'A., AND A. M. KAMAL. 1981. The chondrocranium and the development of the skull in Recent reptiles. Pp. 1–263, *in* Biology of the Reptilia, Volume 11 (C. Gans and T. S. Parsons, eds.). Academic Press, London, United Kingdom.

BRÜHL, C. B. 1886. Zootomie aller Thierklassen für Lernende, nach Autopsien, skizziert. Hoelderer, Vienna, Austria.

CUVIER, G. L. C. F. D. 1829–1830. La règne animale, distribué d'après son organisation, Volumes 2 and 3, Nouvelle édition. Deterville, Paris, France.

ESTES, R. 1983. Sauria Terrestria, Amphisbaenia. Handbuch der Paläoherpetologie/Encyclopedia of Paleoherpetology, Part 10A. Gustav Fischer Verlag, Stuttgart, Germany.

FIORINI, P. 1962. Der Eizahn und die Eischwiele der Reptilien. Eine zusammenfassende Darstellung. Acta Anatomica, 49:328–366.

GANS, C. 1957. "Anguimorph" tooth replacement in *Amphisbaena alba* Linnaeus, 1758 (Reptilia: Amphisbaenidae). Breviora, 70:1–12.

———. 1960. Studies on amphisbaenids (Amphisbaenia: Reptilia). 1. A taxonomic revision of the Trogonophinae and a functional interpretation of the amphisbaenid adaptive pattern. Bulletin of the American Museum of Natural History, 119:129–204.

———. 1962. Notes on amphisbaenids (Amphisbaenia: Reptilia). 5. A re-definition and a bibliography of *Amphisbaena alba* Linné. American Museum Novitates, 2105:1–31.

———. 1974. Biomechanics. Approach to Vertebrate Biology. J. P. Lippincott, Philadelphia, Pennsylvania.

———. 1978. The characteristics and affinities of the Amphisbaenia. Transactions of the Zoological Society of London, 34:347–416.

GANS, C., AND R. MONTERO. In press. Two new fossil amphisbaenids from the Pleistocene of Lagoa Santa (Minas Gerais, Brasil). Steenstrupia (Copenhagen).

GANS, C., AND E. G. WEVER. 1972. The ear and hearing in Amphisbaenia (Reptilia). Journal of Experimental Zoology, 179:17–34.

GILMORE, C. W. 1928. Fossil lizards of North America. Memoirs of the National Academy of Sciences, 22:1–201.

GREER, A. 1970. A subfamilial classification of scincid lizards. Bulletin of the Museum of Comparative Zoology, 139:151–184.

JOLLIE, M. T. 1960. The head skeleton of the lizard. Acta Zoologica, 41:1–64.

KESTEVEN, L. 1957. Notes on the skull and cephalic muscles of the Amphisbaenia. Proceedings of the Linnean Society of New South Wales, 82:109–116.

KRITZINGER, C. C. 1946. The cranial anatomy and kinesis of the south African amphisbaenid *Monopeltis capensis* Smith. South African Journal of Science, 42:175–204.

LAKJER, T. 1927. Studien über die Gaumenregion bei Sauriern im Vergleich mit Anamniern und primitiven Sauropsiden. Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Thiere, 49:57–356.

LOEB, G. E., AND C. GANS. 1986. Electromyography for Experimentalists. University of Chicago Press, Chicago, Illinois.

MAY, E. 1978. Zur Kenntnis der Entwicklung des Schaedels von *Leposternon microcephalum* Wagler, 1824 (Reptilia: Amphisbaenia). Senckenbergiana biologie, 59:41–69.

MCDOWELL, S. B., AND C. M. BOGERT. 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. Bulletin of the American Museum of Natural History, 105:1–142.

MONTERO, R., C. GANS, AND M. L. LIONS. 1999. Embryonic development of the skeleton of *Amphisbaena darwini heterozonata* (Squamata: Amphisbaenidae). Journal of Morphology, 239:1–25.

PRATT, C. W. 1948. The morphology of the ethmoidal region of *Sphenodon* and lizards. Proceedings of the Royal Society of London, 118:171–201.

PRESCH, W. 1976. Secondary palate formation in microteiid lizards (Teiidae: Lacertilia). Bulletin of the Southern California Academy of Science, 75:281–283.

RIEPPEL, O. 1993. Patterns of diversity in the reptilian skull. Pp. 344–390, *in* The Skull. Volume 2: Patterns of Structural and Systematic Diversity (J. Hanken and B. K. Hall, eds.). University of Chicago Press, Chicago, Illinois.

RILEY, J., J. M. WINCH, A. F. STIMSON, AND R. D. POPE. 1986. The association of *Amphisbaena alba* (Reptilia: Amphisbaenia) with the leaf-cutting ant *Atta cephalotes* in Trinidad. Journal of Natural History, 20:459–470.

ROMER, A. S. 1956. Osteology of the Reptiles. University of Chicago Press, Chicago, Illinois.

SMITH, M. A., A. D'A. BELLAIRS, AND A. E. W. MILES. 1953. Observations on the premaxillary dentition of snakes with special reference to the egg-tooth. Journal of the Linnean Society (Zoology), 42:260–268.

UNDERWOOD, G. 1957. *Lanthanotus* and the anguinomorphan lizards: A critical review. Copeia, 1957: 20–30.

VANZOLINI, P. E. 1951*a*. Evolution, adaptation and distribution of the amphisbaenid lizards (Sauria: Amphisbaenidae). Unpublished Ph.D. Dissert., Harvard University, Cambridge, Massachusetts.

———. 1951*b*. *Amphisbaena fuliginosa.* Contribution to the knowledge of the brazilian lizards of the family Amphisbaenidae Gray 1825. 6. On the geographical distribution and differentiation of *Amphisbaena fuliginosa* Linné. Bulletin of the Museum of Comparative Zoology, 106:1–67.

———. 1955. Contribuiçoes ao conhecimento dos lagartos brasileiros da familia Amphisbaenidae Gray, 1825. 5. Distribuiçao geografica e biometrica de *Amphisbaena alba.* Arquivos do Museo Nacional Rio de Janeiro, 42:683–705.

VERSLUYS, J. 1898. Die mittlere und äussere Ohrsphäre der Lacertilia und Rhynchocephalia. Inaugural-Dissert., University of Giessen, Jena, Germany.

WEVER, E. G. 1978. The Reptilian Ear. Princeton University Press, Princeton, New Jersey.

WEVER, E. G., AND C. GANS. 1973. The ear in Amphisbaenia (Reptilia): Further anatomical observations. Journal of Zoology (London), 171:189–206.

WILLISTON, S. W. 1917. The phylogeny and classification of reptiles. Contributions from the Walker Museum, University of Chicago, 2:61–71.

———. 1918*a*. The evolution of vertebrae. Contributions from the Walker Museum, University of Chicago, 2:75–85.

———. 1918*b*. The osteology of some American Permian vertebrates. III. Contributions from the Walker Museum, University of Chicago, 2:87–112.

———. 1925. Osteology of Reptiles. Harvard University Press, Cambridge, Massachusetts.

WU, X.-C., D. B. BRINKMAN, AND A. P. RUSSELL. 1996. *Sineoamphisbaena hexatabularis,* an amphisbaenian (Diapsida: Squamata) from the Upper Cretaceous redbeds at Bayan Mandahu (Inner Mongolia, People's Republic of China), and comments on the phylogenetic relationships of the Amphisbaenia. Canadian Journal of Earth Sciences, 33:541–577.

ZANGERL, R. 1944. Contributions to the osteology of the skull of the Amphisbenidae. American Midland Naturalist, 31:417–454.