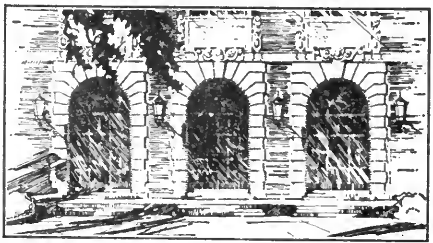


FIELDIANA
Zoology

Published by Field Museum of Natural History

VOLUME 59, No. 2

THE VIPERID SNAKE *AZEMIOPS*:
ITS COMPARATIVE CEPHALIC ANATOMY AND PHYLOGENETIC POSITION IN RELATION TO VIPERINAE AND CROTALINAE

KARAL F. LIEM
HYMEN MARX
and
GEORGE B. RABB

JUNE 30, 1971

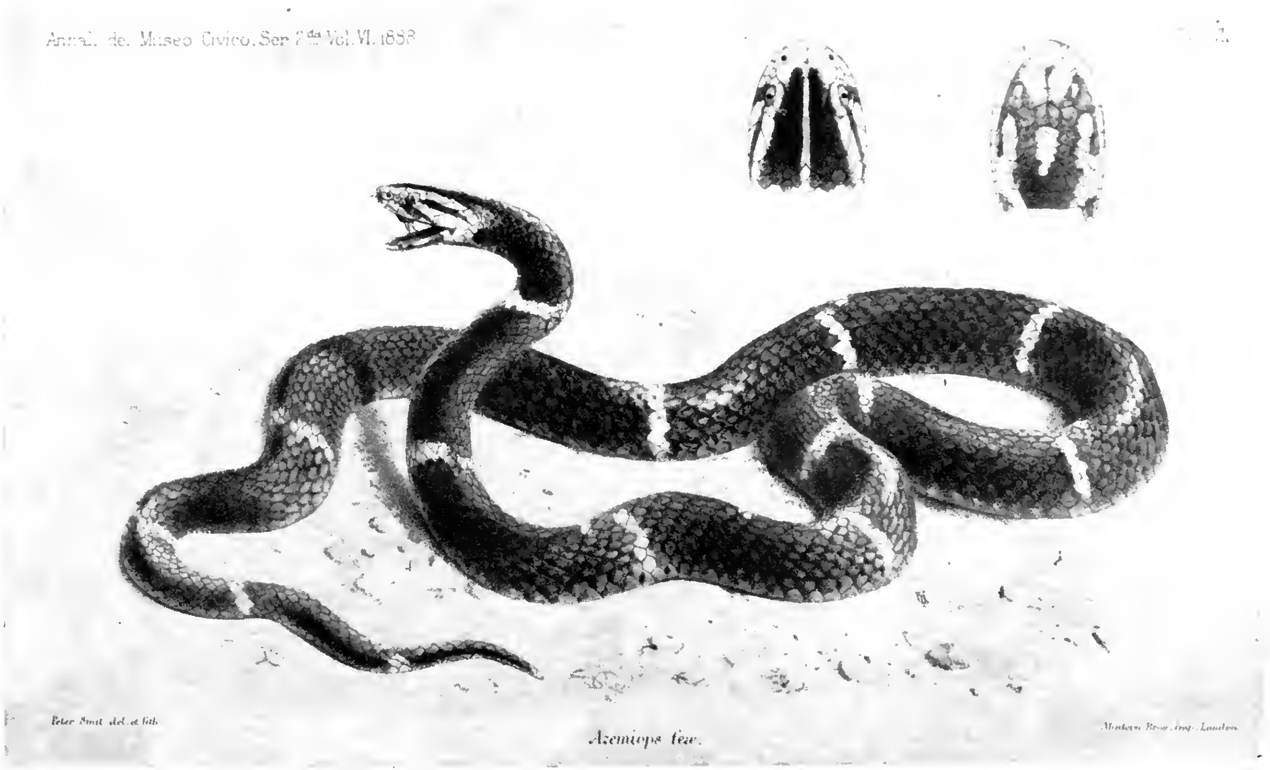


PLATE I. *Azemiops feae* (from Boulenger, 1888, plate 7).

FIELDIANA
Zoology

Published by Field Museum of Natural History

VOLUME 59, No. 2

THE VIPERID SNAKE *AZEMIOPS*:
ITS COMPARATIVE CEPHALIC ANATOMY AND PHYLOGENETIC POSITION IN RELATION TO VIPERINAE AND CROTALINAE

KAREL F. LIEM
Associate Curator, Division of Anatomy
and
Associate Professor, Department of Anatomy
University of Illinois Medical Center, Chicago

HYMEN MARX
Associate Curator, Division of Amphibians and Reptiles

and

GEORGE B. RABB
Research Associate, Division of Amphibians and Reptiles
and
Associate Director, Research and Education
Chicago Zoological Society, Brookfield

JUNE 30, 1971

PUBLICATION 1126

Patricia M. Williams
Editor

Library of Congress Catalog Card Number: 77–156801

PRINTED IN THE UNITED STATES OF AMERICA
BY FIELD MUSEUM PRESS

TABLE OF CONTENTS

INTRODUCTION

Despite their fascination for mankind, the venomous snakes remain incompletely known as to numbers of species, relationships within and among families, and even the basic anatomy of the venom-injecting apparatus. This paper is concerned with using anatomical materials to help unravel one of the evolutionary puzzles in the viperid snakes. It is an outgrowth of a taxonomic study of the viperine snakes by Marx and Rabb (1965), who commented on relationships of three odd, apparently primitive genera: *Causus, Azemiops,* and *Atractaspis.* Except for *Causus,* the anatomy of these forms was little known at the time. Bourgeois (1965) has since established that *Atractaspis,* although possessing a folding-fang venom-injection apparatus, is not a viper but rather has aparallactine colubrid affinities, a viewpoint further substantiated by the work of Kochva et al. (1967) and McDowell (1968). We have subsequently concentrated attention on *Azemiops,* a rare monotypic genus from temperate montane areas of southeastern Asia (Boulenger, 1888; Pope, 1935; Bourret, 1936).

The primitive nature of *Azemiops* is reaffirmed in a concurrent study of various skeletal and integumental characters in taxa representing all the advanced snake groups (Marx and Rabb, in press). To elucidate the position of *Azemiops* among the Viperidae, we have examined in detail parts of the head musculature and certain skull elements. The descriptions form the bulk of this paper. The study includes functional interpretations of the morphology, which we believe contribute to a fuller understanding of the mechanics and evolution of the viperid skull. Analysis of our findings as a whole indicates a distinctive intermediate phylogenetic position for *Azemiops.* We propose that this position be recognized by establishing a separate subfamily to contain this singular genus.

CRANIAL OSTEOLOGY

We follow the nomenclature of Brattstrom (1964), with some minor exceptions. The subdivision of the skull into major components is based on Frazzetta (1959, 1966). There are numerous practical difficulties in describing a highly kinetic skull in meaningful functional subdivisions in a consistent and objective way. We have chosen to follow Frazzetta's method because of its practical usefulness in functional analysis, although Dullemeijer's concept (1956, 1958, 1959) has broader theoretical implications. Recently, Gans (1969) has proposed a new term, the mechanical unit, with the following definition: an assemblage of structural elements that share limited degrees of internal movement. However, the determination of the degree of internal movement and the subsequent delineation of the boundaries of the different mechanical units requires a much more thorough functional analysis than is possible with the extremely rare *Azemiops*. We are therefore following the more conventional approach, which has been widely used by recent authors dealing with functional cephalic anatomy of snakes (e.g., Albright and Nelson, 1959a, b; Boltt and Ewer, 1964; Bourgeois, 1965; Frazzetta, 1966).

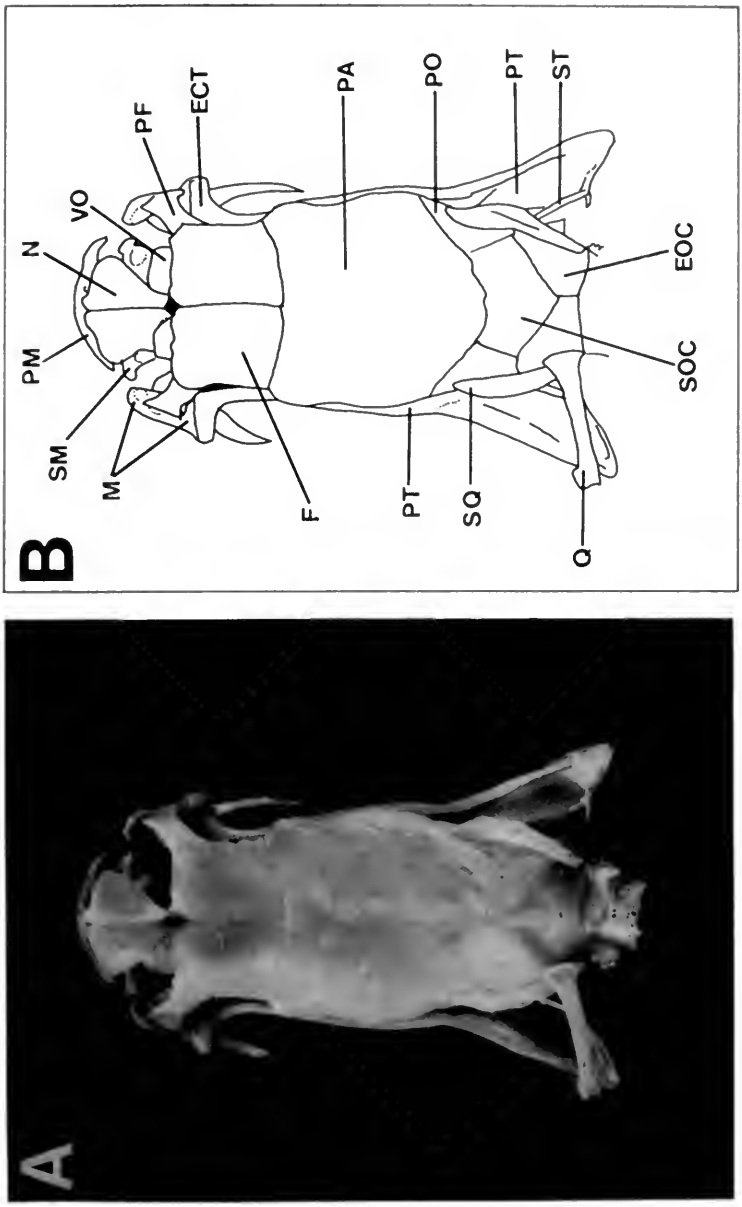
BRAINCASE OR CEREBRAL SKULL

The braincase, including the otic region, is somewhat cylindrical. The roof is flat, the sidewalls convex, and the ventral aspect is characterized by a rather complex relief.

Frontals.—The frontals (figs. 1–4:F) form slightly less than the anterior one-third of the roof of the braincase. On the dorsal surface, anterolaterally each frontal joins the prefrontal along a V-shaped syndesmosis, and posteriorly meets the parietal at a

---

FIG. 1. A. Photograph of dorsal aspect of skull of *Azemiops feae* (USNM 84363). B. Outline drawing adapted from the photograph: Right quadrate has been removed. Abbreviations: ECT, ectopterygoid; EOC, exoccipital; F, frontal; M, maxilla; N, nasal; PA, parietal; PF, prefrontal; PM, premaxilla; PO, prootic, PT, pterygoid; Q, quadrate; SM, septomaxilla; SOC, supraoccipital; SQ, squamosal; ST, stapes; VO, vomer. Total length of skull, 15.7 mm.


A
B
PM
SM
M
N
VO
PF
ECT
F
PA
PT
PO
SQ
PT
ST
Q
SOC
EOC

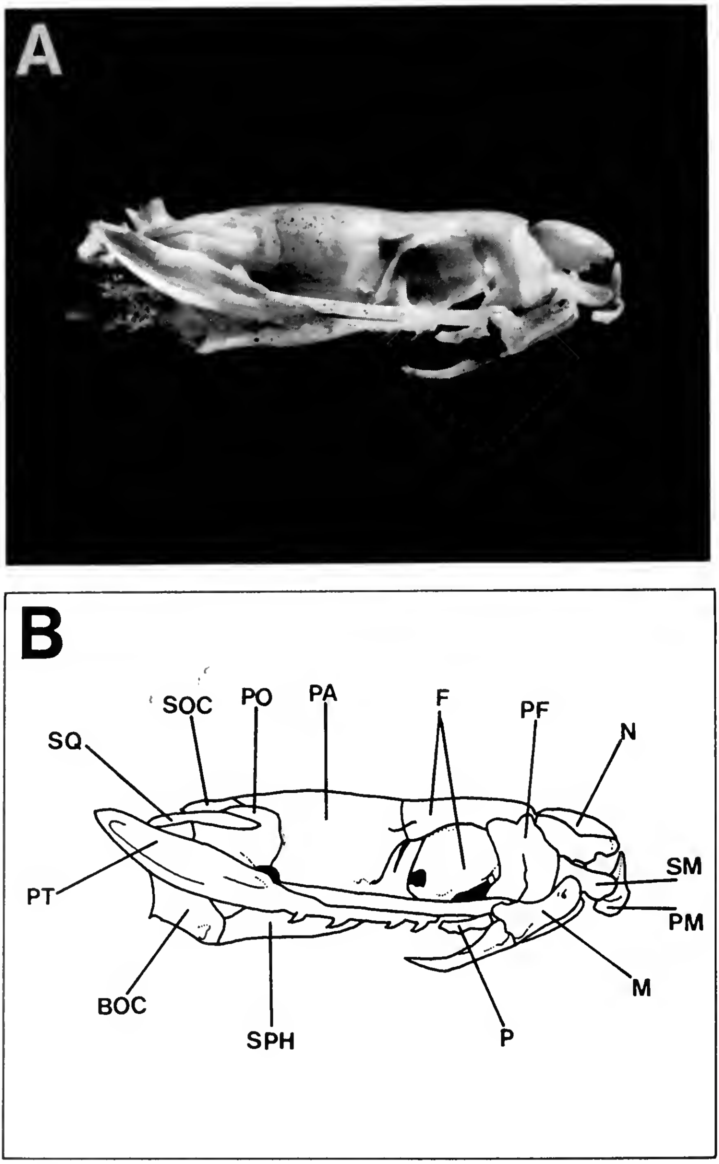


FIG. 2. A. Photograph of lateral aspect of the skull of *Azemiops*. B. Outline drawing adapted from the photograph. Postfrontal and quadrate have been removed. Pterygoid and palatine are separated artificially. Abbreviations: BOC, basioccipital; F, frontal; M, maxilla; N, nasal; P, palatine; PA, parietal; PF, prefrontal; PM, premaxilla; PO, prootic, PT, pterygoid; SM, septomaxilla; SOC, supraoccipital; SPH, sphenoid complex; SQ, squamosal.

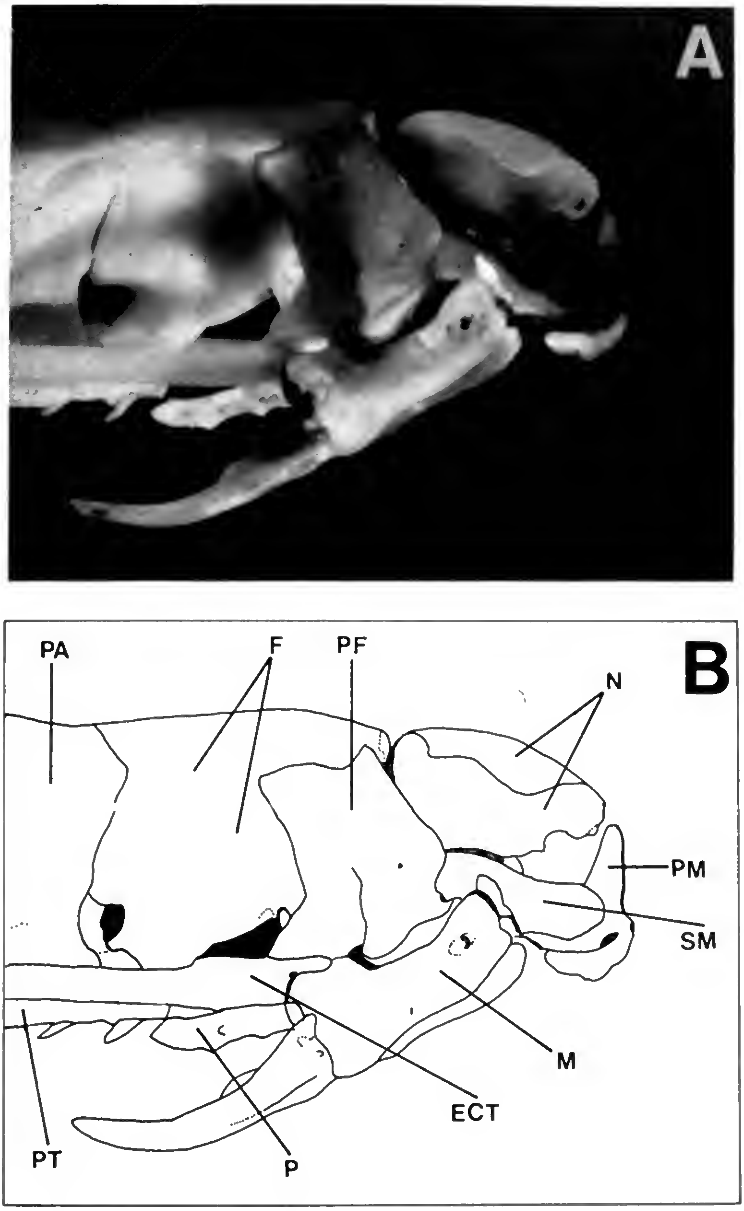
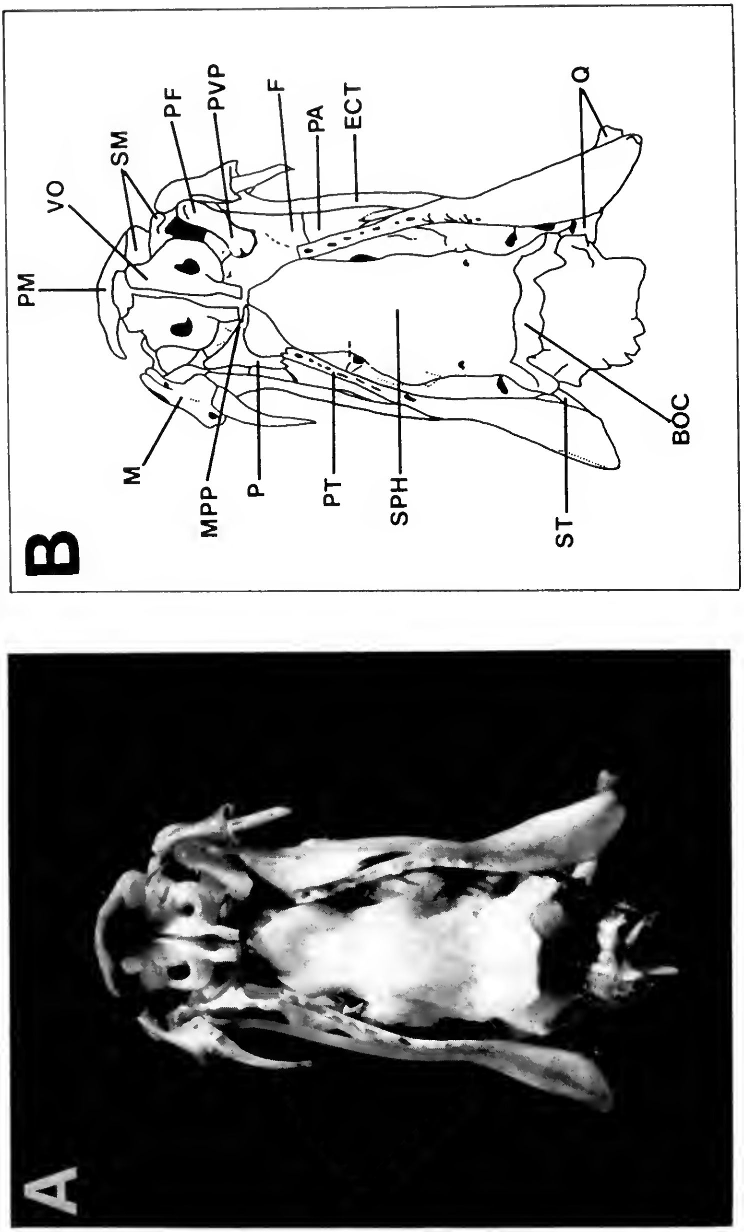


FIG. 3. A. Photograph of lateral aspect of the anterior part of the skull of *Azemiops*. B. Outline drawing adapted from the photograph. Separation of pterygoid and palatine is artificial. Abbreviations: ECT, ectopterygoid; F, frontal; M, maxilla; N, nasal; P, palatine; PA, parietal; PF, prefrontal; PM, premaxilla; PT, pterygoid; SM, septomaxilla.


A
B
PM
VO
SM
PF
PVP
F
PA
ECT
Q
M
MPP
P
PT
SPH
ST
BOC

slightly curved suture. Each frontal extends ventrally to join the anterior portion of the dorsal aspect of the parasphenoid-basisphenoid complex. The frontal forms the major portion of the medial wall of the bony orbit. The posteroventral corner of the orbital portion of the frontal is distinctly notched to form the anteromedial half of the rim of the optic foramen. On the anterior face, a large vacuity forms the olfactory or ethmoid foramen (fig. 5:OF); lateral to it a wing of the frontal extends across the mid-medial surface of the prefrontal (fig. 5:ML). Dorsally the frontal has a close ligamentous connection with the nasal. The ventral anteromedial corner of the frontal is joined loosely to the nasal. Lateral to the ventral nasal articulation, the frontal meets the posterior process of the septomaxilla. A rounded parasagittal ridge runs forward from the sphenoid border on the ventral surface of the frontal. The frontal does not articulate with the postfrontal (postorbital).

Parietal.—The parietal (figs. 1–4:PA) forms the largest part of the cranial roof. It is bordered anteriorly by the frontals, posteriorly by the supraoccipital and the prootic, and ventrally by the parasphenoid-basisphenoid complex. The anterolateral corner of the parietal has a distinct groove in which the dorsal part of the postfrontal is lodged. The attachment between parietal and postfrontal is very loose. In the orbit the descending lamina of the parietal forms the lateral margin of the optic foramen.

Prefrontals.—Each prefrontal (figs. 1–4:PF) is a large bone which forms the anterior bony wall of the orbit. The posterior surface of the prefrontal is concave, the ventral surface flat, while the lateral surface is convex. It articulates with the frontal dorsally and medially and with the maxilla anteroventrally. The lateral aspect of the anteroventral corner of the prefrontal is differentiated into a distinct condyle that forms a joint with the maxilla. Medial to the condyle is a shallow, elongate fossa which lodges a corresponding crest on the maxilla. The dorsal junction with the frontal is V-shaped with the prefrontal having short limbs of equal lengths (fig. 3).

FIG. 4. A. Photograph of ventral aspect of the skull of *Azemiops*. B. Outline drawing adapted from the photograph. Right quadrate and left palatine have been removed. Abbreviations: BOC, basioccipital; ECT, ectopterygoid; F, frontal; M, maxilla; MPP, medial process of palatine; P, palatine; PA, parietal; PF, prefrontal; PVP, posteroventral medial process of prefrontal; PM, premaxilla; PT, pterygoid; Q, quadrate; SM, septomaxilla; SPH, sphenoid complex; ST, stapes, VO, vomer.

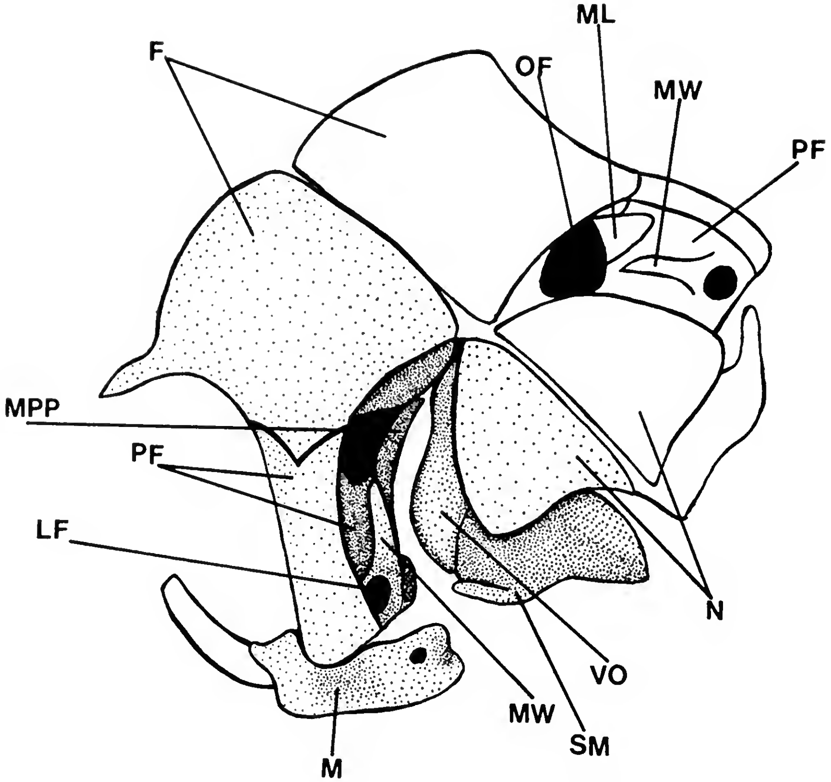


FIG. 5. Anterodorsolateral view of the anterior portion of the skull of *Azemiops*. Right side shaded. Premaxilla not included. Abbreviations: F, frontal; ML, midlateral wing of frontal; M, maxilla; MPP, medial (choanal) process of palatine; MW, medial wing of the prefrontal; N, nasal; LF, lacrimal foramen; PF, prefrontal; OF, olfactory foramen; SM, septomaxilla; VO, vomer.

A large lacrimal foramen is present on the anteromedial aspect of the prefrontal (fig. 5:LF). Just medial to the lacrimal foramen is a prominent, but slender, elongate process, the medial wing of the prefrontal (fig. 5:MW). It extends nearly vertically from the medial wall of the lacrimal foramen in a dorsomedial direction.

Posteroventrally the prefrontal projects as a large process extending posteromedially. It becomes nearly horizontal distally (fig. 4:PVP). The distal margin of the process is somewhat scalloped and has one deep and very narrow indentation (USNM 84363). The ventral surface of this posteroventromedial process of the prefrontal overlies the dorsal surface of the palatine, including the proximal section of the choanal process.

Postfrontals.—Each relatively small postfrontal (fig. 8:POF) is roughly sickle-shaped. The bone forms the posterior margin of the orbit. It is lodged in a fossa in the anterolateral expansion of the parietal. The connection between postfrontal and parietal is very loose, causing the former to be lost in two skull preparations examined. The postfrontal does not articulate with the frontal.

Supraoccipital.—There is one large, heart-shaped supraoccipital (figs. 1, 2:SOC), which is suturally united with the parietal anteriorly, with the prootics laterally, and the exoccipitals posteriorly. The junction between supraoccipital and parietal is a syndesmosis, but there is no fusion of the two bones.

Exoccipitals.—The two exoccipitals (which are indistinguishably fused with the opisthotics) form the posterior boundary of the roof of the braincase (fig. 1:EOC). The exoccipitals meet in the dorsal midline posterior to the supraoccipital. The exoccipitals, together with the basioccipital, surround the foramen magnum. Anteriorly the exoccipital is connected to the supraoccipital, laterally to the prootic, and ventrally to the basioccipital. The exoccipitals, together with the basioccipital, form the occipital condyle. Only the outer portions of the occipital condyle are formed by the exoccipitals.

Basioccipital.—The large basioccipital (fig. 2:BOC) articulates with the sphenoid complex anteriorly and with the exoccipitals and prootics dorsally. It forms the ventral margin of the foramen magnum. The basioccipital contributes to the major, median portion of the occipital condyle. A spinous median ventral process is absent, but there are three knobby points in a transverse row near the sphenoid suture. The bone forms the posterior part of the cranial base, the larger part of which is formed by the sphenoid complex.

Prootics.—Each large prootic (figs. 1, 2:PO) forms slightly less than half of the lateral wall of the braincase. Anteriorly the prootic is joined to the parietal, medially to the supraoccipital, posteriorly to the exoccipital, ventrally to the basioccipital and the sphenoid complex. The squamosal is loosely connected to the prootic by a ligament, which prevents ventral excursion of the squamosal. The prootic contains anterior and posterior prootic foramina. Between the foramina is a distinct bony crest. The anterior foramen accommodates the maxillary division of the trigeminal nerve and a small branch of the facial carotid artery, while the posterior foramen

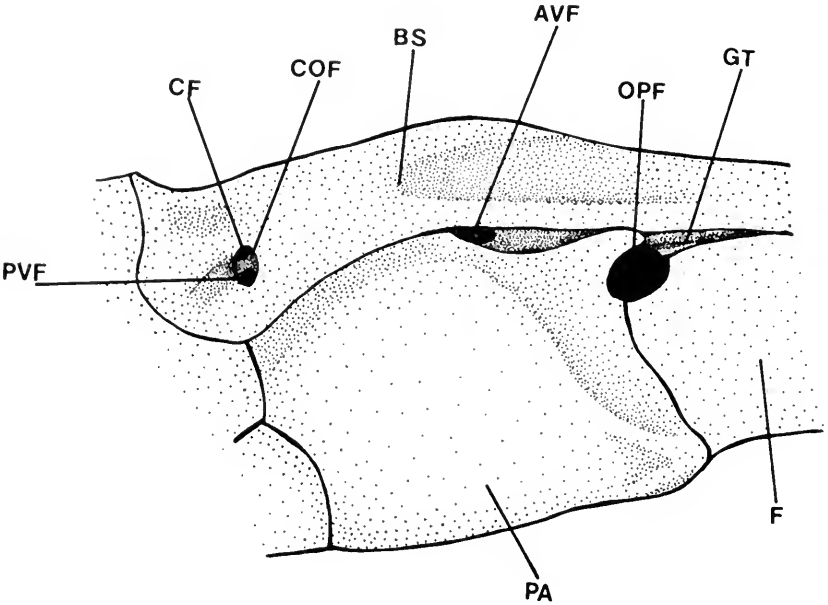


FIG. 6. Ventrolateral view of part of braincase of *Azemiops*. Abbreviations: AVF, anterior Vidian foramen; BS, basisphenoid; CF, cerebral foramen; COF, common foramen; F, frontal; GT, groove for trabecula; OPF, optic foramen; PA, parietal; PVF, posterior Vidian foramen.

contains the facial nerve and the mandibular division of the trigeminal nerve and a small branch of the facial carotid artery to the brain.

Sphenoid complex.—The sphenoid complex (fig. 4:SPH) is ontogenetically composed of the parasphenoid and basisphenoid, but the two components are completely fused in the adult. The sphenoid complex is suturally united with the frontal anterodorsally, the parietal and prootic dorsally, and the basioccipital posteriorly. Its broad anterior part (fig. 4) is separated from the snout complex by the ventral surface of the frontal. The sphenoid complex forms the major portion of the cranial base and lacks a median ventral process. The parasphenoid serves as the ventral bony floor of the optic foramen, although the cartilaginous trabecula clearly forms the external ventral border of the foramen.

Posterolaterally, and symmetrically on each side, the basisphenoid possesses an ovoid foramen of which the long axis is transversely oriented (fig. 6:COF). This foramen functions as a common opening for the cerebral foramen and the posterior Vidian foramen (fig. 6:CF, PVF). Posterior to the optic foramen (fig.

6:OPF) and between the parietal and basisphenoid, is a relatively large opening, the anterior Vidian foramen (fig. 6:AVF).

Columella.—The stapes is an elongate rodlike bone (figs. 1, 4:ST) extending posteriorly and laterally from a circular footplate covering the fenestra ovalis to a distal expansion which fits in a nodular fossa on the quadrate.

SNOUT COMPLEX

The seven bone complex is composed of the premaxilla, nasals, septomaxillae, and vomers. This unit has been called snout complex by Frazzetta (1959) and the ethmoidal region by Dullemeijer (1956).

Nasals.—The dorsal part of each nasal (figs. 1–3:N) is a thin, flat bone slightly curved laterally and anteriorly. The nasal has a vertical, ventrally directed, descending (or medial) lamella. There is a slight embayment of the posterior margin of the descending lamella. However, this margin is closely juxtaposed to the corresponding medial lamella of the frontal, with a close ligamentous connection dorsally as well as a close ventral junction in fibrous connective tissue. At this latter site, the snout unit forms a movable articulation with the frontals. The descending lamellae and the dorsal transverse laminae of the nasals form, respectively, the median bony septum and bony roof of the nasal cavity.

Premaxilla.—The premaxillae (figs. 1–4:PM) are fused into a single T-shaped bone, with the crossbar of the T forming the ventral part of the bone. The vertical part of the T of the toothless premaxilla projects dorsally and contributes to the median septum between the nasal capsules. The premaxilla articulates with all the bones of the snout unit, except the vomer.

Septomaxillae.—Each septomaxilla (figs. 1–4:SM) is a flat, long bone wedged between the nasal and vomer. From the lateral aspect originates a dorsally directed flat and narrow process, which supports the long and narrow caudal conchae. Posteriorly a long process makes contact with the anteroventral surface of the frontal. The septomaxilla forms the posterior part of the ventral wall of the nasal cavity.

Vomers.—Each vomer (figs. 1, 4:VO) is a spherical bone with three processes: an anteriorly, a posteromedially, and a posterolaterally directed process. The latter two processes are between the choanae. The medial vertical lamina has a small round fenestra.

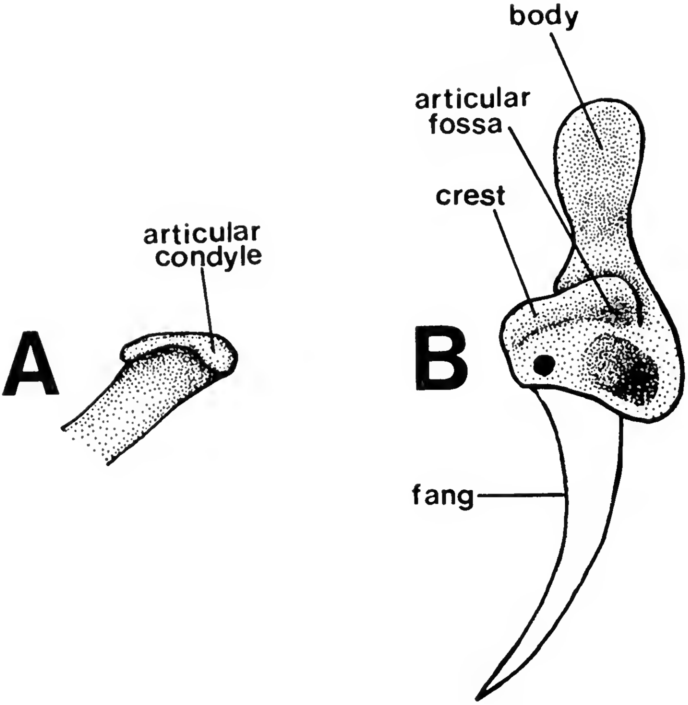


FIG. 7. A. Cranial aspect of anterior margin of left ectopterygoid of *Azemiops*. B. Posterior aspect of left maxilla of *Azemiops*.

The organ of Jacobson is enclosed in the vomer. The vomer forms the greater part of the ventral wall of the nasal cavity.

Conchae.—Two conchae originate from the lateral wall of the nasal capsule. The anterior one is a curved cartilaginous plate with no bony support. The posterior one is long and narrow and is supported by a flat, narrow dorsal process of the septomaxilla.

PALATOMAXILLARY UNIT

Each half of this unit consists of a pterygoid, ectopterygoid, maxilla, and palatine. Only the ectopterygoid has no teeth. This unit is called upper jaw by Dullemeijer (1956).

Maxillae.—The maxilla (figs. 1–4:M) resembles a prism with its apex pointed dorsally. The upper face of the bone adjoining the prefrontal is slightly expanded into a distinctly concave, triangular articular surface. On the posterior aspect, dorsal to the base of the venom fang, the maxilla has an elongate, rather deep fossa (fig. 7B).

Just dorsal to this fossa is a very prominent crest. A less distinct crest borders the fossa ventrally. The medial extremity of the fossa is distinctly expanded. The long axis of the fossa is not horizontal, but makes an approximately 10 degree angle with the horizontal plane. The fossa lodges the anterior end of the ectopterygoid. The medial fang socket extends slightly anterior to the lateral socket. The functional fang is relatively long: in retracted position the tip extends beyond the posterior margin of the orbit. The distal lumen of the fang (discharge orifice of the venom canal) is small and lanceolate in shape, its proximal end continuous with a distinct longitudinal groove on the surface that runs to the entrance lumen. Cutting ridges are present, the anterior one just lateral to the distal lumen.

Pterygoids.—The toothed pterygoid (figs. 1–4:PT) has a shaft that is essentially a posterior continuation of the palatine. However, at the junction with the ectopterygoid the body of the pterygoid increases in height. There are 11 to 14 teeth on the pterygoid, not extending beyond the posterior tip of the ectopterygoid. Posterior to the joint with the ectopterygoid, the pterygoid expands into a broad vane, which is twisted around its long axis in such a way that this portion of the bone presents a dorsomedial and ventrolateral surface. Posteriorly the shaft and the vane of the pterygoid terminate in an oval, thickened articular head for the joint with the quadrate. The joint with the palatine is quite mobile. The anterior end of the pterygoid is distinctly notched, resulting in a blunt, short ventral process and a slightly more elongate, pointed dorsal process (fig. 4). The dorsal and ventral processes embrace the posterior end of the palatine.

Ectopterygoids.—The ectopterygoid (figs. 1, 4:ECT) is an elongate, flat bone that articulates with the pterygoid posteriorly and with the posterior wall of the maxilla anteriorly. The shaft of the bone is somewhat twisted around its long axis. Anteriorly the bone is distinctly expanded laterally, with its straight anterior border running lateromedially. The medial corner of the anterior border is expanded into a knob for articulation with a corresponding fossa in the posterior wall of the maxilla (fig. 7A). Laterally the ectopterygoid possesses a distinct laterally directed process overlying the superior wall of the maxilla dorsal to the base of the lateral fang socket (figs. 1, 3).

Palatines.—The palatine (figs. 2–4:P) is medial to the maxilla. It is a thin, subvertical bony plate in a parasagittal position. In a lateral view the bone is triangular. Its posterior part is a direct continuation of the shaft of the pterygoid. About halfway the length of the bone a broad vane extends dorsomedially from the shaft. This vane dwindles to a long, slender medial choanal process underlying the frontal and the posteroventral medial process of the prefrontal (fig. 4:MPP). The medial choanal processes of left and right palatines nearly touch each other in the midline. The posterior end of the palatine is distinctly forked, forming two posterior processes: a somewhat elongate, pointed lateral, and a short, medial process. These processes embrace the anterior end of the pterygoid. The ventral surface of the palatine bears four teeth.

SQUAMOSAL (SUPRATEMPORAL) UNIT

The squamosal (figs. 1, 2:SQ) is an elongate flat bone that articulates with the dorsolateral aspect of the prootic. The anterior tip does not reach the parietal. The posterior extremity of the bone overlies the anterolateral corner of the exoccipital. The squamosal is slightly curved, the medial border being somewhat concave and the lateral margin faintly convex.

QUADRATE UNIT

The quadrate (figs. 1, 4:Q) is a long, straight, flattened bone interposed between squamosal and the mandible. Dorsally the bone is somewhat expanded to articulate with the squamosal. Ventrally it forms two knobs. Between the two knobs is a saddle-shaped fossa. The lateral knob is rounded while the medial one is smaller and somewhat flattened. The medial knob articulates with the pterygoid. Midway on the shaft, and oblique to its axis, is a raised area with an oval fossa that accommodates the distal end of the stapes. This nodule is the intercalare, according to Kamal and Hammouda (1965).

MANDIBULAR UNIT

Albright and Nelson (1959a) included the squamosal and quadrate in the "mandibular component." We prefer to separate the squamosal and quadrate as independent entities from the mandible. Functionally the quadrate and squamosal play an important role in protruding the palatomaxillary arch.

As in all snakes each mandibular unit moves freely distally. In *Azemiops*, it is composed of four bones: the compound bone (articular of Brattstrom, 1964), angular, dentary, and splenial.

Compound bones.—The compound bone is the largest bone, forming the posterior half of the mandible. Anteriorly it is firmly attached to the splenial, angular, and dentary bones. On the lateral aspect of the mandible is the large posterior Meckelian vacuity which is open dorsally. The medial wall of the posterior Meckelian vacuity is formed by a thin vertical dorsal elevation of the compound bone. This dorsal elevation is restricted to the posterior half of the compound bone. A small foramen is present on the lateral aspect of the long, narrow anterior half of the compound bone. Posterodorsally the bone is differentiated into a saddle-joint for articulation with the quadrate. Posterior to the quadratomandibular joint is a distinct retroarticular process, which curves slightly medially.

Splenials.—The splenial is a small but elongate bone on the medial aspect of the mandible wedged between the ventral posterior process of the dentary and the anteroventral corner of the compound bone. The Meckelian vacuity is open dorsal to the splenial.

Angulars.—The angular is a very small bone that is united with the splenial, dentary, and compound bone. Anteriorly it meets the posterior margin of the splenial (Marx and Rabb, 1965, fig. 34).

Dentaries.—The toothed dentary forms the anterior one-fourth of the mandible. Posteriorly the dentary is produced into two posterior processes, a ventral and a dorsal between which the distal end of the compound bone is lodged. The dentary is also connected to the angular and splenial. The 15 to 16 teeth on the dentary extend almost to the posterior tip of the posterior dorsal process. The three most anterior teeth are distinctly longer than the rest. The dorsal process of the dentary extends farther posteriorly than does the ventral. The Meckelian groove is open from the vacuity above the splenial to the anterior tip of the dentary; the groove becomes ventral in position in the anterior third of the bone.

CEPHALIC ARTHROLOGY AND ASSOCIATED LIGAMENTS

We discuss only those joints and ligaments that play an important role in the striking and feeding mechanism of *Azemiops*.

Squamosal-braincase Articulation

The squamosal-braincase articulation is quite mobile. The parietal possesses an elongate shallow fossa that is covered with cartilage. The squamosal can swing its posterior end dorsally from its resting position. Ventral displacement of the posterior tip of the bone is made impossible by the strong *parieto-squamosal ligament,* which runs from the posterolateral part of the parietal to the medial aspect of the squamosal. The caudal part of the squamosal can swing dorsally in the parasagittal plane using the anterior tip as the center of rotation.

Squamosal-quadrate Articulation

This joint allows limited mobility. The concave articular surface of the squamosal is on the dorsal aspect of the posteroventral corner. The dorsal part of the quadrate is covered with cartilage, which is thicker on the medial side, forming the articular surface. The joint is provided with a strong capsule and a short squamosal-quadrate ligament that runs from the posteroventral corner of the squamosal to the anterodorsal corner of the quadrate. This joint permits the quadrate to swing in the parasagittal and transverse planes, and transmits vertical movements of the quadrate to the squamosal.

Prefrontal-frontal Articulation

Dorsally the prefrontal is joined to the frontal by a syndesmosis. The prefrontal is slightly differentiated into a medial and posterior dorsal process. These processes are of equal length and relatively short. This V-shaped junction allows limited, mainly anterolateral, movement of the prefrontal. However, extensive excursions in the parasagittal plane as described for *Bitis* (Boltt and Ewer, 1964) and the Crotalinae (Dullemeijer, 1959) are prohibited in *Azemiops* by the medial dorsal process of the prefrontal and the large midlateral anterior wing of the frontal.

QUADRATOMANDIBULAR ARTICULATION

This joint is a typical saddle-shaped one. The posterior end of the compound bone is differentiated dorsally into an anterior knob and a posterior knob between which is a longitudinal saddle-shaped articular fossa. Ventrally the quadrate is correspondingly shaped as a transverse saddle-like articular fossa between a lateral and a medial knob. The lateral knob serves as an attachment for the *quadratomaxillary ligament.* These saddle-shaped articular surfaces allow depression of the mandible about the quadratomandibular joint and extensive rotation about its own longitudinal axis.

ATTACHMENT BETWEEN QUADRATE AND PALATOMAXILLARY UNIT

The only bony connection between the quadrate and the palatomaxillary unit is the *quadratopterygoid articulation,* which allows sliding movements between quadrate and pterygoid in many directions. The medial aspect of the medial knob on the distal end of the quadrate forms a flat articular surface with the caudal end of the pterygoid. A narrow *quadratopterygoid ligament* joins the dorsal surface of the caudal tip of the pterygoid to the medial knob at the ventral end of the quadrate. Translational movements of the quadrate relative to the pterygoid are possible (Boltt and Ewer, 1964). Brattstrom (1964) has stated that there is a joint between the pterygoid and the articular (compound). We have not found such a junction in *Azemiops* or in any other viperid we have examined.

The *quadratomaxillary ligament* runs from the lateral knob of the quadrate at the quadratomandibular joint to the maxilla. The ligament is attached and fused to the connective tissue around the venom gland. Anteriorly it reappears below the orbit as a conspicuous ligament that is attached to the ventral tip of the postfrontal and to the maxilla. At the corner of the mouth the ligament splits, one branch attaching to the skin at that site. This branch is the lateral ligament of Wolter (1924).

INTRINSIC JOINTS OF THE PALATOMAXILLARY UNIT

Pterygopalatine articulation.—Posteriorly the palatine is forked, being differentiated into a longer lateral posterior palatine process and a shorter medial posterior palatine process. Between the processes is a saddle-shaped articular fossa flanked by a shorter dorsal anterior pterygoid process and a longer ventral anterior pterygoid process. This arrangement of opposing saddle-shaped articular surfaces allows extensive movements of the palatine: (1) slight rotation of the palatine around its longitudinal axis so that the teeth are turned medially; (2) medial displacement of the anterior tip of the palatine over a considerable distance accompanied by lateral movement of the posterior tip of the palatine so that an angle is formed between pterygoid and palatine (the opposite movement is inhibited by the short and strong pterygopalatine ligament and the ventral surface of the posteroventral medial process of the prefrontal against which the triangular vane of the palatine abuts); (3) both dorsal and ventral displacements of the anterior tip of the palatine about a transverse axis. However, dorsal movements are very limited because of the long choanal process of the palatine, which abuts against the ventral surface of the frontal.

Ectopterygoid-maxillary articulation.—This joint is nearly a pure hinge joint. The anterior part of the ectopterygoid is broadened in the horizontal plane and flattened dorsoventrally. The anterior margin of the ectopterygoid is rounded and covered with cartilage. The medial end of the margin is expanded into a rounded knob that is covered with cartilage. Just dorsal to the fang the posterior surface of the maxilla has an elongate, cartilage-lined fossa, which is expanded medially. The fossa is bordered dorsally and ventrally by distinct crests. The fossa lodges the anterior margin of the ectopterygoid. The maxilla rotates about this joint in the parasagittal plane. However, because the fossa deviates from the horizontal plane by about 10 degrees, the hinge movement does not occur exactly in the parasagittal plane but deviates slightly laterally.

CONNECTIONS BETWEEN BRAINCASE AND PALATOMAXILLARY UNIT

Prefrontal-maxillary articulation.—This joint is formed by two opposing articular facets. A small triangular and somewhat concave articular facet can be found on the posterior aspect of the dorsal portion of the maxilla. The anteroventral part of the prefrontal possesses a rectangular surface, which is wider transversely. The convex articular facet lies on the lateral half of this rectangular area. The convexity of the prefrontal facet and the concavity of the maxillary facet allow rotation of the maxilla in the parasagittal plane, a slight rotation of the maxilla around its long axis so that the fang turns laterally over a very short distance, and sliding of the maxilla along the posteroventral slope of the elongate prefrontal facet. The maxilloprefrontal joint is provided with two ligaments. The lateral *maxilloprefrontal ligament* runs from the posterolateral corner of the maxilla dorsally to the posterolateral margin of the prefrontal. This lateral ligament limits the anterior rotation of the maxilla in the parasagittal plane. The medial *maxilloprefrontal ligament* runs from the posteromedial ridgelike corner of the maxilla to the ventral aspect of the prefrontal. The medial ligament limits the twisting of the maxilla around its long axis.

Palatoprefrontal connection.—This is a very loose connection between the anterior dorsal surface of the palatine and the flat ventral surface of the prefrontal. This connection inhibits dorsal excursion of the palatine and rotation of the palatine about its long axis so that the teeth cannot turn very far laterally.

Palatofrontal connection.—The exceptionally well developed medial or choanal process of the palatine extends to the midline of the braincase, where it lodges in the interchoanal septum. The process lies under, but is not directly connected to, the ventral surface of the frontal anterior to the rostral border of the sphenoid complex. The long medial process limits some movements of the palatine, e.g., rotation so that the teeth turn laterally, and dorsal movement. However, some sliding of the medial process is possible, i.e., ventral movement of the palatine, and rotation so that the teeth turn medially.

ATTACHMENTS OF THE POSTEROVENTROMEDIAL PROCESS OF THE PREFRONTAL

A very extensive and well differentiated fibrous horizontal ligament runs between the posteroventromedial process, the ventrolateral margins of the frontal and the sphenoid complex, and the connective tissue capsule of the eyeball. This ligament has a topographical relationship very similar to the septum interorbitale in *Vipera berus*, as described by Dullemeijer (1956). However, the condition in *Azemiops* differs from that in other Viperidae. The horizontal fibrous ligament of *Azemiops* is differentiated into three distinct parts.

The posterior part runs from the medial half of the distal margin of the posteroventromedial process of the prefrontal to the anterolateral margin of the sphenoid and continues anteriorly on to a distinct longitudinal ridge on the ventral surface of the frontal. The attachment to the sphenoid complex extends posteriorly to the level of the posterior wall of the optic foramen. The tensile forces of this ligament may be responsible for molding the scalloped pattern seen in the distal margin of the posteroventromedial process. This part of the ligament underlies the rostral part of the Harderian gland beneath the eye.

The anterior section of the ligament runs between the lateral half of the distal margin of the posteroventromedial process to the connective tissue capsule of the eye. This part runs mediolaterally.

The third part is a specialization within the posterior section appearing as a distinct aponeurosis associated with both the belly and proximal tendon of the retractor vomeris muscle. The fibers of the aponeurosis run from the retractor vomeris anterolaterally to the posteroventromedial process of the prefrontal.

The horizontal ligament (interorbital septum) of *Azemiops* differs from that of other Viperidae in its differentiation into three distinct parts and in the strong development anteriorly, which is correlated with the presence of the posteroventromedial process of the prefrontal. Apart from its possible role in controlling the degree of anterolateral movements of the prefrontal, the horizontal ligament may play a role in emptying the large anteroventral part of the Harderian gland by means of contraction of the retractor vomeris muscle.

MYOLOGY

The terminology of Kochva (1962) is followed. Haas (1962) has illustrated the superficial cranial musculature of *Azemiops* and has mentioned the absence of a levator anguli oris muscle.

Muscles Between Braincase and Mandibular Unit

Adductor externus superficialis muscle.—This muscle (figs. 8, 9:add. ext. S.) is composed of one part only. It is a straplike parallel-fibered muscle that runs from the postorbital region of the braincase to the posteroventral margin of the mandible.

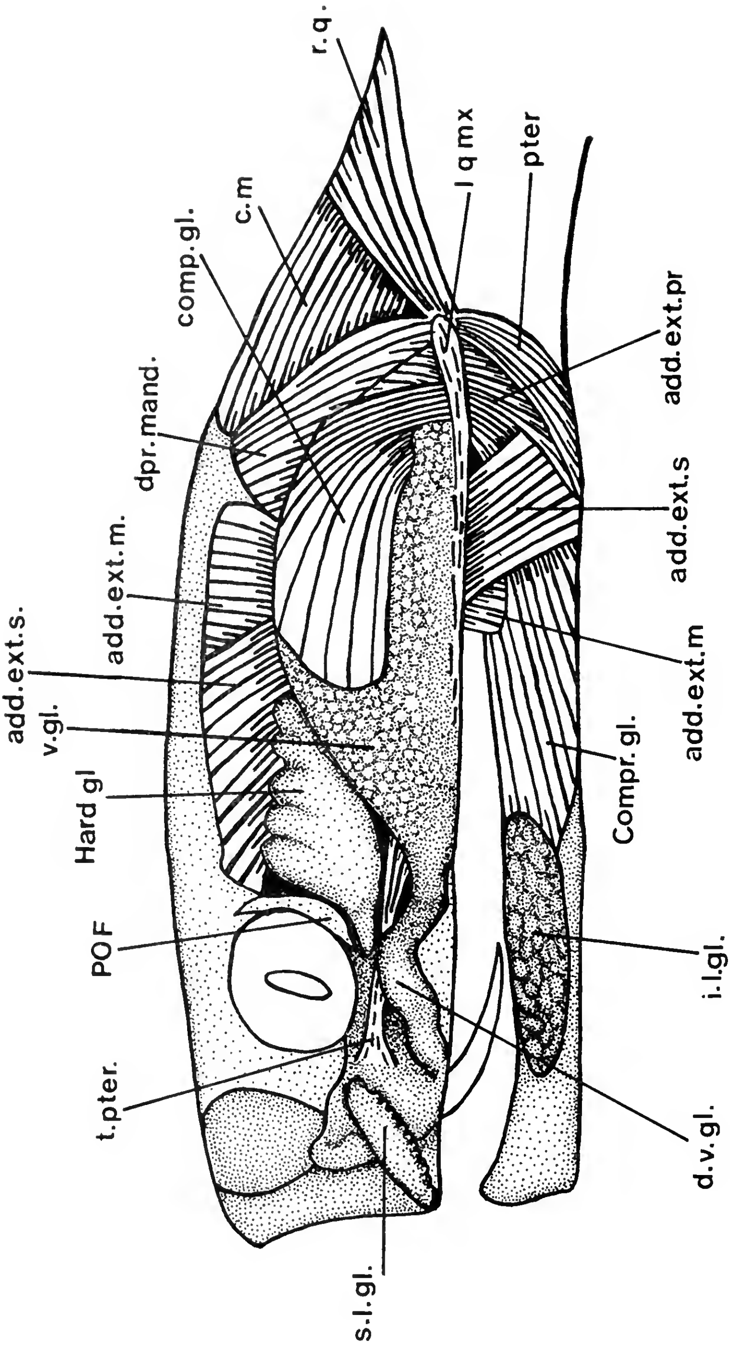
The fleshy origin is a narrow area that extends from the base of the postorbital process along the parietal to a point just anteroventral to the anterior end of the squamosal.

The tendinous insertion is on the lateral surface of the mandible in a line parallel to the ventral border of the mandible. The insertion line begins anteroventral of the quadratomandibular joint and reaches anteriorly beyond the rostral margin of the foramen of the primordial canal.

The muscle fibers run in a posteroventral direction lateral to the large posterior body of the Harderian gland and medial to the venom gland, passing through the loop formed by the compressor glandulae muscle. Ventrally the muscle turns into an aponeurosis, which crosses the adductor externus profundus muscle.

A deep portion of the adductor externus muscle, which is differentiated as a separate levator anguli oris muscle inserting at the corner of the mouth and at the lower lip in other vipers, is absent in *Azemiops*.

Adductor externus medialis muscle.—This vertical, parallel-fibered muscle (figs. 8, 9:add. ext. m.) lies just posterior to the adductor externus superficialis muscle. It originates from the parietal and squamosal. The lateral fibers are attached to a narrow area of the parietal, which is a direct posterior continuation of the area of origin of the adductor externus superficialis muscle. The deeper fibers are attached to the squamosal.


r.q.
c.m
comp.gl.
l q mx
pter
dpr.mand.
add.ext.pr
add.ext.s
add.ext.m.
add.ext.s.
v.gl.
Hard gl
add.ext.m
Compr. gl.
POF
i.l.gl.
t.pter.
d.v.gl.
s.l.gl.

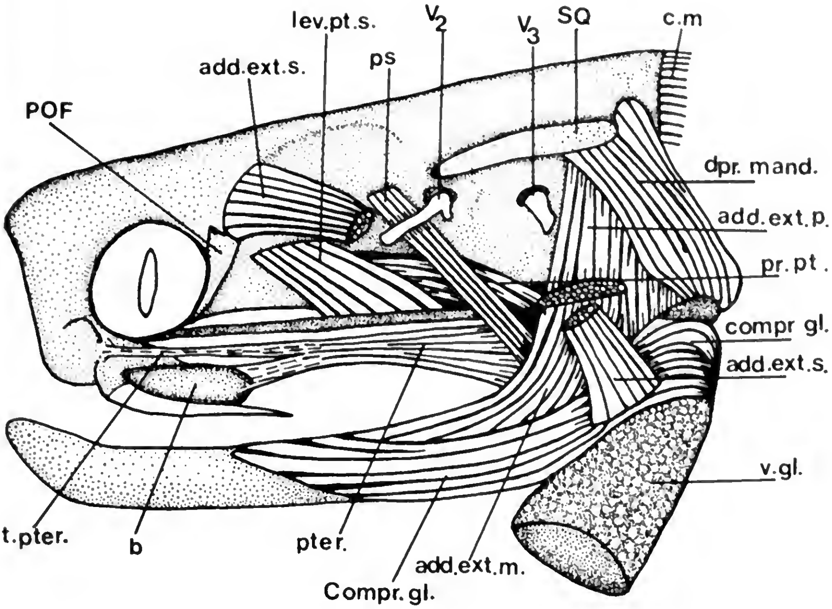


FIG. 9. Lateral aspect of deep cephalic musculature of *Azemiops* after removal of superficial muscles. Posterior half of venom gland displaced in such a way that medial aspect is exposed. Anterior portion of venom gland and posterior body of Harderian gland have been removed. Abbreviations: add. ext. m., adductor externus medialis muscle; add. ext. p., adductor externus profundus muscle; add. ext. s., adductor externus superficialis muscle; b., bag of teeth; c. m., cervical muscles; compr. gl., compressor glandulae muscle; dpr. mand., depressor mandibulae muscle; lev. pts., levator pterygoidei muscle; POF, postfrontal; pr. pt., protractor pterygoidei muscle; ps., pseudotemporalis muscle; pter., pterygoideus muscle; SQ, squamosal; t. pter., tendon of pterygoideus muscle; V_2, maxillary nerve; V_3, mandibular nerve; v. gl., medial aspect of venom gland.

FIG. 8. Lateral aspect of cephalic musculature of *Azemiops*. Posterior body of Harderian gland has been displaced in such a way that it lies lateral to the adductor externus superficialis muscle. Abbreviations: add. ext. m., adductor externus medialis muscle; add. ext. pr., adductor externus profundus muscle; add. ext. s., adductor externus superficialis muscle; c. m., cervical muscles; compr. gl., compressor glandulae muscle; d. v. gl., duct of venom gland; dpr. mand., depressor mandibulae muscle; Hard. gl., Harderian gland; i.l.gl., infralabial gland; l. q. mx., quadratomaxillary ligament; POF., postfrontal; pter., pterygoideus muscle; r. q., retractor quadrati muscle; s.l.gl., supralabial gland; t. pter., tendon of pterygoideus; v. gl., venom gland.

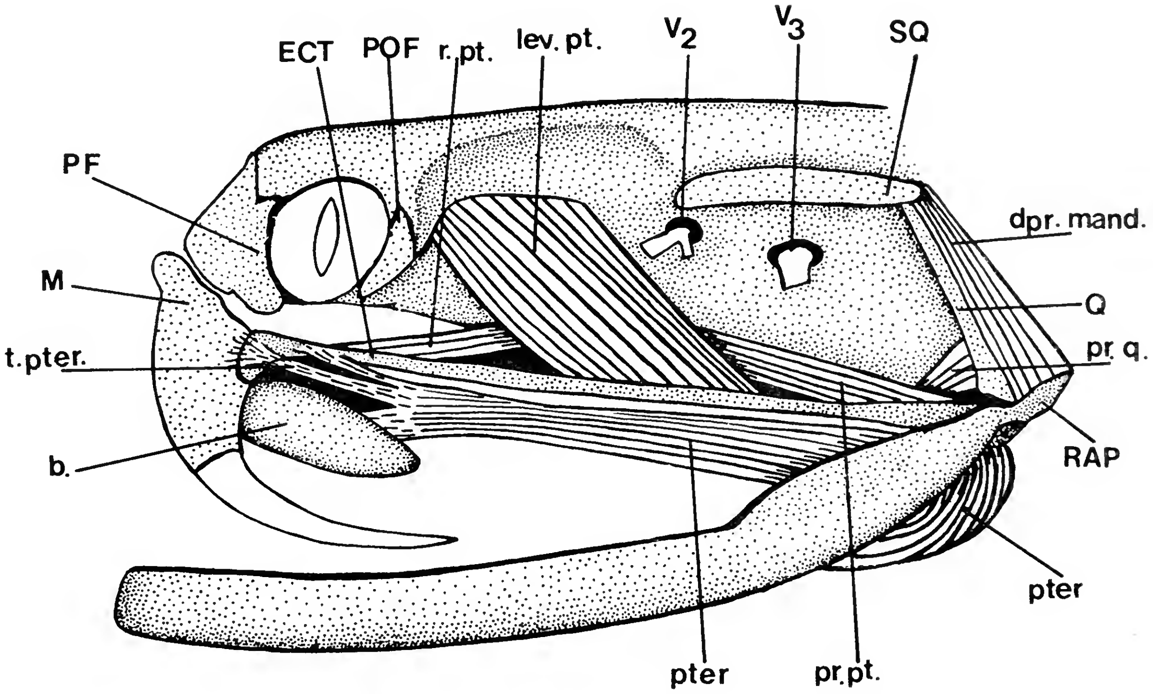


FIG. 10. Lateral aspect of deepest layer of cephalic musculature of *Azemiops*. Abbreviations: b., bag of teeth; dpr. mand., depressor mandibulae muscle; ECT, ectopterygoid; lev. pt., levator pterygoidei muscle; M, maxilla; PF, prefrontal; POF, postfrontal; pr. pt., protractor pterygoidei muscle; pr. q., protractor quadrati muscle; pter., pterygoideus muscle; Q, quadrate; RAP, retroarticular process; r. pt., retractor pterygoidei muscle; SQ, squamosal; t. pter., tendon of pterygoideus muscle; V_2, maxillary nerve; V_3, mandibular nerve.

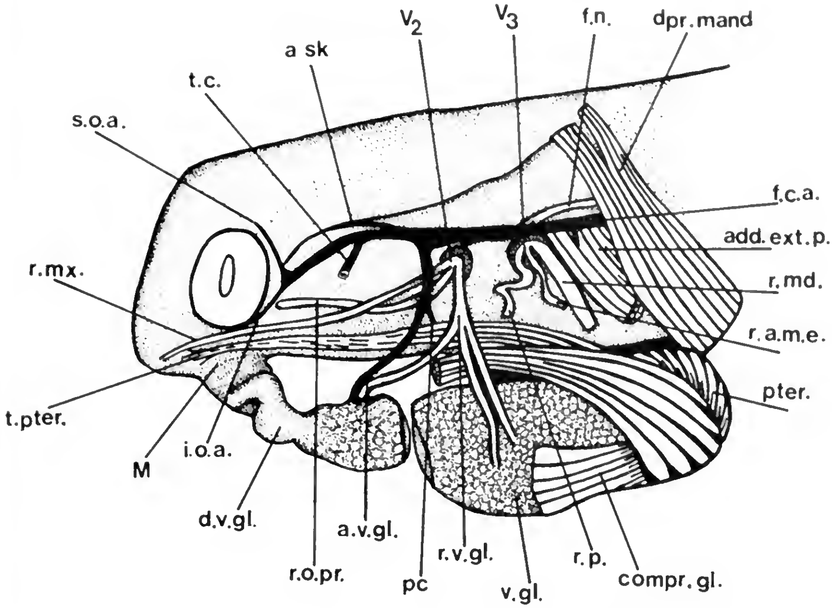


FIG. 11. Lateral view of deep aspect of head of *Azemiops* exhibiting facial carotid artery and some cranial nerves. Abbreviations: add. ext. p., adductor externus profundus muscle; a. sk., artery to skin; a. v. gl., artery to venom gland; compr. gl., compressor glandulae muscle; d. v. gl., duct of venom gland; dpr. mand., depressor mandibulae muscle; f. c. a., facial carotid artery; f. n., facial nerve; i. o. a., infraorbital artery; M, maxilla; pc., artery to pterygoid complex; pter., pterygoideus muscle; r.a.m.e., ramus to adductor mandibulae externus; r. md., ramus mandibularis; r. mx., ramus to maxilla; r. o. pr., ramus ophthalmicus profundus; r. p., ramus to pterygoideus; r. v. gl., ramus to venom gland; s. o. a., supraorbital artery; t. c., artery to temporalis complex; t. pter., tendon of pterygoideus muscle; V_2, maxillary nerve; V_3, mandibular nerve; v. gl., venom gland.

The muscle inserts with an aponeurosis on the dorsolateral surface of the mandible just medial to the attachment of the compressor glandulae muscle.

The muscle fibers pass medially to the adductor externus superficialis, the venom gland, and the compressor glandulae muscle.

Pseudotemporalis muscle.—This is a long, thin, parallel-fibered straplike muscle, which lies deep to the adductor externus superficialis and adductor externus medialis muscles (fig. 9:ps).

Its fleshy origin is from the braincase just ventral to the posterior part of the origin of the adductor externus superficialis muscle. The parallel fibers run posteroventrally to insert with an aponeurosis on the upper edge of the mandible, dorsal and medial to the anterior half of the insertion of the adductor superficialis externus muscle. The maxillary subdivision of the trigeminal nerve passes lateral to the pseudotemporalis muscle.

MUSCLES BETWEEN QUADRATE AND BRAINCASE

There is only one small muscle in this category. The *protractor quadrati muscle* runs from the ventral surface of the braincase posterodorsally to the quadrate. The tendinous origin is from the transverse crest on the sphenoid complex. The fleshy origin is medial to the area of attachment of the adductor posterior muscle.

MUSCLES BETWEEN QUADRATE AND CERVICAL VERTEBRAE

The *retractor quadrati* (*cervicomandibularis*) *muscle* (fig. 8:r.q.) runs from the ventrolateral corner of the quadrate to the cervical region. The origin is an aponeurosis attached to the connective tissue that is fused to the spinal processes of the fifth, sixth, and seventh vertebrae. The insertion is on the lateral knob of the quadrate at the quadratomandibular joint. A short aponeurosis functions as an insertion. This aponeurosis is continuous with the quadratomaxillary ligament. The muscle fibers converge on the aponeurotic insertion. None of the fibers inserts on the retroarticular process of the mandible.

MUSCLES BETWEEN QUADRATE AND MANDIBLE

Adductor posterior muscle.—This relatively small muscle runs between the lower one-fourth of the quadrate and the mandible. It lies medial to the adductor externus profundus muscle. Origin and insertion are fleshy. The origin is from the anteromedial aspect of the distal one-fourth of the quadrate. The insertion on the mandible is on the medial aspect of the posterior part of the mandible, just anterior to the quadratomandibular joint.

Adductor externus profundus muscle.—The bulk of this muscle (fig. 8:add. ext. pr., fig. 9: add. ext. p.) runs from the quadrate to the mandible just anterior to the quadratomandibular joint. A small part also attaches to the venom gland.

The fleshy origin is from the rostromedial surface of nearly the entire length of the body of the quadrate. The insertion of this muscle on the mandible is also fleshy. The area of attachment is on the lateral surface of the mandible just dorsal to the insertion of the adductor externus superficialis muscle. The posterior limit of the insertion area is just anterior to the quadratomandibular joint, while the anterior limit is a short distance beyond the primordial canal.

A small lateral bundle of the anterodorsal part of the muscle is attached to the connective tissue covering the posteroventral surface of the venom gland.

Depressor mandibulae muscle.—This muscle (figs. 8–11:dpr. mand.) runs from the quadrate and the occipital region of the braincase to the mandible.

The origin is from the posterolateral surface of the upper four-fifths of the quadrate and from both the parietal ridge and exoccipital. The attachment to the quadrate is fleshy, while those to the parietal ridge and exoccipital are aponeurotic. The fleshy insertion on the mandible occupies the entire dorsal surface of the retroarticular process.

The muscle is indistinctly divided into two parts. The subdivision is evident in the dorsal part of the muscle only.

COMPRESSOR GLANDULAE MUSCLE

The *compressor glandulae muscle* runs from the connective tissue around the venom gland to the lower jaw (figs. 8, 9:Compr. gl.).

The attachment of the compressor glandulae muscle to the strong connective tissue surrounding the venom gland is restricted to the dorsal, lateral, and posterior aspects of the gland. There is no attachment to the medial aspect of the gland. The attachment to the lateral and ventral aspects of the mandible is partially aponeurotic. The ventral part of the compressor represents the most anterior insertion on the lateral aspect of the mandible among the adductors, and fills the trough formed by the caudally situated adductor externus profundus muscle.

The muscle fibers run from the dorsal and lateral surfaces of the venom gland posteroventrally to the posterior extremity of the gland from which point the fiber direction turns anteroventrally. In this way a muscular U-shaped loop is formed around the base of the venom gland.

MUSCLES BETWEEN BRAINCASE AND PALATOMAXILLARY UNIT

Levator pterygoidei muscle.—This large muscle (figs. 9, 10, 12:lev. pt.) runs from the braincase to the palatopterygoid arch. The fleshy origin is posteroventral to the base of the postorbital process of the parietal. The fleshy insertion on the pterygoid occupies the area around and posterior to the articulation with the ectopterygoid. The muscle is devoid of any tendons and the fibers run parallel.

Protractor pterygoidei muscle.—This parallel-fibered muscle (figs. 9, 10, 12:pr. pt.) runs from the ventral surface of the braincase to the dorsal surface of the caudal part of the pterygoid.

The origin on the ventral surface of the braincase is caudal to the orbits and occupies part of the sphenoid complex. The origins of left and right protractor pterygoidei muscles are separated by a blunt ridge on the sphenoid complex. The fleshy insertion is in a groove on the dorsal aspect of the caudal extremity of the pterygoid.

The parallel fibers run from their origin mainly anteroposteriorly, but also somewhat laterally.

Retractor pterygoideus muscle.—This parallel-fibered muscle (fig. 10:r. pt.) runs from the ventral surface of the braincase to the palatine. The fleshy origin from the sphenoid complex is ventral and slightly caudal to the postorbital process in between the origins of the levator pterygoidei and protractor pterygoidei muscles. The fleshy insertion is on the caudolateral surface of the palatine and on the dorsal surface of the ectopterygoid.

The parallel fibers run from their origin anteroposteriorly and somewhat ventrally.

MUSCLES BETWEEN PALATOMAXILLARY AND MANDIBULAR UNITS

Pterygoideus muscle complex.—This muscle complex (figs. 8–11: pter.) is composed of four subdivisions. Generally, the muscle complex runs from the maxilla, ectopterygoid, and pterygoid to the mandible.

The four subdivisions can only be distinguished at the origin. The subdivisions fuse completely toward the insertion.

The *first subdivision* (*pterygoideus proper*) attaches with an aponeurosis to the ventral half of the maxilla. It runs posteroventrally to attach on the medial aspect of the posteroventral corner of the mandible and at the retroarticular process. The fleshy insertion of this part can be recognized as a bulky muscular mass just behind the mandible.

The *second subdivision* is split off anteriorly as a small but distinct bundle that attaches to the dorsal side of the bag in which the teeth grow.

A *third subdivision* can be recognized near its attachments at the ectopterygoid. The origin of the third subdivision is slightly caudal to that of the first subdivision.

The *fourth subdivision*, the *pterygoideus accessorius muscle*, originates from the posterolateral part of the pterygoid and inserts on the medial surface of the mandible just posterior to the fleshy attachment of the remainder of the pterygoideus muscle, which occupies the entire medial surface of the posteroventral part of the mandible ventral to both the quadratomandibular joint and the insertion of the adductor posterior muscle.

The *pterygoideus glandulae muscle*, which is a separate subdivision attaching to the posteromedial surface of the venom gland in some crotalines, is absent in *Azemiops*. The muscle fibers of all parts of the pterygoideus muscle run parallel to the adducted mandible.

POSITIONAL RELATIONSHIPS OF THE FACIAL CAROTID ARTERY

The internal carotid artery passes ventral to the stapes (columella) and quadrate, running along the laterodorsal part of the braincase. Just anterior to the base of the stapes it bifurcates into the facial carotid and cerebral carotid arteries. The facial carotid artery is a tributary that starts just posterior to the quadratomandibular joint to turn dorsally, running in close association with the vagus and hypoglossal nerves.

The facial carotid artery (fig. 11:f.c.a.) continues to run anteriorly along the laterodorsal part of the braincase to the orbit, passing dorsal to both the maxillary and mandibular nerves as they exit from the skull through their respective foramina. Anteriorly the facial carotid artery curves ventrally along the posteromedial margin of the postfrontal bone and splits into a dorsal supraorbital and ventral infraorbital artery (fig. 11:s.o.a., i.o.a.).

Between the anterior bifurcation and its origin from the internal carotid artery, the facial carotid artery gives rise to the following branches:

1) Small branches that accompany the maxillary and mandibular nerves into the foramina of the skull.

2) Small branches going to the skin (fig. 11:a. sk.).

3) A small branch to the adductor externus profundus muscle just posterior to the foramen of the mandibular nerve.

4) A large artery to the venom gland (fig. 11:a. v. gl.). The venom gland artery branches on the medial aspect of the gland and gives off tributaries to the roof of the mouth and upper lip. About halfway its length the venom gland artery gives rise to an artery which is the source of the "pterygoid complex" (fig. 11:pc), i.e., small branches supplying the protractor pterygoidei, levator pterygoidei, and pterygoideus complex muscles.

5) Midway between the origin of the venom gland artery and the origin of the infraorbital artery the facial carotid artery gives

off a relatively large branch (fig. 11:te), which is the major source for the "temporalis complex", i.e., small branches supplying the adductor mandibulae externus superficialis and adductor mandibulae externus medialis muscles.

THE FEEDING MECHANISM

Because *Azemiops* seems to occupy such a unique position among the Viperidae, an understanding of its feeding and envenomation mechanisms is of great interest. In an extremely rare form such as *Azemiops,* interpretation of function from structure is the only possible approach, although we recognize that there are dangers in this approach (cf. Gans, 1966). In our analysis of *Azemiops* we have depended heavily on the publications by Dullemeijer (1956, 1959) and Boltt and Ewer (1964) on viperid anatomy and mechanics.

The feeding habits of *Azemiops* are poorly known. Marx and Olechowski (1970) have recovered a specimen of the Common Gray Shrew, *Crocidura attenuata,* from the stomach of a juvenile female.

Opening of the Jaws and Protraction of the Palatomaxillary Unit

Opening of the mouth is initiated by depression of the mandible through contraction of the part of the depressor mandibulae muscle that originates from the braincase. The mandible will rotate around the quadratomandibular joint so that its anterior tip will move ventrally. The quadratomandibular joint will also move medially because the squamosal is displaced in such a way that its posterior tip travels dorsomedially. The indirect side-effect of the contraction of the part of the depressor mandibulae muscle that originates from the braincase is that quadrate and pterygoid are forced to move dorsomedially (fig. 10). Depression of the mandible and protraction of the palatomaxillary unit occur simultaneously because of the mechanical interconnections and mobility between the squamosal and braincase, the quadrate and the squamosal, the quadrate and the pterygoid, and the quadrate and the mandible. The fibers of the depressor mandibulae muscle that originate from the braincase cross the braincase-squamosal, the quadrate-squamosal, the quadratopterygoid, and quadratomandibular joints. Contraction of these particular fibers will result in dorsomedial movement of the posterior tip of the squamosal, dorsomedial movement of the quadrate and pterygoid, and depression of the mandible.

The fibers of the depressor mandibulae muscle that run between quadrate and mandible function solely to depress the mandible. The bulk of the depressor mandibulae muscle does not attach to the braincase, indicating that a greater force is exerted by this muscle in lowering the mandible than in protracting the palatomaxillary unit.

The levator pterygoidei, protractor pterygoidei, and protractor quadrati contract in very close co-ordination to protract and to lift the palatomaxillary unit. We disagree with Boltt and Ewer (1964), who suggest that the protractor quadrati is active during closing of the jaws. The protractor quadrati forces the ventral end of the quadrate to swing forward. However, this movement deviates from the parasagittal plane, because the levator pterygoidei muscle lifts the pterygoid dorsally and pulls the posterior end of the palatomaxillary unit medially. The latter movement forces the anteriorly rotating ventral end of the quadrate to deviate toward the median plane. The protractor pterygoidei muscle pulls the entire palatomaxillary unit forward (fig. 12).

The movements caused by the combined actions of the levator pterygoidei, protractor pterygoidei, and protractor quadrati are: 1) direct displacement of the palatomaxillary unit anteriorly, accompanied by dorsomedial movement of the posterior part of the palatomaxillary unit; 2) the dorsomedial displacement of the posterior part of the palatomaxillary unit will force the anteriorly rotating ventral end of the quadrate to deviate medially; 3) the dorsomedial displacement of the posterior part of the palatomaxillary unit forces the dorsal end of the quadrate and, consequently, also the posterior tip of the squamosal to move dorsally (fig. 12).

The anteriorly directed force of the palatopterygoid is transmitted to the maxilla via the ectopterygoid-maxillary joint, causing the maxilla to swing anteriorly but not in a pure hinge fashion. Because the axis of the ectopterygoid-maxillary joint is slightly dorsomedially directed, the maxilla will also rotate slightly, so that the fang moves somewhat laterally.

Dullemeijer (1959) has stressed the importance of the position of the prefrontal-maxillary joint. In *Azemiops* the joint is anteroventral to the eye, and consequently the ectopterygoid-maxillary joint will move anteroventrally during protraction of the palatomaxillary unit, while the posterior end of the palatomaxillary unit moves forward and dorsally.

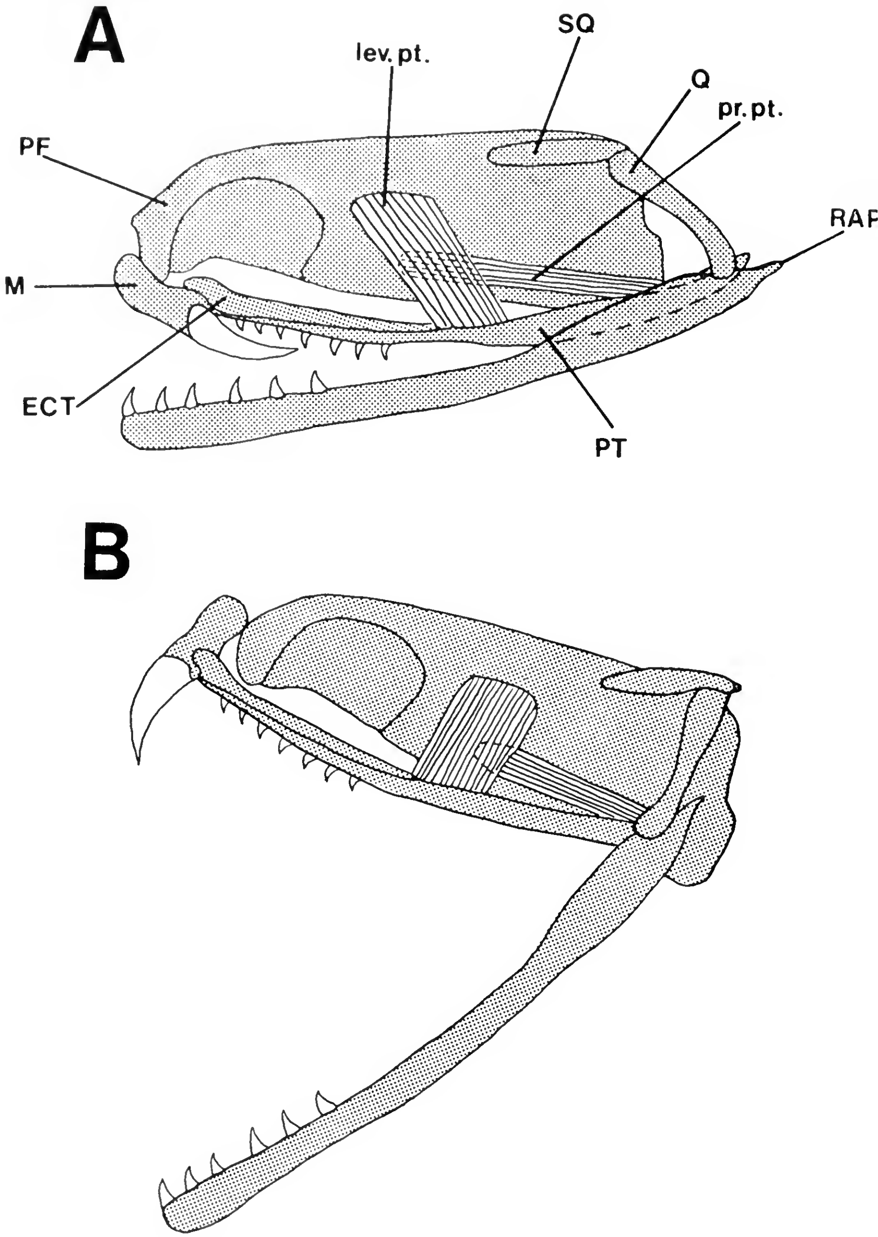


FIG. 12. Simplified diagram of movements of cranial components in *Azemiops*. A. Adducted and retracted condition. B. Opened and protracted condition. Abbreviations: ECT, ectopterygoid; lev. pt., levator pterygoidei muscle; M, maxilla; PF, prefrontal; pr. pt., protractor pterygoidei muscle; PT, pterygoid; Q, quadrate; RAP, retroarticular process; SQ, squamosal.

We emphasize that protraction of the palatomaxillary unit is accompanied by dorsomedial displacement of both the posterior tip of the squamosal and the posterior portion of the palatomaxillary unit. Gadow (1901), Phisalix (1922), and Haas (1931) maintained that the squamosal moves ventrally during protraction of the palatomaxillary unit. However, ventral excursion of the squamosal from the resting position is impossible because of the strong parietosquamosal ligament, which inhibits ventral movement of the squamosal and because the muscles involved (protractor pterygoidei, levator pterygoidei, and protractor quadrati) lift the posterior portion of the palatomaxillary unit dorsally while protracting it. There are no muscles to execute the opposite, i.e., ventral movement of the squamosal.

Klauber (1939, 1956) and Boltt and Ewer (1964) have assumed that the squamosal is stationary during protraction of the palatomaxillary unit. However, movements of the squamosal can be observed easily during feeding of most Viperidae (e.g., Van Riper, 1953). In *Azemiops* the posterior portion of the palatomaxillary unit moves dorsally during protraction because of the action of the levator pterygoidei muscle. This pattern agrees with that of all other Viperidae as described by Dullemeijer (1956, 1959). The pattern in which the entire palatomaxillary unit moves ventrally during protraction as illustrated by Klauber (1939, 1956) is erroneous, since the protractor pterygoidei, levator pterygoidei, and protractor quadrati cannot possibly move the palatomaxillary unit ventrally. The only possible combined effect of these three muscles is protraction and dorsomedial movement of the palatomaxillary unit, as is the case in *Azemiops* and the viperids studied by Kathariner (1900), Dullemeijer (1956, 1959), and Boltt and Ewer (1964).

Adduction of the Mandible

The major adductors that elevate the mandible are the adductor mandibulae externus superficialis, the adductor externus medialis, the adductor posterior, and the pseudotemporalis muscles. During contraction of these muscles the mandible is elevated, i.e., the angle between mandible and quadrate is diminished. However, the quadratomandibular joint also moves posteriorly during elevation of the mandible. When the quadratomandibular joint moves posteriorly, it pulls the palatomaxillary unit along. Adduction of the mandible and retraction of the palatomaxillary unit are interdependent and take place simultaneously. The adductor system is divided into many separate muscles. The adaptive significance of such an organization is that the mandible can move over a large angle and that at any position of the mandible there is always a muscle or part of a muscle that runs perpendicularly to the long mandibular axis (Dullemeijer, 1956). Boltt and Ewer (1964) have suggested that the adductor externus superficialis plays an important role in opening the jaws in *Bitis*. However, the anatomical situation in *Azemiops* indicates that the adductor externus superficialis adducts the mandible.

RETRACTION OF THE PALATOMAXILLARY UNIT

Retraction of the palatomaxillary unit takes place simultaneously with adduction of the mandible. Some adductors also move the quadratomandibular joint and consequently the palatomaxillary unit posteriorly (Dullemeijer, 1956).

The first subdivision of the pterygoideus complex (pterygoideus proper), which runs between the maxilla and the medial surface of the posteroventral part of the mandible (fig. 10), retracts the maxilla back into its resting position. Haas (1929), Kochva (1958), and Boltt and Ewer (1964) have suggested that the pterygoideus complex is a major retractor of the maxilla and the palatomaxillary unit. However, Dullemeijer (1956) objected to this suggestion, because it necessitates a fixed mandible. We agree with Haas (1929), Kochva (1958), and Boltt and Ewer (1964) that the general function of the pterygoideus complex muscle is retraction of the palatomaxillary unit. The mandible can function as a rather stabilized unit when there is prey in the buccal cavity, and stabilization of the mandible can be achieved by regulation of antagonistic muscles. Even if the mandible is not stabilized, the muscle will draw both the palatomaxillary unit and the mandible together. The working-line of the muscle force is perpendicular to the axis of the mobile ectopterygoid-maxillary joint and is parallel to the axis of the quadratomandibular joint (fig. 10). This arrangement favors movement of the maxilla rather than of the mandible.

The large retractor quadrati muscle plays a very important role in retracting the palatomaxillary unit. It pulls the quadrate posteriorly, ventrally, and somewhat laterally. The posteriorly moving quadrate will pull the entire palatomaxillary unit backward and functions as an important synergist of the pterygoideus complex. Kochva (1958) has assigned two antagonistic functions to the retractor quadrati muscle: lowering the mandible and drawing back the quadrate. However, it has been demonstrated in the first subchapter that mandibular depression is accompanied by displacement of the ventral end of the quadrate anteriorly and dorsally, never posteriorly. Kochva's suggestion should therefore be rejected. The functions of the retractor quadrati muscle are to draw back the quadrate and to retract the entire palatomaxillary unit.

The small retractor pterygoidei muscle of *Azemiops* does not play an important role in retracting the palatomaxillary unit because the saddle-joint between pterygoid and palatine allows extensive movements between the two bones without influencing the palatomaxillary unit as a whole.

Compressor Glandulae Muscle

As discussed by Kochva (1963), the compressor glandulae muscle is totally unrelated to the adductor externus superficialis. The compressor glandulae muscle of *Azemiops* resembles that of other viperids. It is a large muscle that is attached to the dorsal and lateral surface of the venom gland. Many of the fibers are very long and envelop the venom gland in U-shaped loops. The muscle attaches to the lateroventral side of the mandible. Haas (1952), Kochva (1958, 1962), Boltt and Ewer (1964), and Rosenberg (1967) have demonstrated that this muscle plays an important role in ejecting venom from the gland in viperids.

DISCUSSION

Some of the functional morphological problems touched on in the preceding pages deserve further exploration. However, we confine ourselves here to the basic question in this study—the phylogenetic position of *Azemiops*. That *Azemiops* is a viperid seems clear from its cephalic anatomy: protraction of the palatomaxillary unit takes place in typical viperid fashion (see pp. 98–101 and Anthony, 1954); the presence and mode of emptying the venom gland are typically viperid (Haas, 1962; Rosenberg, 1967); and the histological anatomy of the venom and accessory glands conforms to the pattern of other viperids (Kochva et al., 1967). Various other characteristics support this familial assignment (see family description, p. 120). The phylogenetic question thus reduces to the nature of the relationships of *Azemiops* to other viperids. In an attempt to answer, our information is here analyzed and integrated with relevant previous studies on the Viperinae and Crotalinae. Attention is concentrated on characters thought to be diagnostic of or peculiar to these subfamilial groups.

PTERYGOIDEUS GLANDULAE MUSCLE

According to Dullemeijer (1959) the pterygoideus musculature of the Viperinae differs from that of the Crotalinae in the absence of a distinct pterygoideus glandulae muscle. Dullemeijer (1959) reported that in Viperinae the adductor profundus functions as an antagonist of the compressor glandulae muscle in emptying the venom gland. In the Crotalinae, on the other hand, the antagonist function is executed by the pterygoideus glandulae muscle. However, Dullemeijer did not study the myology of any species of *Agkistrodon*. Kochva (1962) reported an exceptional case in which the pterygoideus glandulae is absent in *Agkistrodon contortrix,* thus abolishing this character as distinguishing between viperines and crotalines. In our studies we found that *Agkistrodon hypnale, A. bilineatus,* and *A. halys* also lack the pterygoideus glandulae muscle. There is, however, a well-developed pterygoideus glandulae muscle in *Agkistrodon piscivorus, A. acutus,* and *A. rhodostoma.* The dichotomy in this character does not conform well to the phyletic intra-generic groups outlined by Brattstrom (1964). In any event, the presence or absence of the pterygoideus glandulae muscle is not a valid character for distinguishing the Viperinae from the Crotalinae. *Azemiops* lacks the pterygoideus glandulae muscle (fig. 10) and resembles the Viperinae and four species of *Agkistrodon*.

DUCT OF VENOM GLAND

Kochva (1962) described a difference between the Viperinae and Crotalinae in the shape of the duct of the venom gland. In crotalines the duct is characteristically coiled, while in the viperines it is straight. In the large adult specimen of *Azemiops* (FMNH 152987) the duct is coiled (see fig. 8), while in the juvenile individual (FMNH 170643, 285 mm. long) the duct is completely straight. We also found variation in the shape of the duct in adults of the genus *Agkistrodon*. The duct is straight in *A. hypnale* and *A. halys*, while it is coiled in *A. acutus* and *A. rhodostoma*. The shape of the duct is therefore not an absolutely diagnostic character in distinguishing the Crotalinae from the Viperinae. The difference in the shape of the duct between the juvenile and adult *Azemiops* seems to indicate that coiling of the duct takes place during ontogeny. We have found that the duct is straight in juveniles of *Trimeresurus mucrosquamatus* (FMNH 127245) and *Agkistrodon bilineatus* (CZS), while it is distinctly coiled in adults (FMNH 127243 and 39093, respectively). It seems that the duct coils in the Crotalinae only in the later stages of ontogeny. All Viperinae, both juveniles and adults, possess a straight duct of the venom gland. Thus *Azemiops* exhibits a pattern otherwise confined to the Crotalinae.

LEVATOR ANGULI ORIS MUSCLE

In most solenoglyphs a deep and anterior portion of the adductor externus muscle originates medially to the lateral part, and inserts at the corner of the mouth and at the lower lip. This separate bundle of fibers appears as a distinct muscle, the levator anguli oris (Haas, 1962). Underwood (1967b) has stressed the importance of this muscle as a primitive phylogenetic character in snakes. Haas (1962) has shown that the levator anguli oris is absent in *Azemiops* (figs. 8, 9). Our studies on the adult specimen (FMNH 152987) confirm Haas's observation. However, in the juvenile specimen (FMNH 170643) some anterior fibers of the adductor externus superficialis deviate from the main course to attach to the skin at the corner of the mouth. A typical levator anguli oris muscle is absent in *Azemiops*.

All viperines possess a well-developed, distinct, and separate levator anguli oris muscle. All Crotalinae mentioned by Kochva (1962) have a separate levator anguli oris muscle, although it is not so well developed as in the Viperinae. We have found a levator anguli oris muscle in *Agkistrodon hypnale, A. acutus, A. halys, A. piscivorus, A. rhodostoma, A. bilineatus, Bothrops atrox, Lachesis mutus,* and *Trimeresurus mucrosquamatus.* We may therefore conclude that all Viperidae possess a levator anguli oris muscle, except *Azemiops feae,* which is a remarkable and unique exception.

The absence of this muscle is regarded as a derived state by Haas (1962) and Underwood (1967b) because it is present in what they regard as primitive and advanced Colubridae, *s.l.* We refrain from assignment of great phylogenetic importance to this character, and the argument for the presence of a levator anguli oris being a primitive state is not fully satisfactory. A contrary possibility suggested by cases like *Azemiops* is that a tripartite adductor mandibularis externus is primitive, and that developments of a muscle called levator anguli oris took place independently in several taxa. Certainly the anatomical homology of this muscle has not been well documented in more than a few taxa, the origin and relative position vary substantially from one taxon to the next, and it is strange that such a muscle occurs in many specialized taxa (particularly fossorial ones) rather than in more generalized relatives.

An intermediate explanation is that the levator anguli oris is a primitive feature of snakes but its development is ordinarily suppressed in many evolved stocks. The genetic potency could be retained in some or all of these stocks as a latent characteristic, to be expressed as the exigencies of specialization called for such a structure. The argument for this kind of evolutionary process has been set forth by deBeer (1958), and more recently by Throckmorton (1962). Thus, in phyletic analysis of viperid characters, the actual presence of this muscle could well be considered a derived state, since its absence is usual in presumptive ancestral colubroid stocks and in taxa indubitably primitive within the group (*viz., Azemiops*).

Foramina on Ventral Surface of the Skull

Underwood (1967a) has pointed out the potential taxonomic usefulness of the position of various cephalic foramina, and particularly those reflecting the course of the Vidian canal. He has indicated that a diagnostic characteristic of the Viperinae and Crotalinae is that there are separate openings for the posterior end of the Vidian canal and for the cerebral artery. Our examinations of skull specimens confirm this pattern, although in *Causus* and *Crotalus* the two openings may be enclosed in a common, shallow, sharply emarginated depression. In *Azemiops* the two openings are enclosed in a relatively small common external foramen (fig. 6). This condition is almost certainly unique among the viperids. Variation has not been adequately studied throughout the Colubroidea.

FACIAL CAROTID ARTERY

Recently, Van Bourgondien and Bothner (1969) have suggested that the topographical relationships between the facial carotid artery and the maxillary and mandibular branches of the trigeminal nerve at their points of passage through the cranial foramina may indicate phylogenetic relationships. The facial carotid artery passes dorsal to the maxillary and mandibular nerves at their points of passage through the cranial foramina in *Agkistrodon contortrix, A. piscivorus, Sistrurus catenatus, S. miliarius, Crotalus horridus, C. viridis,* and *C. atrox* (Van Bourgondien and Bothner, 1969). We have found a similar pattern in *Agkistrodon hypnale, A. acutus, A. halys, A. rhodostoma, A. bilineatus, Bothrops atrox, Trimeresurus mucrosquamatus,* and *Lachesis mutus.* Rathke (1856) reported this pattern in *Bothrops jajaraca.* We may therefore conclude that the passage of the facial carotid artery dorsad to both the maxillary and mandibular nerves is a crotaline characteristic.

Published information on the facial carotid artery of the Viperinae is restricted to *Vipera aspis,* in which this artery was said to pass ventral to both the maxillary and mandibular nerves (Phisalix, 1922), and *Vipera berus,* in which the facial carotid artery passes ventral to the mandibular nerve but dorsal to the maxillary nerve (Rathke, 1856; Dullemeijer, 1956). We have found the latter pattern to be characteristic for the Viperinae. We have examined *Vipera ammodytes, V. aspis, V. lebetina, V. persica, Bitis gabonica, B. arietans, Atheris nitschei, A. hindii, A. hispidus, A. squamiger, Echis carinatus, Eristicophis macmahoni, Cerastes cerastes,* and *Causus rhombeatus.* In one specimen of *V. persica* and one of *A. squamiger* the artery was dorsal to both nerves on one side of the head, and in another two *V. persica* the dorsal branch of the maxillary nerve was above the artery on one side. In none of the species did we find the pattern described and illustrated by Phisalix (1922).

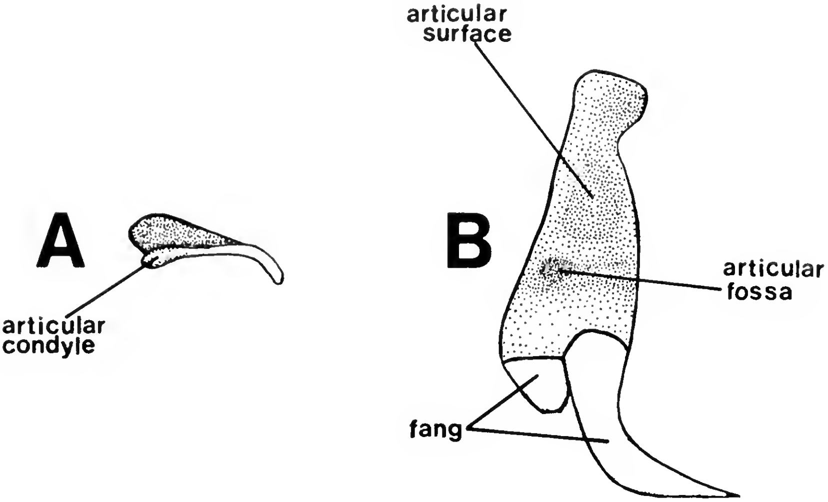


FIG. 13. A. Cranial aspect of anterior margin of left ectopterygoid of *Atheris squamiger*. B. Posterior aspect of left maxilla of *A. squamiger*.

In *Azemiops* the pattern of the facial carotid artery is typically crotaline, i.e., the artery passes dorsal to both maxillary and mandibular branches of the trigeminal nerve (fig. 11). This also seems to be the standard pattern in the few other Colubroidea studied by Rathke (1856) and by us.

ECTOPTERYGOID-MAXILLARY JOINT

The ectopterygoid-maxillary joint of the Crotalinae is very different from that of the Viperinae (Dullemeijer, 1959). In the latter, the horizontal, oblong articular fossa is on the posterior aspect of the maxilla (fig. 13). Medially the fossa is expanded. The anterior margin of the ectopterygoid is differentiated into a distinct ridgelike head which fits into the oblong fossa of the maxilla. Medially the anterior margin of the ectopterygoid swells into a distinct condyle that is lodged in the medial expansion of the fossa on the posterior surface of the maxilla. This viperine ectopterygoid-maxillary articulation (fig. 13) is a pure hinge-joint allowing the maxilla to move in the parasagittal plane (Dullemeijer, 1956, 1959).

In the characteristic crotaline ectopterygoid-maxillary joint, it is the posterior surface of the maxilla that possesses an oblong condyle which becomes narrower laterally (fig. 14). The articular fossa that accommodates this oblong maxillary condyle is found in the anterior surface of the ectopterygoid. This crotaline ectopterygoid-maxillary

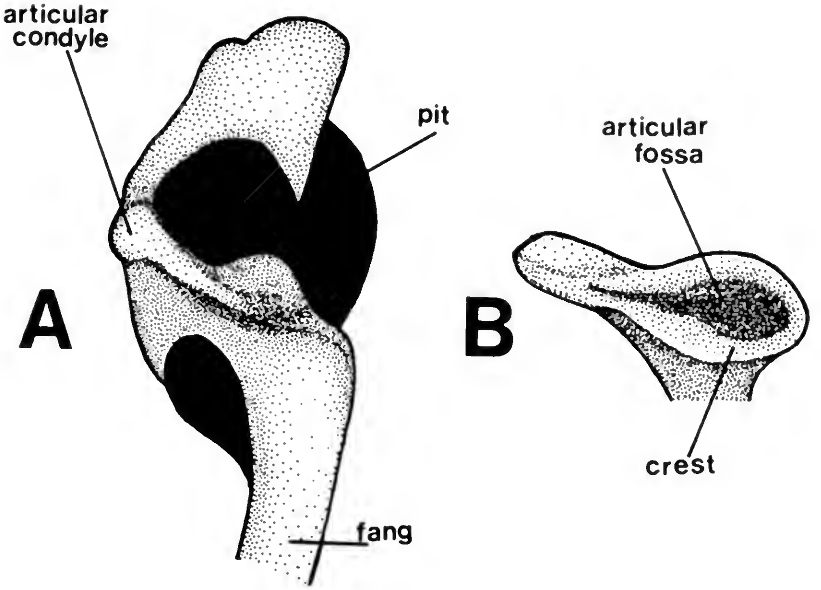


FIG. 14. A. Posterior aspect of right maxilla of *Crotalus atrox*. B. Cranial aspect of anterior margin of right ectopterygoid of *C. atrox*.

articulation is not a simple hinge-joint (Dullemeijer, 1959, p. 914). Dullemeijer (1959, p. 949) has given a mechanical explanation for this crotaline ectopterygoid-maxillary joint. The presence of a pit in the crotaline maxilla creates a weakness in the posterior wall which consequently cannot provide the necessary strength for an articular fossa. Instead, an elongate condyle is developed on the maxilla, while the articular fossa is differentiated on the ectopterygoid.

Azemiops lacks a maxillary pit and exhibits the viperine type of joint, with the fossa in the posterior surface of the maxilla and the articular condyle on the anterior surface of the ectopterygoid (fig. 7). However, the movement in the joint in *Azemiops* foreshadows the condition in Crotalinae. The axis of the ectopterygoid-maxillary joint in *Azemiops* is slightly dorsomedially directed, causing the maxilla to move like a hinge; this action is accompanied by a rotational displacement so that the fang turns laterally.

PREFRONTAL-FRONTAL ARTICULATION

The anterior end of the functional unit involved in the stabbing strike of the folding-fang snakes is the prefrontal bone. In most colubrids it is a practically immobile bone, joining the frontal at its anterolateral dorsal margin by a strong syndesmosis. A midlateral wing of the frontal extends in front of body of the prefrontal and severely restricts any movement in an exact parasagittal plane. The dorsal junction line is generally straight and somewhat oblique to the longitudinal axis of the skull. Variations from this pattern include prefrontals with a flattened horizontal process bordering the anterior dorsal face of the frontal (Marx and Rabb, 1965, figs. 32, 33), or with a similar process on the lateral dorsal face of the frontal (as in many hydrophiids), or with relatively short medial and posterior dorsal processes. The last pattern is shown by *Azemiops* and *Causus*. Without exception, crotalines have no long processes, but the union is not a simple, relatively immobile joint as in most colubrids. Instead, the bones articulate through double saddle joints, the prefrontal having two small knobs or rounded dorsal processes with intervening fossa that meet corresponding surfaces on the frontal, including a modified midlateral wing (see figures in Brattstrom, 1964). The dorsalmost prefrontal process rises above the surface, rather than being simply flush as is the case for the processes in *Azemiops* and *Causus*. In viperines other than *Causus* there is always a single medial dorsal process. The latter fits in a groove on the anterodorsal face of the frontal, although the main juncture in terms of force is still the anterolateral corner of the frontal, where a fossa accommodates a condylar surface of the prefrontal.

Dullemeijer (1959) has stated that the prefrontal-frontal junction is an immobile syndesmosis in the Viperinae, whereas in the Crotalinae it is a very mobile articulation. However, Boltt and Ewer (1964) have demonstrated that the prefrontal of *Bitis* can move to such an extent that the long axis of the main body of the bone becomes horizontal and in a direct line with the dorsal surface of the braincase. Similar potential movement seems indicated by the articular surfaces in the other viperine genera, save *Causus*.

From analysis of colubrid conditions, having double dorsal processes seems to be a derived state, simultaneously allowing and limiting movement. The other viperid conditions allow more mobility. However, stabilizing the thrust of the maxilla and its fang presumably has been important to the evolutionary success of the crotalines and viperines, and we assume that their differing prefrontal-frontal articulations are so adapted. Both of these patterns could conceivably develop from the short double process stage seen in *Azemiops* and *Causus*.

PTERYGOPALATINE JOINT

The pterygopalatine junction in all Viperinae, except *Atheris superciliaris*, is a syndesmosis, allowing only some dorsoventral movement of the palatine relative to the pterygoid. The medial aspect of the anterior tip of the pterygoid is closely applied to the lateral surface of the posterior tip of the palatine. The intervening connective tissue of this fibrous joint will transmit the anterior-posterior movements of the pterygoid directly to the palatine. The palatine does not make a horizontal angle with the long axis of the pterygoid during the excursions of the latter (Boltt and Ewer, 1964). We may generalize that in the Viperinae the palatine principally moves as one unit with the pterygoid and may be regarded as merely an extension of the long axis of the pterygoid. However, in *Atheris superciliaris* the pterygopalatine joint is identical to that of the crotalines.

In the Crotalinae the pterygopalatine joint is a highly mobile, saddle-shaped joint, except in *Agkistrodon hypnale*, *A. nepa*, *A. strauchi*, and *A. rhodostoma*, all of which exhibit the general viperine type of pterygopalatine syndesmosis. In all crotalines, except the species of *Agkistrodon* mentioned above, the palatine is forked posteriorly into lateral and medial posterior processes. Between the processes is a saddle-shaped articular facet. Anteriorly the pterygoid possesses a saddle-shaped articular fossa flanked by dorsal and ventral processes. The opposing saddle-shaped articular surfaces allow (1) extensive movements of the palatine around its longitudinal axis, (2) medial and lateral displacements of its anterior tip so that an angle is formed between the pterygoid and palatine, and (3) dorsal and ventral displacements of the anterior tip of the palatine about a transverse axis of the joint. The pterygopalatine joint of *Azemiops* is highly mobile (fig. 4) and is formed by two opposing saddle-shaped articular surfaces. The joint in *Azemiops* therefore is like that of most Crotalinae.

CHOANAL PROCESS OF PALATINE

Azemiops has a well-developed, long dorsomedial process of the palatine. Such a long choanal process arising from an expanded dorsal margin of the palatine occurs in about 10 per cent of 309 colubrid species examined; 80 per cent have a simple broad dorsal or dorsomedial vane in the middle of the palatine; the remainder have intermediate conditions or no expansion at all. A broad median flange condition occurs in all crotalines (see Brattstrom, 1964), but in none of the viperines examined (a few have a slight anterior dorsal projection). The only viperid species approximating the *Azemiops* condition are *Agkistrodon rhodostoma* (Chernov, 1957) and *A. acutus*. This character state occurs only in two elapids and no hydrophiids.

Albright and Nelson (1959a, b) stated that the palatine of *Elaphe* is involved in transmission of forces between the cranial, nasal, and palatomaxillary units. Although they specify various rotational movements of the bone, no special function is indicated for the dorsomedial flange in this species. It does serve as an insertion point for the retractor pterygoideus (Albright and Nelson, 1959a, fig. 14) and as the attachment site for strong fibrous connective tissue running to the vomer and prefrontal. In *Azemiops* the distal end of the choanal process is well lodged in tough connective tissue of the septum between the choanae. Scott (1967) postulated that the dorsomedial flange or vane provides a needed brace for the palatine in those colubrids seizing and engulfing vertebrate prey. If so, it would be less useful to snakes that kill prey with venom or that feed on small or soft-bodied invertebrates. In any event, the function of a long, slender choanal process as opposed to a simple, broad flange is unclear.

ANTEROVENTRAL MEDIAL WING OF PREFRONTAL

A medial process extends vertically above the lacrimal canal on the anteroventral face of the prefrontal in *Azemiops*. The wing is involved in a posterior concha; mesially it serves as the anchor point for a posterior, internal end of the large nasal gland; laterally it forms part of the wall for a blind prefrontal pocket of the conchal space. The wing is present in well-developed form in over two-thirds of 266 colubrid species examined; an additional 26 species of 21 genera show a vestige of the structure; 44 species of 36 genera have no trace of the wing. The elapids show proportionately fewer taxa with a well-developed process; the hydrophiids lack it entirely. All viperids, save *Azemiops*, lack a well-developed wing, but a pimple-like remnant occurs in at least 12 species (genera *Vipera*, *Echis*, *Bothrops*, *Trimeresurus*, *Crotalus*, *Sistrurus*).

POSTEROVENTRAL MEDIAL PROCESS OF THE PREFRONTAL

A distinct, prominent, posteromedially directed process from the posteroventral border of the prefrontal is unique to *Azemiops* among the Viperidae and probably among the Colubroidea. Ordinarily the posterior face of the prefrontal descends as a simple, often concave, wall fronting the orbital cavity, with at most a ridge at the ventral edge for connective tissue attachment. The posterior projection in *Azemiops*, with its strong ligamentous connections, presumably stabilizes the prefrontal, and the single muscular connection may possibly function in compression of the Harderian gland. Beyond this we hesitate to speculate on the nature of this specialized structure.

Unique Mixture of Morphological Features in *Azemiops*

From published data available and our examinations, five morphological features absolutely separate the Crotalinae from the Viperinae. These characteristics are the presence of a loreal pit and an associated cavity of the maxilla and prefrontal; the presence of a condyle on the posterior surface of the maxilla for articulation with the ectopterygoid; a very mobile prefrontal-frontal articulation without a dorsal horizontal process of the prefrontal; presence of a dorsomedial flange or choanal process of the palatine; and passage of the facial carotid artery dorsal to both the maxillary and mandibular nerves at their exits from the skull. All except the last two appear to be in derived character states. The pit in the maxilla and the condyle on the posterior surface of this bone are functionally interdependent, and from a mechanical point of view they can be considered as parts of a single character complex. Two other characteristics are peculiar to, although not universal in the crotalines: a coiled venom duct in adults and the presence of a pterygoideus glandulae muscle, both apparently derivative states.

The prefrontal-frontal joint in *Azemiops*, as in *Causus*, involves two short horizontal dorsal processes, a possibly precursory state to the crotaline and ordinary viperine conditions. *Azemiops* lacks a pterygoideus glandulae muscle, as do all viperines and also some *Agkistrodon*. *Azemiops* has no pit in the maxilla, and an articular fossa is located in the posterior wall of the maxilla in viperine fashion. However, the apparent movement at the ectopterygoid-maxillary joint approaches the crotaline form. This, in conjunction with sharing crotaline patterns in adult shape of the venom duct and in the pterygopalatine joint, suggests that *Azemiops* has the anomalous position of a "pitless pit-viper." In addition, *Azemiops* retains in common with the crotalines a primitive pattern of the facial carotid artery and a dorsomedial process of the palatine.

To examine the relationships of *Azemiops* further, we have used data from a morphological survey of the advanced snakes that focusses on derived characters seen in the venomous groups (Marx and Rabb, in press). The materials were 24 external integumental features and 26 characteristics of the skull (some have been discussed in the preceding sections). These characters were phyletically analyzed by applying various criteria to the conditions in the ancestral group, which was taken to be phenetically represented by the living colubrids (Marx and Rabb, 1970).

In assessing the phenotype of *Azemiops feae*, we compared its derived states of the 50 characters to the number of derived states of 33 viperine and 45 crotaline species, representing all the known viperid genera (fig. 15). *Azemiops feae* has the fewest derived character states of all species of the Viperidae. The relative amount of derivativeness of the skull characters is fairly constant in all taxa (fig. 15). However, external characters show a gradient of derivativeness, with *Azemiops feae* having only a single external character with a derived state. We conclude that *Azemiops feae* is the least derived taxon in the entire family of vipers.

The 41 characters in which *Azemiops* occurs in a primitive state will not yield any intrafamilial phylogenetic directional information. However, they do indicate a relict nature. Among the viperids, *Azemiops* frequently shares colubroid holdover features with *Agkistrodon* and *Causus*.

Of these primitive state characters, one has been specially noted already since it distinguishes *Azemiops* clearly from all other viperids: the medial or nasal wing of the prefrontal.

In two other characters, *Azemiops* is unusual, but not unique among the viperids in having the primitive state. A supralabial participates in the external ventral border of the orbit in *Azemiops*, as in most colubrids. The majority of the viperids have an intervening row of scales, the interoculabials. In four crotaline species, *Agkistrodon halys*, *A. strauchi*, *A. monticola*, and *Crotalus pusillus*, one of the supralabials still intersects the orbit.

Azemiops shows no carination of the dorsal scales, which is the condition in the majority of colubrids and elapids. In contrast, all but one other viperid have keeled scales. The exception is *Agkistrodon rhodostoma*.

Nine characters have derived states in *Azemiops* (Table 1). Three of the nine characters have all viperid taxa in a derived state when compared to other advanced snakes (Colubroidea): absence of

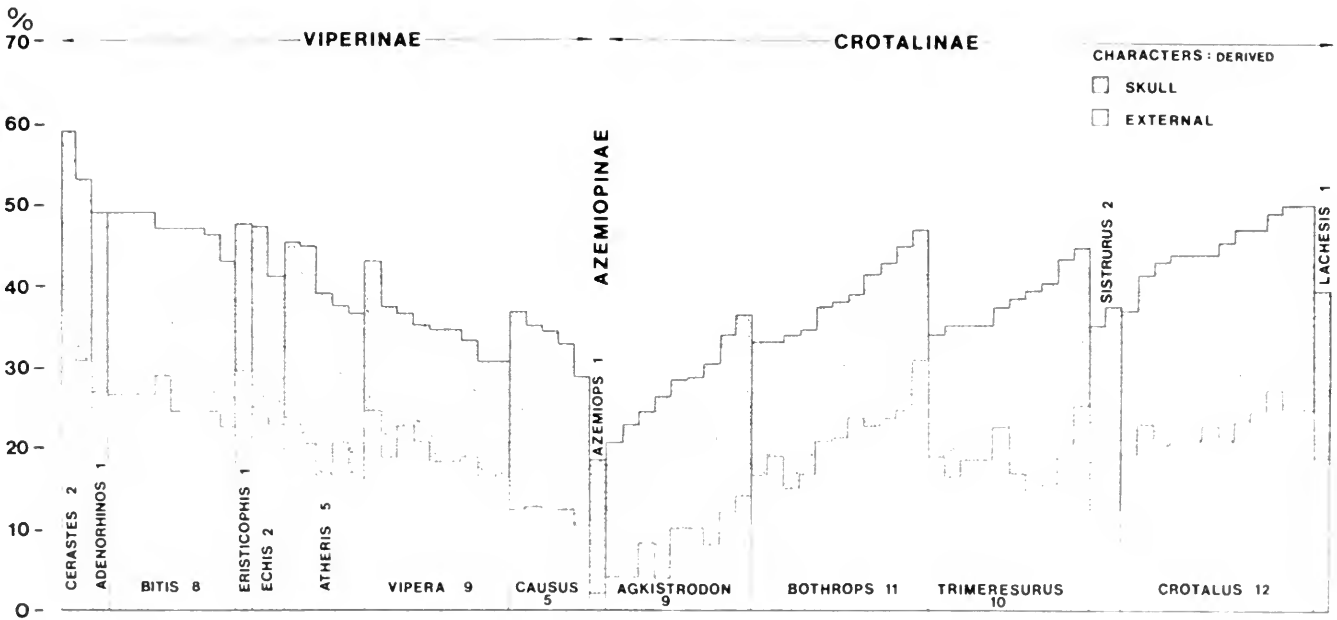


FIG. 15. Relative abundance of derived states of 50 colubroid characters in taxa of Viperidae (see Marx and Rabb, in press). Numbers after generic names indicate number of species examined. Species are represented individually by columns in the graph.

TABLE 1. Derived states of nine colubroid characters[1] present in *Azemiops* compared to Viperinae and Crotalinae.

Character	Viperinae (8 genera)	Crotalinae (6 genera)	*Azemiops*
Apical pits absent (19-I)[2]	0%	4.4% (1)[3]	+/0
Lateral process of palatine absent (29-I)	100.0 (8)	100.0 (6)	+
Palatine-pterygoid articulation notched (31-II)	3.0 (1)	88.9 (6)	+
Prefrontal dorsal process medial and posterior (33-IV)	14.7 (1)	0	+
Parietals bulbous anteriorly (37-III)	23.5 (4)	4.4 (2)	+
Few maxillary teeth (44-II)	100.0 (8)	100.0 (6)	+
Fangs longer than their distance to eye (45-III)	38.9 (4)	63.9 (5)	+
Fangs posterior; grooved anterior (46-III)	100.0 (8)	100.0 (6)	+
Palatine teeth 3 to 5 (48-II)	48.5 (5)	72.1 (3)	+

[1] Marx and Rabb, in press.
[2] *ibid.:* Character and State.
[3] (number of genera)

the lateral maxillary process of the palatine; few maxillary teeth; anteriorly grooved fangs of posterior position on maxilla. However, since they are uniformly present in all Viperidae, these three characters must be considered primitive to the Viperidae, yielding no intrafamilial phylogenetic information.

The remaining six characters (Table 1) have different proportional distributions in the crotalines and viperines. In two cases the derived character state(s) does not occur in one subfamily. This is true of the apical pit character, where the derived condition of absence is found only in two crotalines. *Azemiops* shows an intermediate derived condition in this character, apical pits being present anteriorly on the dorsal scales but not over most of the body. As mentioned above, the presence of two horizontal dorsal processes of the prefrontal occurs only in *Azemiops* and in the presumptively primitive viperine genus *Causus*. This anatomical arrangement apparently was rarely tried among the colubrids, elapids, and hydrophiids.

In two dentitional characters, relative length of fang and number of palatine teeth, the crotalines show a proportionally greater number of species in the derived states. However, at the generic level, the two subfamilies do not diverge greatly in regard to palatine tooth numbers, and long fangs are not rare in the viperines.

As discussed, the pterygopalatine articulation is in the form of a saddle joint in most of the crotalines, occurring in all genera. In contrast, only one viperine was recorded as having this derived condition.

The remaining character of *Azemiops* in a derived state is the nature of the parietal walls. They are expanded in a bulbous fashion anteriorly in *Azemiops*, in one-fourth of the viperines, and in three crotaline species. This feature is rather well correlated with subterrestrial or fossorial habits among the colubrids, and is frequent in the secretive elapids. It is possible that this characteristic is so linked ecologically in *Azemiops*, an explanation that would also account for the apical pit situation, which is anomalous on phylogenetic grounds. Unfortunately, the habits of this snake are a mystery, although there is a hint that it may be subterrestrial. Its rarity in collections also suggests a rather secretive mode of life.

TABLE 2. Certain *Azemiops* characters compared to Viperinae and Crotalinae.

	Viperinae	Crotalinae	*Azemiops*
Anteroventral medial wing of prefrontal well developed (32-II)[1]	0	0	+
Posteroventral medial process of prefrontal present	0	0	+
Cerebral artery and posterior Vidian canal share common external foramen	0	0	+
Levator anguli oris muscle absent	0	0	+
Medial choanal process of palatine present	0	0[2]	+
Facial carotid artery passes dorsal to both maxillary and mandibular branches of the trigeminal nerve	0	+	+
Ectopterygoid-maxillary joint:			
Morphology	+	0	+
Movement	0	+	+
External facial sensory pit absent	+	0	+
Maxilla without pit	+	0	+
Pterygoideus glandulae muscle absent	+	0[2]	+
Venom gland duct coiled in adults	0	+[2]	+

[1] See Marx and Rabb, in press.

[2] Exceptions in *Agkistrodon*, see discussion of these characters.

Table 2 summarizes the characters examined in the main body of the text and in the preceding discussion. Again *Azemiops* can be seen to combine elements of crotaline and viperine morphology.

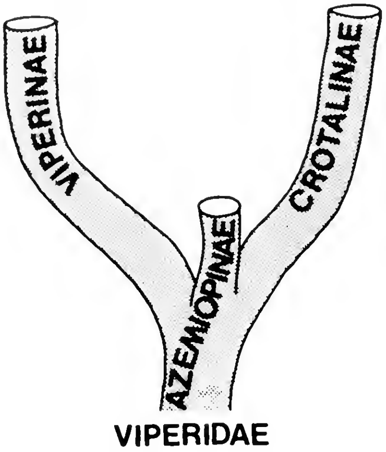


FIG. 16. Suggested phylogenetic relations of the subfamilies of Viperidae.

In addition, there are four conditions otherwise unknown in the Viperidae: a well-developed anteroventral vertical medial wing of the prefrontal, which we have found to be a primitive feature among the Colubroidea; a prominent posteroventral medial process of the prefrontal, a feature perhaps unique among the Colubroidea; the the lack of a distinct levator anguli oris muscle; and sharing of a common external foramen by the cerebral artery and posterior Vidian canal.

We conclude that *Azemiops* represents a distinct, primitive evolutionary line within the Viperidae. *Azemiops* displays few derived character states, and its primitive nature is also suggested by the several characteristics that are held in common with either *Agkistrodon* or *Causus*, generally acknowledged as basal stocks in the viperines and crotalines, respectively. Moreover, in its cephalic anatomy and particularly the feeding and envenomation apparatus, *Azemiops* often combines the morphology of the viperines and crotalines. Within the family context there are also substantial features unique to this taxon. We believe *Azemiops* arose as an early offshoot of the main line of vipers near the evolutionary paths to the crotalines and viperines (fig. 16). We feel that it would be useful for nomenclature to reflect this judgment in some measure, although there is little firm information on mode of life of *Azemiops* and incomplete knowledge of adaptive levels in snakes in general. One way to summarize our conclusions would be to drop subfamilial categories in the Viperidae. Such a recommendation is unlikely to achieve acceptance. The crotalines are well differentiated from the other viperids by the loreal pit organ and associated maxillary modifications. In addition, the geographic distributions of the crotalines and viperines are largely complementary and the ecological radiations of the groups involve many parallels. It has accordingly long been customary to recognize these natural assemblages of genera as subfamilies if not families. The intermediacy of *Azemiops* argues against separation of the groups at the family level. To recognize this intermediate unit thus involves establishment of a separate subfamily.

CLASSIFICATION

Family Viperidae, Bonaparte, 1840.

Definition.—Venomous solenoglyphous colubroid snakes with the following additional characteristics. Maxilla very short but deep-bodied, rotates around the maxillo-prefrontal joint in a parasagittal plane. Maxilla double socketed, and normally bears one hollow fang and its replacement teeth. Fang erection accomplished by anterodorsal movement of the palatomaxillary arch through contraction of the protractor pterygoidei and levator pterygoidei muscles. Adductor externus superficialis present. Quadratomaxillary ligament present. Lateral, maxillary process of palatine absent. Palatine and pterygoid joined. Postfrontal present. Hemipenis bifurcate; sulcus spermaticus bifurcate. Tracheal lung. Hypapophyses are present on the trunk vertebrae.

Contents.—Three subfamilies, 15 genera, about 163 species.

Azemiopinae, new subfamily.

Type genus.—*Azemiops,* Boulenger, 1888.

Subfamily diagnosis.—Anteroventral medial wing of prefrontal well developed; a prominent posteroventral medial process of prefrontal; levator anguli oris muscle absent; cerebral artery and posterior Vidian canal share common external foramen.

Subfamily description.—EXTERNAL CHARACTERS: Nine dorsal head shields; rostral single and rounded; nasal shield in contact with rostral and supralabials; nostril medially situated in nasal shield; no loreal pit; one loreal; one to two anterior temporals; interoculabials absent, eye in contact with supralabials; eye with vertical pupil; gular scales smooth; dorsal scales smooth; paired apical pits on body scales present only in neck area; tubercles on lateral head scales; anal divided or single; subcaudals paired.

SCALE COUNTS.—Mid-body scale rows, 17; supralabials, 6, third entering eye; infralabials, 7–8; preoculars, 2–3; postoculars, 1–2; ventrals, 170–196; subcaudals, 38–54. Maximum length, 770 mm. (Bourret, 1936); tail .114 to .176 of total length.

INTERNAL CHARACTERS.—Choanal process of palatine present; venom gland duct coiled in adult, straight in juvenile; maxillary pit lacking; fossa on maxilla for articulation with ectopterygoid; pterygopalatine junction a saddle joint; facial carotid artery passes dorsal to both maxillary and mandibular branches of the trigeminal nerve; pterygoideus glandulae muscle absent; left lung very small; spinous epizygapophyseal processes present on atlas and axis.

For further description of internal anatomy of head, see pp. 68–119 and tables; for additional characters see Marx and Rabb (in press). The hemipenis has been described by Pope (1935).

Contents.—Solely *Azemiops feae.*

Subfamily Crotalinae.

Subfamily definition.—Posterior Vidian canal separate from cerebral arterial foramen; levator anguli oris muscle present; anteroventral medial process of prefrontal very small or absent; no posteroventral medial process of prefrontal; pupil of eye vertical; loreal pit organ and associated maxillary pit present; fossa on anterior surface of ectopterygoid for articulation with maxilla; prefrontal-frontal articulation highly mobile, without dorsal medial or posterior horizontal processes of prefrontal; dorsomedial flange or long choanal process of palatine; facial carotid artery passes dorsal to both maxillary and mandibular branches of the trigeminal nerve.

Contents.—122 species currently placed in the genera *Agkistrodon, Trimeresurus, Bothrops, Lachesis, Sistrurus, Crotalus.*

Subfamily Viperinae.

Subfamily definition.—Posterior Vidian canal separate from cerebral arterial foramen; levator anguli oris muscle present; pterygoideus glandulae muscle absent; anteroventral medial process of prefrontal very small or absent; no posteroventral medial process of prefrontal; dorsomedial process of palatine not developed; eye separated from supralabials; dorsal scales keeled and possessing apical pits; no loreal or maxillary pit; fossa on maxilla for articulation with ectopterygoid; facial carotid artery ordinarily passes dorsal to the maxillary branch and ventral to the mandibular branch of the trigeminal nerve; venom duct straight in adults.

Contents.—40 species currently placed in the genera *Vipera, Eristicophis, Echis, Cerastes, Causus, Bitis, Atheris, Adenorhinos.*

(Characteristics used in the definitions and description apply to all forms included in the taxon, but are not necessarily exclusive.)

ACKNOWLEDGEMENTS

We appreciate beneficial discussions with, and critical comments from Hobart M. Smith, Thomas S. Olechowski, Garth Underwood, and Robert F. Inger. We wish to thank the National Science Foundation (Grant GB-5814) for financial support. Secretarial skills from Marilyn S. Belka and Adelle Miller, and X-rays by Kraig Adler are appreciated. Photos are the work of Homer Holdren; illustrations by Liem, Marx, Zbigniew Jastrzebski, and Peter R. Solt.

Jean Guibé (MHNP=Museum National d'Histoire Naturelle, Paris) and James A. Peters (USNM=United States National Museum) were kind enough to allow examination of specimens of *Azemiops feae,* particularly the skulls. Chicago Zoological Society (CZS) also furnished viper specimens for additional anatomical dissection. Samuel McDowell has kindly sent information on his own examinations of *Azemiops,* including the type, Museo civico di Storia Naturale di Genova 30891.

ANATOMICAL MATERIAL EXAMINED

Azemiopinae	
Azemiops feae	FMNH 152987, 170643, USNM 84363, MHNP 36-463
Viperinae	
Atheris hindii	FMNH 142082
hispidus	FMNH 154900
nitschei	FMNH 8986, 9902
squamiger	FMNH 58951
superciliaris	FMNH 171373
Bitis gabonica	CZS
Causus defilippii	FMNH 81128
Cerastes cerastes	CZS
Echis carinatus	FMNH 166971-72
Eristicophis macmahoni	FMNH 142681
Vipera ammodytes	CZS
aspis	FMNH 120975, 1599
berus	CZS
lebetina	FMNH 166970
persica	CZS (2 specimens)
	FMNH 166969, 19583, 20933, 170930, 166968, 109993
Crotalinae	
Agkistrodon acutus	FMNH 140109
bilineatus	CZS, FMNH 39093
contortrix	FMNH 110599
halys	CZS, FMNH 170638
hypnale	FMNH 122513, 142399
piscivorus	CZS (3 specimens)
rhodostoma	FMNH 11522, 169434
Bothrops atrox	FMNH 31743
Crotalus atrox	CZS
cerastes	CZS
viridis	CZS
Lachesis mutus	FMNH 154535
Sistrurus catenatus	CZS
Trimeresurus mucrosquamatus	FMNH 127243, 127245

Many additional skull specimens from Field Museum collections were used in comparative examinations (total of 150 viperid, 75 viperine, 75 crotaline).

REFERENCES

ALBRIGHT, R. G. and E. M. NELSON

1959a. Cranial kinetics of the generalized colubrid snake *Elaphe obsoleta quadrivittata*. I. Descriptive morphology. J. Morphol., **105**, pp. 193–240.

1959b. Cranial kinetics of the generalized colubrid snake *Elaphe obsoleta quadrivittata*. II. Functional morphology. J. Morphol., **105**, pp. 241–292.

ANTHONY, J.

1954. La signification des movements de l'os maxillaire chez les Vipéridés lors de la morsure. Compt. rend. sce. acad. Sci., **238**, pp. 2348–2349.

BOLTT, R. E. and R. F. EWER

1964. The functional anatomy of the head of the puff adder, *Bitis arietans* (Merr.). J. Morphol., **114**, pp. 83–106.

BOULENGER, G. A.

1888. An account of the Reptilia obtained in Burma, north of Tenasserim, by M. L. Fea, of the Genoa Civic Museum. Ann. Mus. Civ. Stor. Genova, (2) **6**, pp. 593–604.

BOURGEOIS, M.

1965. Contribution a la morphologie comparée du crane des ophidiens de l'Afrique Centrale. Public. Univ. Off. Congo, Lubumbashi, **18**, pp. 1–293.

BOURRET, R.

1936. Les serpents de l'Indochine. Toulouse. I, 496 pp.

BRATTSTROM, B. H.

1964. Evolution of the pit vipers. Trans. San Diego Soc. Nat. Hist., **13**, pp. 185–268.

CHERNOV, C. A.

1957. Systematic position of the poisonous snake *Ancistrodon rhodostoma* (Boie) (Serpentes, Crotalidae) in connection with its craniology. Zool. Zhurn., **36**, pp. 790–792.

DE BEER, G. R.

1958. Embryos and ancestors. Oxford Univ. Press, 197 pp.

DULLEMEIJER, P.

1956. The functional morphology of the head of the common viper, *Vipera berus* (L.). Arch neerl. zool., **11**, pp. 388–495.

1958. The mutual structural influence of the elements in a pattern. Arch neerl. zool., **13** (suppl.), pp. 74–88.

1959. A comparative functional anatomical study of the heads of some Viperidae. Morph. Jahrb., **99**, pp. 881–985.

FRAZZETTA, T. H.

1959. Studies on the morphology and function of the skull in the Boidae (Serpentes). Part I, Cranial differences between *Python sebae* and *Epicrates cenchris*. Bull. Mus. Comp. Zool., Harvard, **119**, pp. 453–472.

1966. Studies on the morphology and function of the skull in the Boidae (Serpentes). Part II, Morphology and function of the jaw apparatus in *Python sebae* and *Python molurus*. J. Morphol., **118**, pp. 217–296.

GADOW, H.

1901. Amphibia and reptiles. MacMillan, London, 650 pp.

GANS, C.

1966. Some limitations and approaches to problems in functional anatomy. Folia biotheoretica, **6**, pp. 41–50.

1969. Functional components versus mechanical units in descriptive morphology. J. Morphol., **128**, pp. 363–368.

HAAS, G.

1929. Versuch einer funktionellen Analyse des Giftbisses und Schlingaktes von *Lachesis gramineus*. Anat. Anz., **68**, pp. 358–378.

1931. Die Kiefermuskulatur und die Schadelmechanik der Schlangen in vergleichender Darstellung. Zool. Jahrb., Abt. Anat. Ontog., **53**, pp. 127–198.

1952. The head muscles of the genus *Causus* (Ophidia, Solenoglypha) and some remarks on the origin of the Solenoglypha. Proc. Zool. Soc. London, **122**, pp. 573–592.

1962. Remarques concernant les relations phylogéniques des diverses familles d'ophidiens fondées sur la differenciation de la musculature mandibulaire. Problems Actuels de Paléontologie. Colloques internationaux du Centre National de la Recherche scientifique, **104**, pp. 215–241.

KAMAL, A. M. and H. G. HAMMOUDA

1965. The columella auris of the snake, *Psammophis sibilans*. Anat. Anz., **116**, pp. 124–138.

KATHARINER, L.

1900. Die mechanik des Bisses der Solenoglyphen Giftschlangen. Biol. Zbl., **20**, pp. 45–53.

KLAUBER, L. M.

1939. A statistical study of the rattlesnakes. VI. Fangs. Occ. Papers San Diego Soc. Nat. Hist., **5**, 61 pp.

1956. Rattlesnakes, their habits, life histories, and influence on mankind. Univ. Calif. Press. 1,476 pp.

KOCHVA, E.

1958. The head muscles of *Vipera palaestinae* and their relation to the venom gland. J. Morphol., **102**, pp. 23–53.

1962. On the lateral jaw musculature of the Solenoglypha with remarks on some other snakes. J. Morphol., **110**, pp. 227–284.

1963. Development of the venom gland and trigeminal muscles in *Vipera palaestinae*. Acta Anat., **52**, pp. 49–89.

KOCHVA, E., M. SHAYER-WOLLBERG, and R. SOBOL

1967. The special pattern of the venom gland in *Atractaspis* and its bearing on the taxonomic status of the genus. Copeia, **1967**, pp. 763–772.

MARX, H. and T. S. OLECHOWSKI

1970. Fea's viper and the common gray shrew: a distribution note on predator and prey. J. Mammal., **51**, p. 205.

MARX, H. and G. B. RABB

1965. Relationships and zoogeography of the viperine snakes (family Viperidae). Fieldiana: Zool., **44**, pp. 161–206.

1970. Character analysis: an empirical approach applied to advanced snakes. J. Zool., London, **161**, pp. 525–548.

In press. Phyletic analysis of fifty characters of advanced snakes. Fieldiana, Zool.

McDowell, S. B.

1968. Affinities of the snakes called *Elaps lacteus* and *E. dorsalis*. J. Linn. Soc. (Zool.), **47**, pp. 561–578.

Phisalix, M.

1922. Animaux venimeux et venins. Masson, Paris, 2, 864 pp.

Pope, C. H.

1935. The reptiles of China. Nat. Hist. Central Asia, **10**, pp. 1–604.

Rathke, H.

1856. Über die Carotiden der Schlangen. Denkschr. Kais. Akad. Wiss., **11**(2):1–22.

Rosenberg, H. I.

1967. Histology, histochemistry and emptying mechanism of the venom glands of some elapid snakes. J. Morphol., **123**, pp. 133–156.

Scott, N. V., Jr.

1967. The colubrid snake, *Tropidodipsas annulifera*, with reference to the status of *Geatractus*, *Exelencophis*, *Chersodromus annulatus*, and *Tropidodipsas malacodryas*. Copeia, **1967**, pp. 280–286.

Throckmorton, L. H.

1962. The problem of phylogeny in the genus *Drosophila*. Stud. Genetics, **2**, p. 207–343.

Underwood, G.

1967a. A contribution to the classification of snakes. Brit. Mus. (Nat. Hist.), London, 179 pp.

1967b. A comprehensive approach to the classification of higher snakes. Herpetologica, **23**, pp. 161–168.

Van Bourgondien, T. M. and R. C. Bothner

1969. A comparative study of the arterial systems of some New World Crotalinae (Reptilia: Ophidia). Amer. Midl. Nat., **81**, pp. 107–147.

Van Riper, W.

1953. How a rattlesnake strikes. Sci. Amer., **189**, pp. 100–102.

Wolter, M.

1924. Die Giftdrüse von *Vipera berus*. Jena Z. Naturw., **60**, pp. 305–362.

Publication 1126