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**THE CRANIAL ANATOMY OF THE HOG-NOSED  
SNAKES (HETERODON)**

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# THE CRANIAL ANATOMY OF THE HOG-NOSED SNAKES (*HETERODON*)

W. G. Weaver, Jr.<sup>1</sup>

**SYNOPSIS:** The cranial osteology and myology of the Xenodontine snake genus *Heterodon* are described and correlated with certain aspects of the trunk musculature. Comparisons are made with the genus *Xenodon* and the viperidae.

*Heterodon*, and to a lesser extent *Xenodon*, are similar to the Viperidae in many features of their cranial and trunk myology.

A Xenodontine protoviper is hypothesized that gave rise to three present-day snake groups: (1) the advanced xenodontine snakes such as *Xenodon*, (2) the more primitive but specialized *Heterodon*, and (3) the vipers.

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<sup>1</sup> W. G. Weaver, Jr. is a graduate assistant at the Florida State Museum. This paper is a thesis presented to the graduate council of the University of Florida in partial fulfillment of the requirements for the degree of Master of Science. Manuscript submitted 28 Jan. 1965.

## INTRODUCTION

In a study of the lateral jaw musculature of *Causus*, Haas (1952) proposed that the solenoglyphs arose from aglyphous colubrids. Anthony (1955) reached a similar conclusion from his study of fang position. The primitive trunk musculature of the viperids indicates that an investigation of the trunk and cranial morphology of the primitive colubrids is in order. This paper describes briefly the cranial osteology and myology of a specialized primitive colubrid, *Heterodon*, and compares them with those of *Xenodon*, which some authors consider close to *Heterodon*. The cranial anatomy of *Heterodon* has never been described in detail, though Kellicott (1898) used *H. platyrhinos* as a general model for snake dissection. Haas (1931) and Anthony and Serra (1951) described the cranial anatomy of *Xenodon merremi*.

## MATERIALS

The myological descriptions are based on dissections of 25 *Heterodon platyrhinos*, 12 *H. simus*, 6 *H. nasicus*, 3 *Xenodon rabdocephalus*, and 1 *X. severus*. The osteological descriptions are based on skeletons of 11 *H. platyrhinos*, 7 *H. simus*, 2 *H. nasicus*, 1 *X. merrimi*, and 2 *X. rabdocephalus*. In addition I dissected specimens of *Agkistrodon*, *Bothrops*, *Crotalus*, *Trimeresurus*, and *Vipera* among the Viperidae, *Constrictor* and *Eunectes* of the Boidae, and *Coluber*, *Elaphe*, *Lampropeltis*, *Natrix*, and *Thamnophis* of the Colubridae. I have conformed where possible to the myological nomenclature outlined by Kochva (1962).

## SYSTEMATIC POSITION OF *Heterodon* AND *Xenodon*

The poor fossil record of colubrid snakes forces greater reliance on a horizontal classification. Cope (1900) organized the subfamilies of the Colubridae on the basis of hemipenial structure and the presence or absence of vertebral hypapophyses. He placed *Heterodon* in the Dromicinae, a group he reserved for aglyphous colubrids having a calyculate hemipenis with a double sulcus. *Xenodon* and *Lystrophis*, genera he considered superficially similar to *Heterodon*, he placed in the Xenodontinae, aglyphous forms in which the hemipenis has a double sulcus and an apical disk.

Dunn (1928), using Cope's characters plus certain features of the dentary bone, grouped *Heterodon*, *Xenodon*, *Lystrophis*, and most of the South American colubrids into the Ophiinae (Cope's Xenodontinae). He defined the Ophiinae as South American (mostly) aglyphous

or opisthoglyphous colubrids with or without vertebral hypopophyses, and hemipenes with basal spines and distal calyces or apical disks.

Bogert (1940) found Dunn's definition of the subfamilies Natricinae and Ophiinae inadequate for Old World genera. Schmidt (1949) and Romer (1956) concurred in not recognizing the two subfamilies. Smith (1964) proposed resurrecting the Heterodontinae, a name proposed by Bonaparte in 1845 but not widely accepted. It includes *Heterodon*, *Xenodon*, *Lystrophis*, and perhaps *Lioheterodon* and others. The characters of the Heterodontinae, as redefined by Smith (1964; 291), are: "... bufophagous colubrid snakes having greatly enlarged adrenals, a viperid type trunk musculature, a viperid type jaw musculature, and a pro-viperid or viperid type of cranial kinesis." Rossman and Wilson (1965) objected to the name Heterodontinae because of the nomenclatural complexities and inconsistencies its formal adoption would involve. Smith concurred and withdrew his proposal.

Little has been published about the relationships of the species within the genus *Heterodon*, which Auffenberg (1963) split into two groups on the basis of vertebral characters, a *platyrhinos* group and a *nasicus-simus* group. The Pliocene forms, *H. brevis* (Auffenberg, 1963) and *H. plionasicus* (Peters, 1953), are considered ancestral to *H. platyrhinos* and *H. nasicus*, respectively.

#### DISTRIBUTION OF *Heterodon* AND *Xenodon*

The earliest fossil records for *Heterodon* are from the Pliocene of Florida and Kansas (Auffenberg, 1963; Peters, 1953). The geographic range of the genus is completely within North America east of the Rocky Mountain chain (Edgren, 1952). Pleistocene records are all within the ranges of the three extant species. The largest of these, *Heterodon platyrhinos*, is a forest species of the eastern United States, restricted to river bottom forests in the central prairie regions and extending as far as southwestern South Dakota in ecologically suitable localities. *H. simus*, the smallest species, is almost entirely confined to more xeric situations throughout the southeastern coastal plain. *H. nasicus*, intermediate in size, is a snake of sandy areas within the central plains of Canada and south to Tamaulipas and San Luis Potosi, Mexico.

How many species comprise the genus *Xenodon* is not yet clear. Most of them occur in South and Central America, and only one extends northward into Mexico (Smith and Taylor, 1945).

## CRANIAL OSTEOLOGY

The skull is considered in terms of the six functional units set forth by Albright and Nelson (1959): Cranial, nasal, palato-maxillary, mandibular, hyoid, and vertebral.

## THE CRANIAL UNIT

The cranium consists of 2 frontals, 2 pre- and 2 postfrontals, an occipital complex, 1 sphenoid, 2 pro-otics and 2 columellae auris. The pre- and postfrontals and columellae are slightly movable.

**FRONTALS.** The frontals (fig. 1) are rectangular in shape dorsally, and separated anteriorly by a grooved vertical septum. The lateral walls converge ventrally to the narrow anterior projection of the sphenoid. The dorsomedial surface is raised in a longitudinal swelling which expands anterolaterally. The length of the bone in *Heterodon nasicus* is shorter in relation to its width than the same element in *H. platyrhinos*. *H. simus* is intermediate in this respect. In *Xenodon* the frontals have a wide medial posterior extension which fits into a notch in the parietal. The frontoparietal joint in *Heterodon* is nearly straight.

**PREFRONTALS.** The prefrontals articulate dorsally with the frontals and ventrally with the dorsal surface of the anteromedial process of the maxillary and the lateral process of the palatine. These latter two connections are flexible. The bone is wider ventrally than dorsally and is perforated by a large rostrally-directed fenestra in the ventrolateral corner.

**POSTFRONTALS.** The postfrontals are slender, crescent-shaped bones attached dorsally to the anterior edge of the lateral horizontal process of the parietal and by ligaments to the maxillary and prefrontal bones. The pre- and postfrontals of both genera are similar (fig. 2).

**PARIETAL.** The parietal is the largest of the skull bones. Its dorsal surface is shaped like an unequal hexagon (fig. 1). The lateral borders expand posterolaterally into a horizontal lateral process which contains a groove for the postfrontal on its anterior edge. The posterior lateral wall is expanded as a vertical lateral process ventral to the horizontal lateral process. A vertical wall that slants ventro-rostrally forms the posterior border of both these processes and provides an origin for the adductor externus medialis, adductor externus profundus and the levator pterygoidei. The posterolateral border joins the pro-otic and the posteroventral surface joins the sphenoid. The parietal of *Xenodon* has a pair of dorsolateral grooves that start

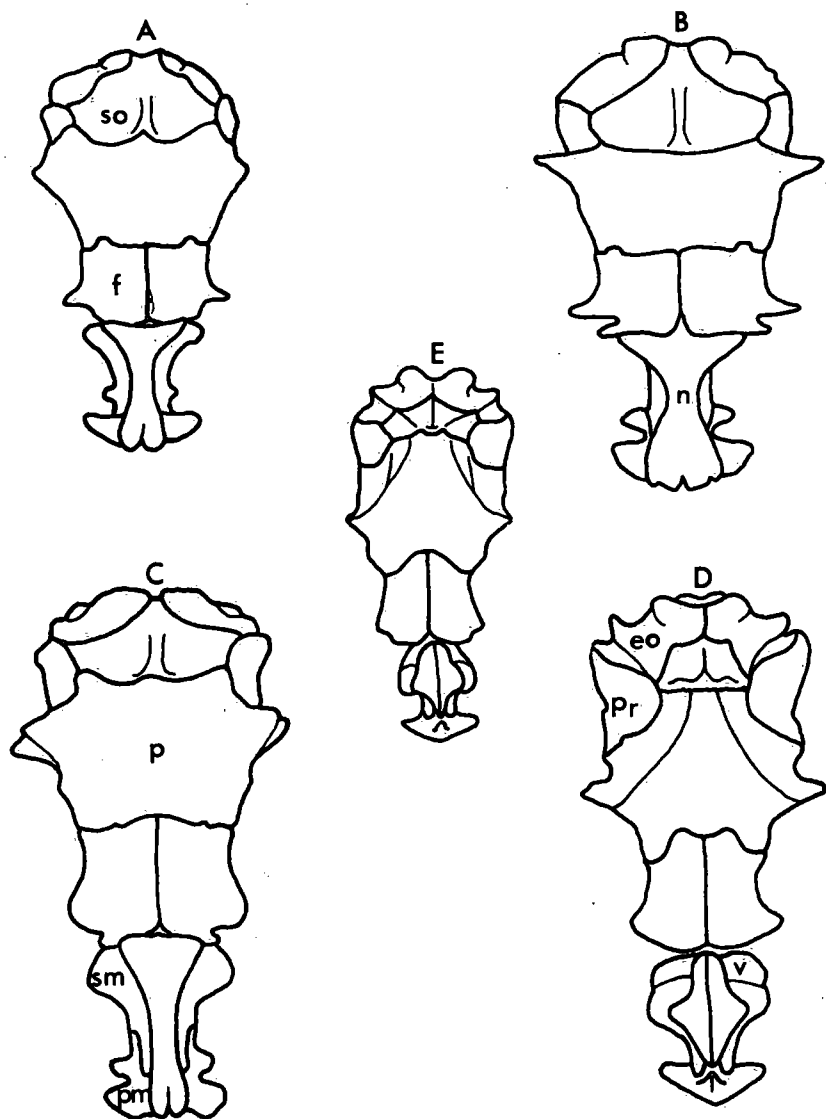


Figure 1. Dorsal view of skull. A, *Heterodon simus*; B, *H. nasicus*; C, *H. platyrhinos*; D, *Xenodon merremi*; E, *X. rabdocephalus*; Abbreviations: eo, exoccipital; f, frontal; n, nasal; p, parietal; pm, premaxillary; pr, pro-otic; sm, septomaxillary; so, supraoccipital; v, vomer.

from the postfrontals and converge posteriorly. These grooves furnish an origin for the muscles listed above. In *Heterodon* the grooves are shortened into the steep ventrorostrally-inclined walls.

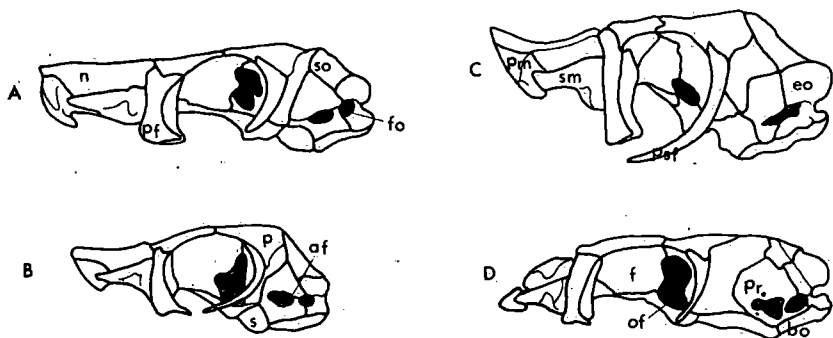


Figure 2. Lateral view of skull. A, *Heterodon platyrhinos*; B, *H. simus*; C, *H. nasicus*; D, *Xenodon rabdocephalus*; Abbreviations: af, anterior pro-otic foramen; bo, basioccipital; eo, exoccipital; f, frontal; fo, foramen ovale; n, nasal; of, orbital foramen; p, parietal; pf, prefrontal; pm, premaxillary; pr, pro-otic; psf, postfrontal; s, sphenoid; sm, septomaxillary; so, suproccipital; v, vomer.

The large orbital foramen in the lateral parietal wall is bilobed in all the species of *Xenodon* examined and in *Heterodon platyrhinos*. The dorsal lobe of the foramen is narrowed in *H. simus* and absent in *H. nasicus* (fig. 2). It is bounded anteriorly by the lateral parietal wall and ventrally by the sphenoid. *H. simus* and *H. nasicus* the parietal is relatively wider than in *H. platyrhinos* and its posterior dorsal surface swells dorsally to meet the supraoccipital; this surface is flattened in *H. platyrhinos*.

**PRO-OTIC.** The pro-otic is pentagonal; it connects with the parietal, the supra- and exoccipitals, and houses the base of the long, slender columella auris. The columella arises from a footplate within the foramen and extends posteriorly, roughly parallel and ventral to the squamosal. The anterior pro-otic foramen is entirely confined to the pro-otic bone. A lateral ridge dorsal to both foramina proceeds from the ventral anterior border posterodorsally to the end of the bone. The foramen ovale is larger in *Xenodon* than in *Heterodon*. In *Xenodon* the anterior foramen is associated with two or three smaller foramina which appear to be incorporated in the anterior pro-otic foramen in *Heterodon*.

**OCCIPITALS.** Four occipital bones comprise the rear of the brain case. In *Heterodon* most of the occipital condyle is on the basioccipital; in



*Xenodon*: it is mostly on the exoccipitals. All the occipital bones in *Heterodon* border on the foramen magnum except in *H. platyrhinos*, in which the supraoccipital sometimes does not. In *Xenodon* the supraoccipital is much smaller than in *Heterodon* and does not intrude into the dorsal border of the foramen magnum. As McDowell and Bogert (1954) note, supraoccipital participation in the border of the foramen magnum is rare in snakes; it has been reported elsewhere only in *Phyllorhynchus* and *Dasypeltis*; in the Tropical American Boinae the supraoccipital overlaps the exoccipitals. The sagittal crest is more prominent in *Xenodon* than in *Heterodon*.

**SPHENOID.** The sphenoid (fig. 3) is an arrow-shaped bone that forms the floor of the braincase. Its anterior portion extends rostrally from its wide posterior end to the frontals as a tapering finger of bone.

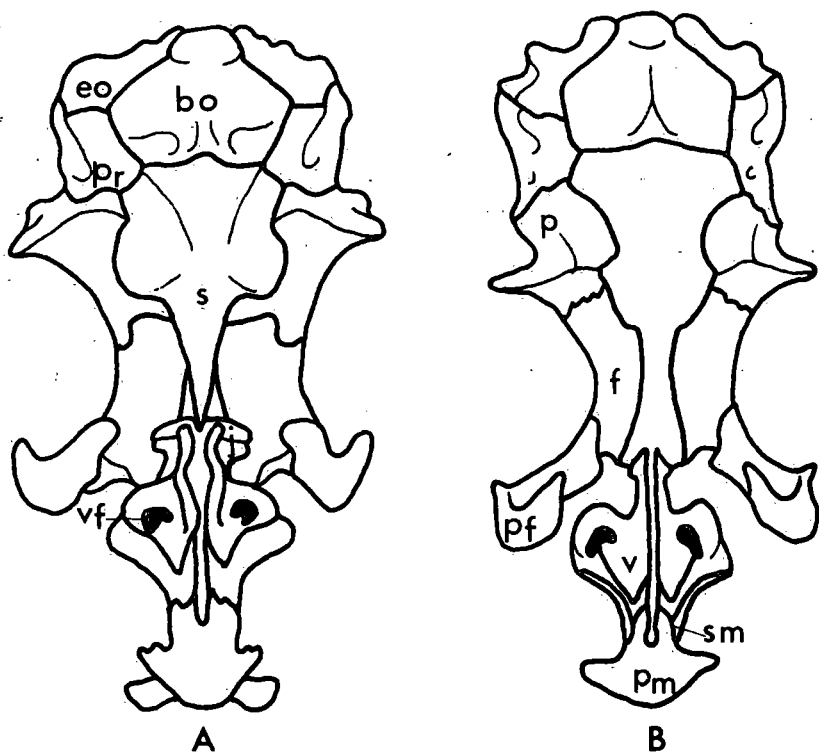


Figure 3. Ventral view of skull. A, *Heterodon platyrhinos*; B, *Xenodon merremi*. Abbreviations: bo, basioccipital; eo, exoccipital; f, frontal; j, septo-maxillary-frontal joint; p, parietal; pf, prefrontal; pm, premaxillary; pr, pro-otic; s, sphenoid; sm, septomaxillary; v, vomer; vf, ventral vomerine foramen.

The broad posterior end of the bone furnishes an origin for most of the constrictor dorsalis complex. On each side near the posterior end is a dorsally concave ventrolateral process. A large groove from the pro-otic extends anteroventrally to the sphenoid for insertion of the retractor pterygoidei. The posterior midline of the sphenoid in both genera tends to project ventrally. The groove from the pro-otic is absent in *Xenodon*, being blocked by an elevated flange along the sphenoid-pro-otic and the sphenoid-basioccipital borders. The bone's general features are more similar to one another in *Heterodon* and *Xenodon* than either are to other genera examined.

#### THE NASAL UNIT

The nasal unit consists of a premaxillary, a nasal, two septomaxillaries, and two vomers.

**PREMAXILLARY.** In *Heterodon* the premaxillary is flattened anteroposteriorly and consists of a vertical median bar arising from a ventrally directed horizontal bar. On each side and posterior to the vertical bar a dorsolateral expansion gives the bone a characteristic flared appearance (fig. 4). In side view the premaxillary is severely inclined forward in *H. nasicus*, less in *H. simus*, and is nearly vertical in *H. platyrhinos* (fig. 2). In *H. nasicus* the dorsal edge of the premaxillary and the anterior edge of the nasal bone show a greater degree of interdigitation than in either *H. simus* or *H. platyrhinos*. The distal borders of the dorsolateral expansions are crenate in *H. platyrhinos* (fig. 4) and smooth in the other two species. Both *H. nasicus* and *H. simus* show depressions on the medial anterior face of the premaxillary. These depressions are most extensive in *H. platyrhinos*. The dorsal edge of the premaxillary is thicker in *H. simus* and *H. nasicus* than in *H. platyrhinos*.

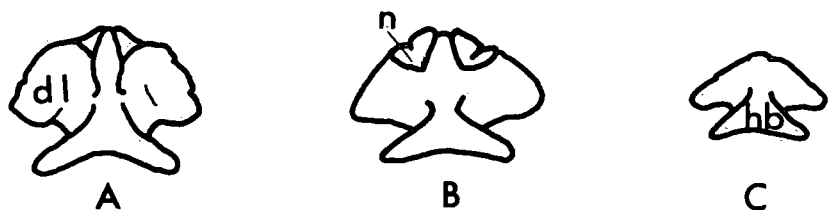


Figure 4. Anterior view of the premaxillary of *Heterodon*. A, *H. platyrhinos*; B, *H. nasicus*; C, *H. simus*; Abbreviations: dl, dorsolateral expansion; hb, horizontal bar; n, nasal.

The premaxillary of *Xenodon* is generalized and resembles that of *Thamnophis*, *Elaphe*, or *Coluber*. In *Heterodon* the premaxillary attaches to the ventral surface of the septomaxillary by a broad, thin process. In *Xenodon* the process is narrow and attaches to the medioventral surface of the septomaxillary.

**NASALS.** The nasals are wedge-shaped in cross-section, medially fused, and expanded posteriorly and anteriorly. The posterior expansion, particularly noticeable in *H. nasicus* (fig. 1), is so placed it restricts vertical rotation of the nasal unit about the frontals. The nasals of *Xenodon* are neither elongate nor posteriorly expanded and are widest in the middle (fig. 1).

**SEPTOMAXILLARIES.** The septomaxillaries lie parallel and ventral to each side of the nasal. Slender anteriorly, they expand posteriorly into a lateral process curved dorsally at its tip. A posterior process acts as an articular projection fitting into the anterior ventro-medial border of the frontal. Thus the two septomaxillaries form a two-pronged point of dorsoventral rotation for the nasal unit (fig. 3). In *Xenodon* the septomaxillary does not cover the entire dorsal surface of the vomer.

**VOMERS.** Posterior and ventral to the septomaxillaries are the vomers. A bulb-like expansion occurs on the lateroposterior border of each. Projecting from its medioposterior border each vomer has a thin vertical process that is pierced ventrally by a foramen. The dorsal edge of the vertical process is the insertion of the retractor vomeris. In *Xenodon* the bulb-like expansion projects dorsally, forming a conspicuous bulge that is completed posteriorly by the posterior portion of the septomaxillary. Both genera have a foramen on the ventral surface of the vomer. The opening is rounded in *Heterodon* and crescent-shaped in *Xenodon*. Medial to each foramen a thin, longitudinal ridge extends posteriorly to take part in the posterior vertical process. The anteromedial border of the ventral vomerine foramen has a rostrally directed ridge medially delimiting the anteroventral border of the bone.

#### THE PALATO-MAXILLARY UNIT

The palatine, pterygoid, maxillary, and ectopterygoid function as a unit on each side of the head.

**MAXILLARIES.** The maxillary forms the anterior lateral border of the chain of associated elements. It has two ventrally-directed medial processes (fig. 5). The posterior process is on the medioventral sur-

face of the bone, anterior to the enlarged teeth. The enlarged anterior tooth arises from a socket on the posterior border of this process. The dorsal surface of the process is connected, via a loose band of connective tissue, to the medial arm of the ectopterygoid fork. Contrary to Ditmar's report (1912), I found no grooves in the two enlarged caudal teeth. The maxillary is shorter relative to basioccipital length in *H. nasicus* and *H. simus* than in *H. platyrhinos*, and in *Xenodon* than in *Heterodon*.

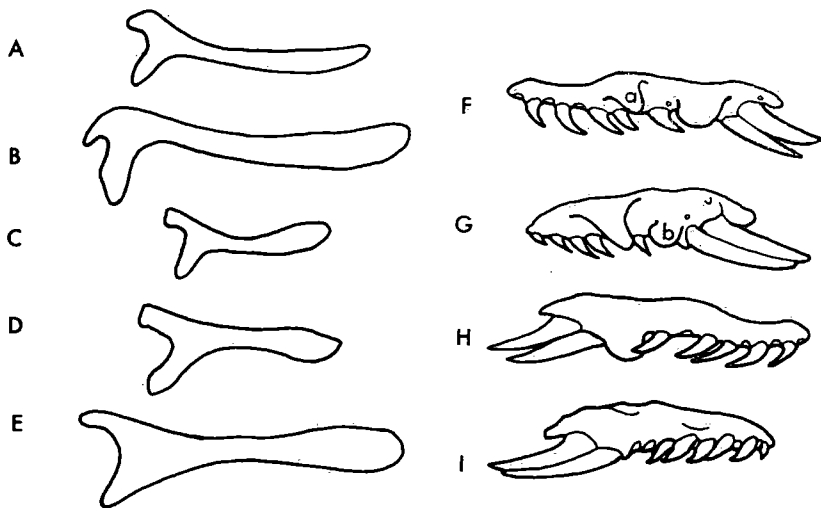


Figure 5. Ectopterygoid and maxillary bones of *Heterodon* and *Xenodon*. Left, dorsal view of right ectopterygoid. Right, medial and lateral view of maxillary. A, *Xenodon rabdocephalus*; B, *Xenodon merremi*; C, *Heterodon simus*; D, *Heterodon nasicus*; E, *Heterodon platyrhinos*; F, *Heterodon platyrhinos* (Medial view); G, *Xenodon merremi* (Medial view); H, *Heterodon platyrhinos* (lateral view); I, *Xenodon merremi* (lateral view); Abbreviations: a, anterior medial process; b, posterior medial process.

**PTERYGOIDS.** The laterally flattened pterygoid (fig. 6) is bent laterally at a point near the posterior end of the tooth row. Dorsal to the middle of the tooth row the bone gives off a lateral process which is widest anteriorly and in *H. platyrhinos* is furnished with an anteriorly directed finger of bone. On the dorsal surface of the lateral process the same species has a wide groove which receives the ectopterygoid. Both these latter features are absent from the pterygoids of the other two species of *Heterodon*. The angle of the lateral bend is greater in *H. nasicus* and *H. simus* than in *H. platyrhinos*. The pterygoid

tooth row is relatively longer in *Xenodon* than in *Heterodon*, and the posteroventral side is deeply grooved as opposed to the flattened posterior end in *Heterodon*. The anterior bony finger of the lateral pterygoid process in *H. platyrhinos* is missing in *Xenodon*. In addition the lateral process arises closer to the anterior end of the tooth row in *Xenodon*.

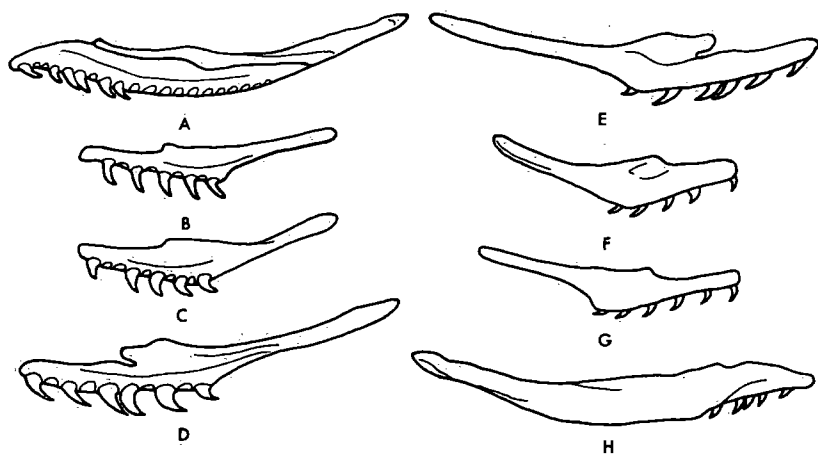


Figure 6. Pterygoid bone of *Heterodon* and *Xenodon*. Left, ventrolateral view. Right, dorsomedial view. A, *Xenodon merremi*; B, *Heterodon simus*; C, *Heterodon nasicus*; D, *Heterodon platyrhinos*; E, *Heterodon platyrhinos*; F, *Heterodon nasicus*; G, *Heterodon simus*; H, *Xenodon merremi*.

**PALATINES.** The palatine lies anterior to the pterygoid. A large anteriorly-arched medial process near the middle of the bone is curved ventroposteriorly at its tip. The medial palatine process extends anteriorly nearly to the vertical posterior process of the vomer. In *Heterodon* it makes contact with the sphenoid, as in *Xenodon* or more generalized colubrids such as *Elaphe* or *Thamnophis*. The medial arched process curves ventrally, but not posteriorly in *Xenodon*. A smaller lateral process expands posteriorly on the anterior end.

**ECTOPTERYGOIDS.** The ectopterygoids (fig. 5) are dorsoventrally flattened and forked anteriorly. The forked end lies over the posterior end of the maxillary. They are longer relative to the basioccipital in *H. platyrhinos* than in *H. simus* or *H. nasicus*. The forked anterior ends are bent sharply mediad in *Xenodon* as opposed to the simple "Y" in *Heterodon*.

## THE MANDIBULAR UNIT

This unit consists of two mandibles, two quadrates, and two supratemporals.

**SUPRATEMPORALS.** The supratemporals are laterally flattened and approximately half the length of the quadrates. The posterior ends are medially twisted to allow for the medial angle of the quadrate. The anterior ends of the supratemporals lie against the parietal posterior to the vertical lateral process. The posterior ends extend over the pro-otic and are supported by the dorsally inclined lateral pro-otic ridge which restricts movement in a ventral arc. In *Xenodon* the supratemporals are longer than half the quadrate length and are not medially rotated.

**QUADRATES.** The quadrates (fig. 7) are elongate, flattened proximally for the supratemporal articulation, and connected to the mandibles by a saddle joint. The proximal edges are expanded posteriorly into a rounded flange. A weak vertical process occurs on the posterior edge of each shank, about one third the length of the bone from the distal end, for a cartilaginous connection with the columella. In

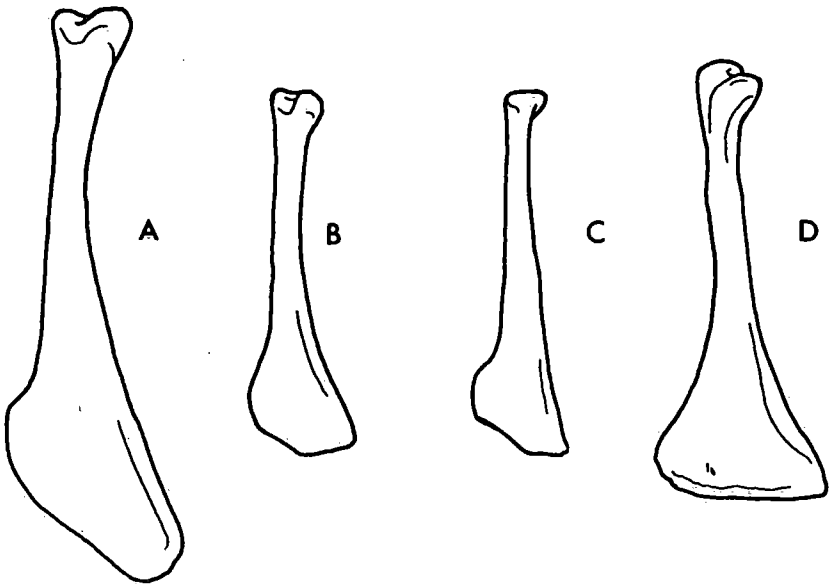


Figure 7. Quadrate bone of *Heterodon* and *Xenodon*. A, *Heterodon platyrhinos*; B, *H. nasicus*; C, *H. simus*; D, *Xenodon merremi*. Proximal end of bone is expanded.

*Xenodon* the proximal end is truncated and the vertical process on the shank is strongly developed.

**MANDIBLES.** The mandibles (fig. 8) consist of four bones, the compound, dentary, angular, and splenial. Only the dentary bears teeth. The angular is fused to the anterior ventrolateral border of the compound bone. The sliver-like splenial lies on the medial posterior surface of the dentary and is pierced at the posterior end by a foramen.

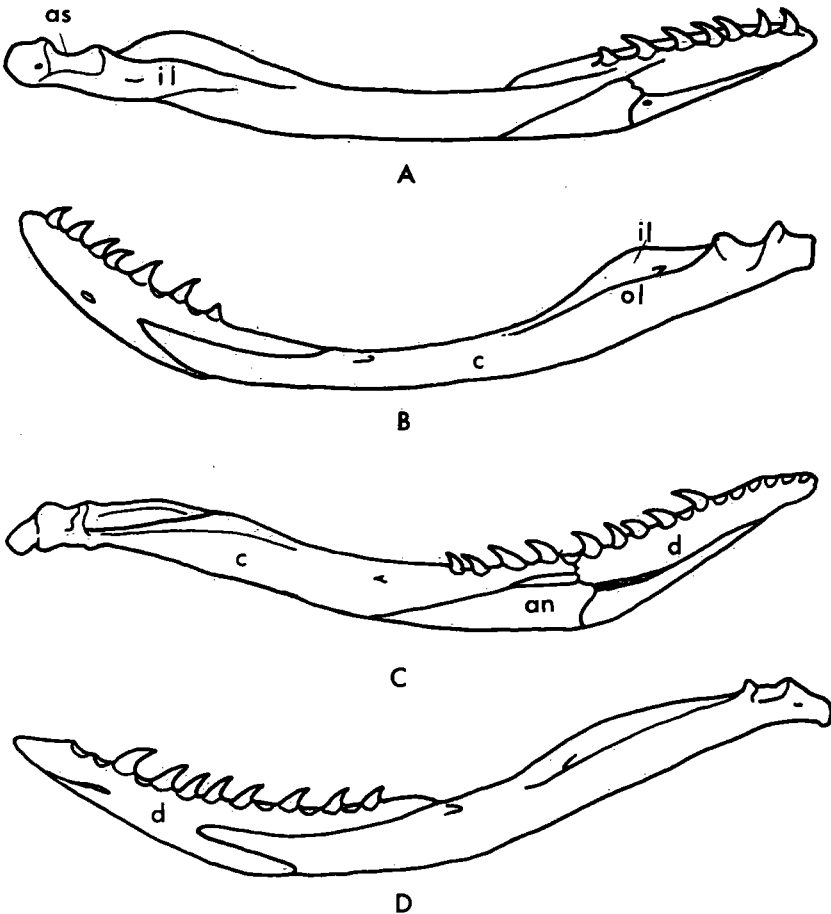


Figure 8. The mandible of *Heterodon* and *Xenodon*. A, *Heterodon platyrhinos* (medial view); B, *Heterodon platyrhinos* (lateral view); C, *Xenodon merremi* (medial view); D, *Xenodon merremi* (lateral view). Abbreviations: as, articular surface for quadrate; an, angular; c, compound; d, dentary; il, inner lamella; ol, outer lamella, Mandibular fossa located between outer and inner lamellae.

The dentary is relatively shorter with respect to the compound bone in *Heterodon* than in *Xenodon*, *Elaphe*, *Coluber*, or *Thamnophis*. As the laminae are weakly developed, the mandibular fossa is shallow. In *H. nasicus*, and to some degree in *H. simus*, the inner lamina is conspicuously higher and more pointed than in *H. platyrhinos*. However (Auffenberg, 1955) has shown the shape of the laminae to vary ontogenetically in *Coluber*. The medial side of the inner surangular lamina is recessed for attachment of the adductor posterior profundus and the lateral head of the pterygoideus. In *Heterodon* the mandible is relatively shorter than in *Xenodon* and the angular bone is very thick and offset medially along its entire length. The dentary of *Xenodon* is approximately half the mandibular length, as opposed to one third the mandibular length in *Heterodon*. The lateral dentary foramen extends anteriorly as a shallow groove in *Xenodon* and the mandibular fossa is shallow, as in *Heterodon*. Considerable lateral movement of the dentary is possible in both genera.

#### THE HYOID UNIT

The hyoid apparatus is shaped like a hairpin with the loop anterior. In *Heterodon* the basihyal is round and has no anterior projection. In *Xenodon* a cartilaginous anterior projection from the basihyal is present, as it is in *Vipera palestinae* and *Bothrops*. I could find no separation into a first or second ceratohyal as Cowan and Hick (1951) reported in *Thamnophis*. The pattern of the hyoid apparatus fits Smith's (1948) classification which combines the Colubridae, Solenoglyphae, Elapidae, and Hydrophiidae into a single group with regard to hyoid configuration.

#### THE VERTEBRAL UNIT

This unit is not strictly within the scope of this paper; it is treated only where the description of muscle attachments warrants.

### CRANIAL MYOLOGY

#### THE ADDUCTORES MANDIBULAE

The fibers of these muscles are directed dorsoventrally except those of the pterygoideus which are more or less horizontal to the longitudinal plane of the skull. Embryologically the adductors are derived from the adductor externus medialis. This suggests that the sauropsidians evolved from forms having a single adductor which subsequently split into three major parts. In turn each of the major



parts may undergo various divisions (Edgeworth, 1935). The adductores mandibulae unite the mandibular unit of the skull with the cranial and palato-maxillary unit.

**M. ADDUCTOR EXTERNUS SUPERFICIALIS.** This is the most lateral cranial muscle. It originates from the posterior side of the postfrontal and passes medially to the large Harderian gland and around the posterior angle of the mouth to the dorsolateral posterior end of the dentary. This muscle differs from its counterparts in *Thamnophis*, *Elaphe*, and *Natrix* in that: (1) it curves anteriorly after passing the posterior mouth angle and (2) it is not associated with an aponeurosis. The forward curve of this muscle (fig. 9) is reminiscent of the vipers and was used by Smith (1964) as one of the characters of the Heterodontinae. In *Xenodon* the muscle lies over the dorsolateral surface of the Harderian gland. It extends posteroventrally from the postfrontal to the anterior lateral surface of the adductor externus profundus where it becomes involved in a large aponeurosis. Haas (1931) reported some fibers curving forward around the posterior

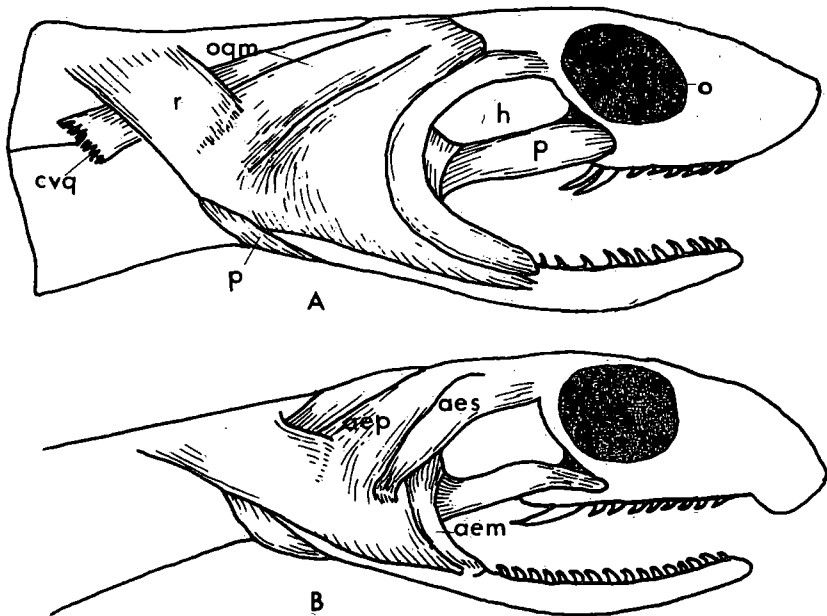


Figure 9. Lateral view of superficial cranial muscles of *Heterodon* and *Xenodon*. A, *Heterodon platyrhinos*; B, *Xenodon rabdocephalus*; Abbreviations: aes, adductor externus superficialis; aep, adductor externus profundus; aem, adductor externus medialis; p, pterygoideus; r, retractorquadrati; cvq, cervico-quadratus; h, harderian gland; o, orbit; o-q-m, depressor mandibulae.

angle of the mouth to insert on the mandible in *X. merremi*, a condition I found duplicated in *X. severus*. Specimens of *X. rabdocephalus* show no clear-cut mandibular attachment.

M. ADDUCTOR EXTERNUS MEDIALIS. This muscle originates from the posterolateral surface of the parietal. Its fibers are closely associated with the medial posterior border of the adductor externus superficialis and the medial anterior border of the adductor externus profundus. The insertion is on the compound bone posterior and medial to the insertion of the adductor externus superficialis. This muscle is more distinct in *H. simus* and *H. nasicus* than in *H. platyrhinos*. In *Xenodon* the adductor externus medialis is very distinct and makes a slight bend forward as it does in *Heterodon*.

M. ADDUCTOR EXTERNUS PROFUNDUS. This is a thick triangular muscle with the apex at the quadrato-mandibular joint. It arises from the anterior lateral surface of the quadrate and inserts on the lateral border of the mandibular fossa forward and lateral of the insertion of the adductor externus superficialis.

M. ADDUCTOR POSTERIOR SUPERFICIALIS. This thin muscle arises from the entire anterior surface of the quadrate and inserts in the mandibular fossa. The anterior border is bounded by the mandibular branch of the trigeminal nerve.

M. ADDUCTOR POSTERIOR PROFUNDUS. This thick columnar muscle originates from the medial surface of the quadrate and inserts on the posterior medial border of the mandibular fossa. In *Xenodon* it is triangular, as in *Elaphe* and *Thamnophis*.

M. PTERYGOIDEUS. This heavy, two-headed muscle arises from the lateral arm of the ectopterygoid via a strap-like tendon. The lateral head extends posteroventrally from the dorsal surface of the tendon to the anterior medial side of the mandibular fossa. The mandibular branch of the fifth cranial nerve separates the posterior edge of this slip from the anterior border of the adductor posterior superficialis. The posterior head is the largest part of the muscle and forms a conspicuous belly near its origin on the posterior medial end of the compound bone and the quadrate-compound joint. In *Xenodon* the lateral head is reduced.

M. PTERYGOIDEUS ACCESSORIUS. The pars posterior is a flat muscle originating from the pterygo-ectopterygoid joint and the adjacent portion of the pterygoid. It extends posterolaterally to insert on the medial posterior end of the compound bone.

**M. PSEUDOTEMPORALIS.** This thin flat muscle lies medial to the pterygoideus accessorius. The origin is the posterior dorsal edge of the postfrontal. It extends posteroventrally to the dorsolateral surface of the compound bone anterior to the lateral head of the pterygoideus. This muscle is best developed in *H. nasicus* and *H. simus*.

#### THE CONSTRICTOR DORSALIS

The constrictor dorsalis (fig. 10) is derived embryologically from the dorsal masticatory muscle plate which subsequently divides into slips inserting on the pterygoid, vomer, and quadrate. The simplest condition of this group is found in *Sphenodon*, a rhynchocephalian (Edgeworth, 1935). The presence of a constrictor dorsalis is characteristic of forms with kinetic skulls, and its degree of development in reptiles reflects the degree of cranial kinesis (Ostrom, 1962). The constrictor dorsalis unites the cranium with the mandibular unit, the palatamaxillary unit, and the nasal unit.

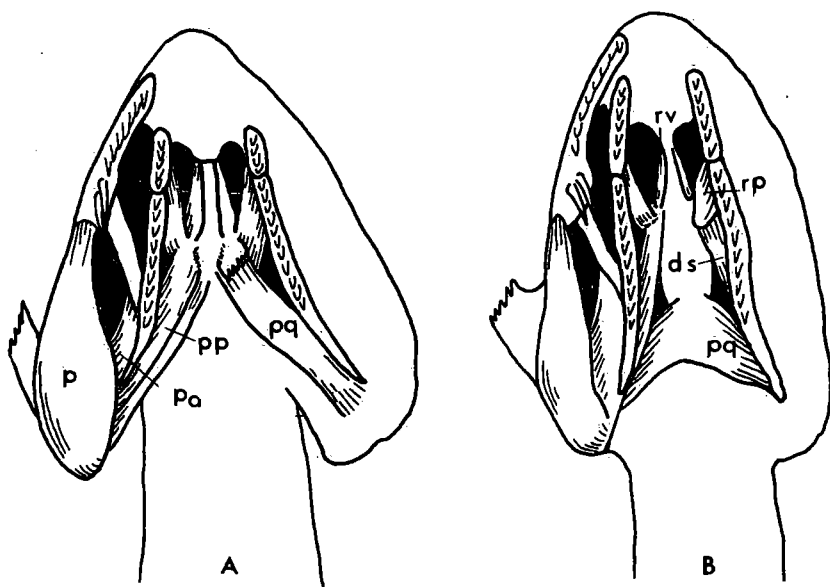


Figure 10. Ventral view of cranial musculature in *Heterodon* and *Xenodon*. A, *Heterodon platyrhinos*; B, *Xenodon rabdocephalus*; Abbreviations: ds, dorsal slip of protractor pterygoidei (pp removed on right side); pa, pterygoideus accessorius; p, pterygoideus; pp, protractor pterygoidei; pq, protractor quadrati; rp, retractor pterygoidei; rv, retractor vomeris.

**M. PROTRACTOR QUADRATI.** The protractor quadratus is a flat, thin muscle arising from the fascia over the ventral semispinalis muscles. It extends posterolaterally to the distal end of the quadrate and lies dorsal to the entire length of the protractor pterygoideus. In *Xenodon* it arises posterior to the protractor pterygoidei and extends laterally, dorsally overlapping the latter only with its distal end.

**M. PROTRACTOR PTERYGOIDEI.** This strap-like muscle issues from the midline of the sphenoid anterior to the sphenoid-basioccipital junction. It extends posterolaterally to the medial side of the pterygoid near the pterygoid-quadrate junction. In *Xenodon* the muscle attaches medially to the pterygoid from the end of the tooth row to the distal end of the bone. In addition all the *Xenodon* examined had a thin, narrow muscle located dorsally to the protractor pterygoidei. This muscle, here considered a slip of the protractor pterygoidei, originates from the lateral sphenoid border anterior to the pro-otic and extends posterolaterally to the dorsomedial surface of the pterygoid at a point medial and midway to the insertion of the levator pterygoidei.

**M. LEVATOR PTERYGOIDEI.** This fan-shaped muscle arises from the lateral vertical wall of the parietal medial to the dorsal end of the post-frontal. The ventrally directed fibers fan out posteriorly for insertion on the posterior dorsolateral edge of the pterygoid. The wide insertion extends from the rear pterygoid teeth to the distal end of the bone.

**M. RETRACTOR PTERYGOIDEI.** The origin of this thick muscle is the groove extending ventroanteriorly through the pro-otic and sphenoid bones. It extends anteroventrally to the medial border of the pterygoid and palatine bones at their junction. The muscle arises from the sphenoid midline in *Xenodon*, *Thamnophis*, *Elaphe*, and *Natrix* (Cowan and Hick, 1951; Adams, 1925; Albright and Nelson, 1959). A high origin, not unlike the one in *Heterodon*, exists in *Crotalus adamanteus* and *Agkistrodon picivorus* among the vipers.

**M. RECTRACTOR VOMERIS.** This short cylindrical muscle originates from the sphenoid anterior to the origin of the protractor pterygoidei. The insertion is on the ventral posterior end of the vomer.

#### THE INTERMANDIBULAR MUSCLES

The intermandibular muscles are presumed to have developed from a primordial single muscle sheet as indicated by the common midline insertion of the intermandibularis anterior and posterior (Cow-

an and Hick, 1951; Edgeworth, 1935). The intermandibular muscles are associated only with the mandibular unit.

**M. INTERMANDIBULARIS ANTERIOR.** This is a two-headed muscle arising from a bar of connective tissue that lies on the midline between the anterior tips of the mandibles. The dorsal head extends vertically to the lateral anterior tip of the tongue sheath. The lateral head is directed anterolaterally to the ventromedial tip of the dentary. No glandular portion was detected as reported for *Elaphe* (Albright and Nelson, 1959) or *Thamnophis* (Cowan and Hick, 1951). However a short muscle that originates from the connective tissue bar and extends posteriorly to enclose the posterior end of the sublingual gland may represent the glandular portion these workers describe.

**M. TRANSVERSUS BRACHIALIS.** This narrow, thin muscle arises from the skin between the origin of the intermandibularis posterior, pars posterior, and intermandibularis anterior. It extends dorsally in an anterolateral direction to insert by two heads at (1) the ventral posterior end of the sublingual gland and (2) the mucus membrane covering the floor of the mouth. The glandular attachment is the stronger.

**M. INTERMANDIBULARIS POSTERIOR: PARS ANTERIOR.** This is a flat muscle which originates from the midline at a level approximately even with the dentary-angular joint. A few fibers arise from the posterior end of the sublingual gland and merge in their anterior length with the glandular attachment of the transversus brachialis. The muscle extends posterolaterally, dorsal to the neuro-costo-mandibularis, to the ventral edge of the compound bone opposite the anterior border of the mandibular fossa.

**M. INTERMANDIBULARIS POSTERIOR: PARS POSTERIOR.** This straplike muscle lies ventral to the neuro-costo-mandibularis. It arises from the midline and extends posterolaterally to the posterior lateral side of the compound bone at a level even with the posterior border of the mandibular fossa.

#### THE HYPOBRANCHIAL SPINAL MUSCLES

The hypobranchial musculature develops from downgrowths of two or more spinal myotomes. The resulting primordium divides into an anterior geniohyoideus and a posterior rectus-cervicis. The tongue is formed from a median elevation of the floor of the mouth. The hyoglossus is derived from the hypobranchial primordium before separation. The anterior geniohyoideus becomes the geniotrachealis and the genioglossus. The hyolaryngeus arises from the posterior

end of the hyoglossus in *Tropidonotus-Natrix*, (Edgeworth, 1935). These muscles are essentially the extrinsic tongue muscles; some of their members unite the hyoid and mandibular skull units.

**M. HYOGLOSSUS.** The tongue consists of two adjacent muscles which are bifurcated anteriorly. They arise from the posterior ends of the ceratohyals and extend anteriorly to become sheathed in the extrinsic tongue musculature.

**M. GENIOGLOSSUS.** This is a cylindrical two-headed muscle originating from (1) the anterior tip of the midline cartilage and (2) the anterior medial end of the dentary in conjunction with the geniotrachealis. The anterior head (1) extends posteriorly along the lateral side of the tongue. The anterior medial head (2) passes posteromedially from the dentary and merges with the anterior head at a point even with the dentary-angular joint. The lateral head constitutes the dorso-lateral half of the tongue sheath and the anterior head forms the ventrolateral half.

**M. GENIOTRACHEALIS.** This muscle originates in conjunction with the lateral head of the genioglossus from the anterior tip of the dentary. It passes posterodorsally to the dorsolateral area of the trachea at a point posterior to a line drawn through the dentary-compound joints of the mandibles.

**M. HYOLARYNGEUS.** This thin strand of muscle arises from fascia over the Neuro-costo-mandibularis between the ceratohyals and the posterior end of the mandible. It extends anterodorsally to the trachea where its fibers become closely applied to the dorsal surface of the insertion of the geniotrachealis.

**M. CERVICO-HYOIDEUS.** This broad sheet of fibers arises from the gastro-steges in the anterior trunk region and inserts on the basihyal and anterior ceratohyals.

**M. CERVICO-QUADRATUS.** This thin, flat muscle arises from skin and fascia over the costal head of the neuro-costo-mandibularis. It extends anterodorsally, medial to the retractor quadrati, to attach to the posterior edge of the quadrate. This muscle is better developed in *H. nasicus* than in the other species of *Heterodon*.

**M. CUTANEO-QUADRATUS.** This is a thin flat muscle arising from the skin around the distal end of the quadrate, lying lateral to the retractor quadrati, and inserting on the mid-proximal end of the quadrate. This muscle is best developed in *H. nasicus*. Haas (1931)

reported it in *Xenodon merremi*, and I have found it in *X. severus* and *X. rabdocephalus*. I have not found it in *Elaphe* or *Thamnophis*.

#### THE HYOID MUSCLES

The hyoid muscle plate lies in front of the trunk myotomes as a vertical band of cells extending posteriorly and giving rise to the constrictor colli. The anterior fibers of the colli separate to form several muscles. In the Ophidia the depressor mandibulae, the retractor quadrati, and the neuro-costo-mandibularis are the products of this separation (Edgeworth, 1935; Romer, 1956). The hyoid musculature unites the mandibular and vertebral skull units.

**M. RETRACTOR QUADRATI.** This is a wide flat muscle arising from fascia over the spinalis-semispinalis muscles at the level of vertebrae VI to IX in *H. simus* and *H. platyrhinos*, and from vertebrae IV to VI in *H. nasicus*. In all species of *Heterodon* the insertion is on the distal, lateral side of the quadrate and over the quadrate-compound joint. Both origin and insertion appeared constant in *Heterodon*. Albright and Nelson reported variations at the insertion in *Elaphe*. In *Xenodon merremi* it is two headed at its insertion, one head attaching to the inner band of the quadrate-maxillary ligament, the other making a normal insertion (Haas, 1931; Anthony and Serra, 1951). The arrangement of these muscle heads is similar in both *Xenodon severus* and *X. merremi*. In *X. rabdocephalus* the muscle does not show a clear-cut division into two heads, but its anterior part attaches to the inner band of the ligament at its insertion.

**M. DEPRESSOR MANDIBULAE.** This thick muscle lies on the posterior edge of the quadrate. The origin is from the supraoccipital by a few strands of connective tissue, and from the posterior border of the quadrate. The insertion is the quadrate-mandibular joint.

**M. NEURO-COSTO-MANDIBULARIS.** This large, flat muscle arises from three heads. The vertebral head is from the dorsal surface of the trunk posterior to the origin of the retractor quadrati, the costal head from the distal end of the first few ribs, and the hyoid head from the lateral border of the anterior ceratohyals. All heads merge ventrally at a point anterior to a line through the quadrate-mandibular joints. The insertion is on the medioventral border of the mandible.

**M. CONSTRICTOR COLLI.** This thin, subcutaneous muscle is closely applied to the skin in the neck region. It encircles the anterior trunk region and extends rostrad on the ventral surface as far as the mandibular attachment of the intermandibularis posterior pars posterior.

## THE GLANDS AND LIGAMENTS

No attempt is made to describe these structures in detail. Those that seem especially pertinent are described briefly.

**LABIAL GLANDS.** The labial glands lie under the skin of the sides of the mouth. The inferior gland is moderately enlarged in *Heterodon*. In *H. simus* and *H. nasicus* the superior gland is markedly enlarged posteriorly and the parotid element is well differentiated. In *Xenodon severus* and *X. rabdocephalus* the posterior superior gland is not usually enlarged, but the parotid gland is well developed and a pale cream color in preserved specimens.

**QUADRATE-MAXILLARY LIGAMENT.** This is a flat thin band divided into two parts anteriorly. The ligament arises from quadrate-mandibular capsule and passes rostrally to attach by a medial band to the posterior end of the upper labial gland and by a lateral band to the skin over the posterior end of the upper labial gland. In *Xenodon* the ligament is also doubled, but the inner band connects to the posterior end of the maxillary bone and the lateral band attaches to the rear of the parotid gland. The maxillary attachment is present in *Natrix*, *Thamnophis*, and *Elaphe*. In *Xenodon* the anterior part of the retractor quadrati attaches to the inner band near its origin.

**POSTFRONTAL-MAXILLARY LIGAMENT.** This tendon extends from the distal end of the postfrontal to the ventrolateral side of the maxillary anterior to the maxillary-ectopterygoid joint.

**PALATO-MAXILLARY LIGAMENT.** This structure provides a tendinous connection between the anterior lateral process of the palatine and the anterior medial process of the maxillary.

**HARDERIAN GLAND.** This is a large, oval gland projecting from the posterior ventral floor of the orbit medial to the postfrontal (fig. 9).

## FUNCTIONAL ASPECTS

The upturned, projecting premaxillary and the compact nasal structure reflect *Heterodon's* burrowing behavior (Bogert, 1947). In his study of *Heterodon's* burrowing Davis (1946) described the modified rostrum as a double-shared plow that forces soil to the side. This structure is not only used in burrowing but also to procure food. Goin (1947) reports that *Heterodon simus* digs up spadefoot toads (*Scaphiopus h. holbrookii*) with its snout. I have watched *H. platyrhinos* seek and root out common toads (*Bufo terrestris*). The elon-



gate nasals and the series of widened dorsal cranial bones provide a median line of support, while the shortened head has an increased mechanical advantage and is thus more efficient for rooting.

The enlarged ungrooved caudal maxillary teeth are separated by a diastema from the smaller anterior teeth in both *Heterodon* and *Xenodon*. These enlarged teeth are directed posteriorly and medially and rise from the maxillary at such an angle that the end of the tooth is nearly parallel to the bone. This suggests the existence of a mechanism for moving the tooth tips to a more perpendicular position. Boulenger (1915) describes a forward rotation of the maxillary in *X. merremi* to engage the enlarged teeth in solenoglyph fashion. Haas (1931) suggests that the postfrontal-maxillary ligament prevents the vertical rotation Boulenger described and ascribes the erection of the enlarged teeth to a lateral rotation of the maxillary (see also Anthony and Serra, 1951). Albright and Nelson (1959) describe a lateral rotation of the maxillary when *Elaphe* opens its mouth. I have noticed that a similar movement in *Heterodon* brings the enlarged maxillary teeth into play. The ventrolateral attachment of the postfrontal-maxillary ligament increases the lateral rotation of the maxillary. A slight lateral movement of the postfrontals increases the lateral rotation of the maxillaries and widens the lateral gape between their posterior ends. This increase in gape helps the snake puncture inflated toads.

Enlargement of the posterior position of the upper labial gland is often accompanied by modifications of the maxillary teeth (Smith and Bellairs, 1947). In view of the well developed parotid gland in *Heterodon*, Bragg's report (1960) of toxic effects from a *H. nasicus* bite is not surprising. W. T. Neill (personal communication) reported a fence swift, *Sceloporus undulatus*, killed by the apparently toxic bite of *H. simus*. The snake seized the lizard by the hind leg, chewed, and imbedded its rear maxillary teeth. It held the prey for less than a minute. The lizard was dead when the snake released it to seize another lizard.

McAlister (1953) investigated the toxic effects of the parotid gland of *H. platyrhinos* and found that after injection of a parotid solution anurans died within 24 hours but mice were unaffected. The pronounced enlargement of the superior labial gland in *H. simus* and *H. nasicus* compared to those of other snakes and its relative normality in *H. platyrhinos* offer a possible explanation of the contrary findings. The morphology of the gland and the reports published so far suggest that all *Heterodon* species are mildly toxic. In *H. simus* and *H. nasicus* the toxin is probably useful in subduing prey.

There is (Stejneger, 1895) at least one record of a poisonous bite from *Xenodon severus*, although a bite by *X. rabdocephalus* produced no ill effects.

### DISCUSSION

The cranial osteology of *Heterodon* supports the relationship of *H. simus* and *H. nasicus* and confirms a similar conclusion based on vertebral characters (Auffenberg, 1963). Table 1 lists the major points of comparison and indicates the groupings. The greater number of osteological differences may be attributed to the fact that muscles are more protean than bones and consequently less easily compared. Kochva (1962), however, found significant intrageneric variations in musculature in *Vipera*, as did Haas in *Causus* (Haas, 1952).

TABLE 1. MYOLOGICAL AND OSTEOLOGICAL COMPARISONS WITHIN THE GENUS *HETERODON* \*

	<i>H. platyrhinos</i>	<i>H. simus</i>	<i>H. nasicus</i>
Premaxillary		X	X
Maxillary		X	X
Nasal	X	X	
Ectopterygoid		X	X
Pterygoid		X	X
Frontals		X	X
Parietals		X	X
Supraoccipital		X	X
Orbital foramen	X	X	
Foramen magnum		X	X
Adductor extenus medialis		X	X
Pseudotemporalis		X	X
Retractor quadrati	X	X	
Cutaneo quadratus	X	X	
Retractor quadrati	X		X
Labial glands		X	X

\* The X's indicate the species that are most similar for the structures listed in the column at the left.

The increased osteological specializations in *H. simus* and in *H. nasicus* indicate that these species represent advanced *Heterodon* evolution. Thus the more generalized species, *H. platyrhinos*, is probably representative of the generic ancestor. The presence of a bilobed orbital foramen in *H. platyrhinos* and *Xenodon* and its graduated diminuation in *H. simus* and *H. nasicus* respectively add support to this conclusion.

Other than the gross features mentioned by Smith uniting the Heterodontinae and Dunn's characters for the Ophiinae, *Heterodon* and *Xenodon* have cranial characters in common. The prefrontals and to some degree the postfrontals, the maxillary and the method of engaging the maxillary teeth, the sphenoid, the shape of the orbital foramen, and the trunk musculature (see below) leave little doubt about the *Heterodon-Xenodon* affinity. This does not imply that other genera are excluded from this grouping. The presence of an aponeurosis on the lateral jaw musculature, the more typically colubrid features of the head, and the colubrid tendency of the trunk musculature point to the general colubridization of *Xenodon* as opposed to *Heterodon*.

When considering the relationships of *Heterodon* to other genera one must distinguish specialized features from those having phylogenetic or taxonomic importance. It is also necessary to estimate what effect, if any, osteological changes have on associated musculature. In *Heterodon* the major areas of specialization are the nasal bones and the median series of dorsal cranial bones. The anterior lateral and ventral cranial elements remain rather unspecialized. The pre- and postfrontals, the maxillaries, the sphenoid, and the orbital foramen show characters of some phylogentic or taxonomic importance.

The maxillaries are an important diagnostic tool because they are usually the site of dental modifications and ordinarily carry any specialized teeth that may occur (Bogert, 1943). The pre- and postfrontals and the sphenoid are similar in both genera, as is the orbital foramen. I believe this similarity has at least some taxonomic import.

The skull specializations of *Heterodon* are illustrated in the widening of the frontals, parietals, and supraoccipitals, and in the extreme shortening of the skull behind the postfrontals. This shortening is most obvious in the incorporation of the various small pro-otic foramina into the anterior pro-otic foramen, and in the loss of the dorso-lateral parietal groove, which is present in *Xenodon* and other unspecialized colubrids such as *Thamnophis*, *Elaphe*, and *Coluber*. The loss of this groove might be expected to alter the adductor externus muscles which normally arise from it, but the effect is slight. Only the adductor externus medialis suffers, being smaller in *Heterodon* than in *Xenodon* and the above genera, which places the adductor externus superficialis and profundus closer together. The presence of a large and well developed adductor externus superficialis in *Heterodon* is not correlated with osteological specializations of the skull.

The development of this muscle may actually be correlated with the absence of a well developed aponeurosis.

The shortened maxillary and its enlarged caudal teeth, the highly developed parotid gland, and the viper-like appearance of *Heterodon* invite speculation on the role of the xenodontine snakes in the evolution of the solenoglyphs. Anthony (1955) notes two points for fang location, a maxillo-prefrontal locus (proterodont) and a maxillo-transverse locus (opisthodont). The vipers developed along the opisthodont line from aglyphous colubrids. *Heterodon* and *Xenodon* demonstrate the opisthodont condition. Haas (1952) arrived at a similar conclusion on studies centered around *Causus*; he hypothesized that the ancestral solenoglyph would be a primitive colubrid with a double adductor externus superficialis, whose posterior member being derived from the adductor externus profundus gave rise to the gland muscle. He cited *Sibon* as an example close to the hypothetical ancestor. In a later paper (1962) Haas considered the levator anguli oris (arising from the postfrontal and inserting at the posterior corner of the mouth) a primitive character of the lateral jaw musculature, and one probably present in the viper ancestor. *Heterodon* and *Xenodon* show an advanced colubrid plan of lateral jaw musculature since the levator anguli oris is missing. However both show a primitive characteristic in the forward curving of the adductor externus superficialis.

More impressive is Mosauer's observation of the similarity between the trunk musculature of *Heterodon platyrhinos* and *Crotalus horridus*. My dissections, which confirm those of Mosauer, also show that the trunk musculature of *Xenodon (rabdocephalus)* resembles that of *Crotalus*. Both *Xenodon* and *Heterodon* are similar to *Crotalus* which is similar to *Vipera*, *Causus*, and *Agkistrodon* in the fibrous association of the semispinalis and the interarticularis superior (personal observation, not in Mosauer), the osseous attachment of the semispinalis to the neural arch (a tendinous attachment to the longissimus in *Coluber* and the other advanced colubrids), and in a fibrous association of the spinalis and the multifidus. The trunk musculature of *Heterodon* is very close to the pre-Colubrid stage "F" of Auffenberg (1961). *Xenodon* differs from *Heterodon* only in the increased length of the muscle fibers, particularly in the spinalis complex. This lengthening of fibers is a step in the colubridization of trunk musculature (Auffenberg, 1962).

Haas (1952) stresses the "logical necessity" of double adductor externus superficialis in the viper ancestors and points out the fruitlessness of relying on osteological characters alone. I believe osteology

must be considered because profound osteological changes eliminate sites for muscular attachment and force muscles to conform to a new topography. The shortened posterior of the skull in *Heterodon* places the adductor externus superficialis and profundus close together. From this condition the development of a gland muscle from an anterior splitting off of the profundus seems reasonable. A subsequent anterior migration of the insertion of the separated member, largely accomplished in the existing single adductor externus profundus of *Heterodon*, and a posterior migration of the superficialis would form the characteristic muscular loop seen in the solenoglyphs. This path of gland-muscle development eliminates the necessity of a double adductor externus superficialis in the viper ancestor.

While head musculature must be considered in solenoglyph phylogeny, the trunk myology appears more reliable. The extreme shortening of the maxillary and the corresponding elongation of the ectopterygoid, the development of a poison gland and of a compressor for the gland impose severe changes in the muscular construction of the head. In a sense these changes are adaptive and tend to mask phylogenetic affinities. In the absence of such drastic osteological changes in the vertebral structure, the trunk myology is more conservative and reflects evolution more accurately. The occurrence of an aglyphous colubrid with enlarged maxillary teeth in the opisthodont position, with at least one primitive characteristic of the lateral jaw musculature and a viperid-like trunk myology, merits serious consideration as a viper ancestor. In view of these characteristics, it is conceivable that a xenodontine protoviper gave rise to (1) *Xenodon* (advanced *Heterodontinae* or *Xenodontinae*), (2) a *Heterodon* type which, although it became specialized, retained many primitive features, and (3) the solenoglyphs.

It is hypothesized that the xenodontine proto-viper possessed the following characters: (1) a viperid trunk musculature with short fibers in the spinalis complex, (2) enlarged opisthodont maxillary teeth and a corresponding shortening of the maxillary, (3) a well developed parotid gland, (4) a well developed adductor externus superficialis closely associated with the adductor externus profundus, (5) a rostrally extended insertion of the adductor externus profundus, (6) the presence of a levator anguli oris, and (7) no aponeurosis involving the adductor externus superficialis, thus allowing that muscle to make a fleshy insertion on the mandible.

*Heterodon* resembles this condition except that it lacks a levator anguli oris. *Xenodon* is farther along the colubridization process, retaining only the enlarged opisthodont maxillary teeth on a short-

ened maxillary (point 2 above), and a well developed parotid gland (point 3 above) and to some extent the close association of the adductor externus superficialis and profundus (point 4 above).

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