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Smilisca baudini, by Linda Trueb**

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**Transcriber's Notes**

Except for several minor typographical corrections which were made (missing periods, commas, etc.) that are not detailed here, the text presented is that which appeared in the original printed version.

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**BY**

**LINDA TRUEB**

**UNIVERSITY OF KANSAS  
LAWRENCE  
1968**

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**Cranial Osteology of the Hylid Frog, *Smilisca baudini***

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**BY**

**LINDA TRUEB**

**INTRODUCTION**

The paucity of descriptive cranial anatomical work dealing with hylid frogs was pointed out by Trueb (1966) in her paper describing the cranial osteology of *Hyla septentrionalis*. Comparative studies on the cranial osteology of the genus *Smilisca* (Duellman and Trueb, 1966), along with other more brief descriptions, reveal variation among cranial characters of hylids. Since these external characters have been useful in defining species, species groups, and genera, it seems

worthwhile to pursue correlated studies on internal cranial structure. The following account dealing with the Neotropical tree frog, *Smilisca baudini* Duméril and Bibron, 1841, is the first published description of the internal cranial anatomy of a hylid frog, and supplements the recent account (Duellman and Trueb, 1966) of external cranial osteology of the same species. Comparative studies of hylid skulls are expected to yield information of taxonomic importance.

I am grateful to Richard J. Baldauf of Texas A & M University and William E. Duellman of the University of Kansas for critically reading the manuscript and offering helpful suggestions. The findings reported here result from research on Middle American hylids supported by a grant from the National Science Foundation (GB-1441) to William E. Duellman.

## Materials and Methods

The serial sections illustrated beyond are from an adult male of *Smilisca baudini* (KU 89924) having a snout-vent length of 53.0 mm. and a head width (measured at angle of jaws) of 17.0 mm. The specimen was collected 5.2 kilometers east-southeast of Córdoba, Veracruz, México. Transverse sections were cut at thicknesses of 10 and 15 microns on a rotary microtome and stained according to the technique described by Baldauf (1958). Cleared and stained specimens and dried skeletons also were used. [Figure 1](#) is based on KU 68183-4 and [Fig. 9](#) on KU 55614. All other drawings are made from KU 89924. In all cross-sectional figures, bone is represented by solid black, cartilage by stippling, and connective tissue by cross-hatching. Unless otherwise noted all descriptions are given in an anterior-posterior sequence.

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Commonly accepted English terms are used. For example, dentary is used in preference to dentale and maxillary process instead of processus maxillaris. If no commonly accepted English term is available for a given structure, the Latin name is retained. For example, the cartilaginous plate separating the cavum principale from the cavum medium is termed the lamina superior.

## DESCRIPTION OF INTERNAL CRANIAL OSTEOLOGY

### Olfactory Region

*Alary cartilage.*—The anterior end of the alary cartilage (*al. c.*, [Figs. 2-5](#)) lies within the posterior concavity of the alary process (*al. proc.*, [Figs. 1-3](#)) of the premaxillary (*pmax.*). In posterior sections the cartilage assumes a dorsolateral position ([Fig. 3](#)), ventral and slightly lateral to the tectum nasi. The alary cartilage remains narrowly separated from the tectum nasi but fuses ventromedially with the septum nasi and forms a nearly complete cartilaginous capsule around the anterior end of the cavum principale. Posterior to the anterior end of the cavum medium and the lamina superior, the alary cartilage separates ventrally from the lamina. In subsequent posterior sections, the cartilage, arcuate in cross section, becomes progressively smaller and terminates at the level of the union of the medial and lateral recesses of the cavum inferior.

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*Prenasal cartilages.*—The superior prenasal cartilage is small; it lies adjacent to the posterodorsal surface of the alary process of the premaxillary, and anterior to the alary cartilage. The inferior prenasal cartilage (*inf. pnas. c.*, [Figs. 2-6, and 8](#)) appears posterior to the appearance of the alary cartilage. The anterior terminus lies at the base of the alary process; the cartilage extends dorsally ([Fig. 3](#)) along the posterior surface of the alary process and then curves posterodorsally and joins the solum nasi medioventral to the posterior end of the septomaxillary ([Fig. 8d](#)).

*Tectum nasi.*—The anterolateral corner of the tectum nasi (*tect. nas.*, [Fig. 2](#)) appears just posterior and dorsomedial to the anterior end of the alary cartilage. The anterior process is short; it fuses medially with the septum nasi forming a complete roof to the cavum principale ([Figs. 3 and 4](#)). The oblique cartilage (*obl. c.*) diverges laterally from the tectum nasi just posterior to the terminus of the alary cartilage ([Fig. 6](#)). Medially, the tectum nasi persists, overlaid by the nasal bone laterally.

*Septum nasi.*—Posterior to the appearance of the septum nasi (*sept. nas.*) and its union with the tectum nasi ([Fig. 3](#)), the septum abruptly expands across the width of the skull medial to the alary cartilage. The septum is entirely cartilaginous posterior to the level of the olfactory eminence, except for a small amount of secondary membranous ossification dorsomedially at a level anterior to the nasal bones. Perichondral ossification commences in the dorsal part of the septum nasi at the level of the olfactory eminence. Endochondral ossification first appears dorsally in the vertical part of the septum at the level of the internal nares. Ossification of dorsal parts of the septum precedes ossification of ventral parts. Perichondral ossification of the ventral part of the septum nasi is first noted at the level of transition between the planum antorbitale and solum nasi. Perichondral ossification gradually gives way to endochondral ossification

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posteriorly.

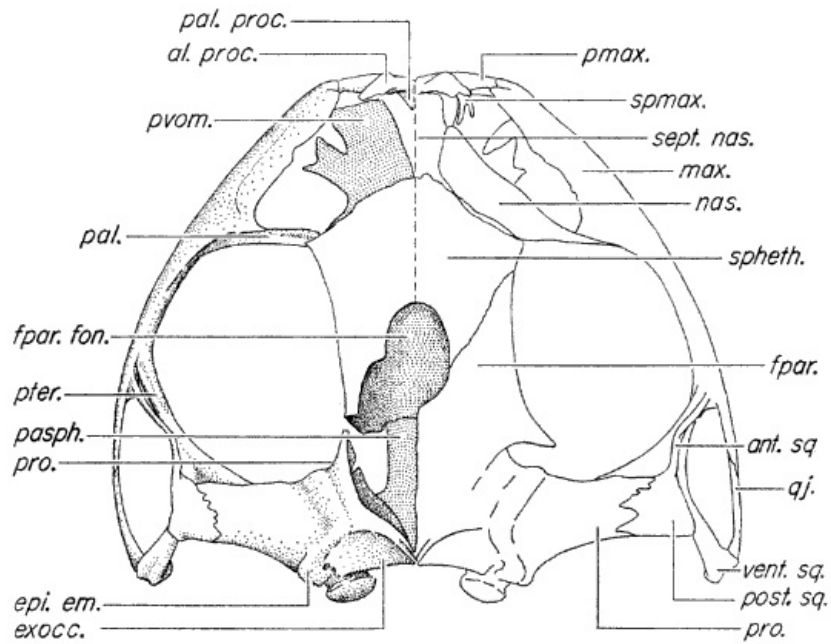
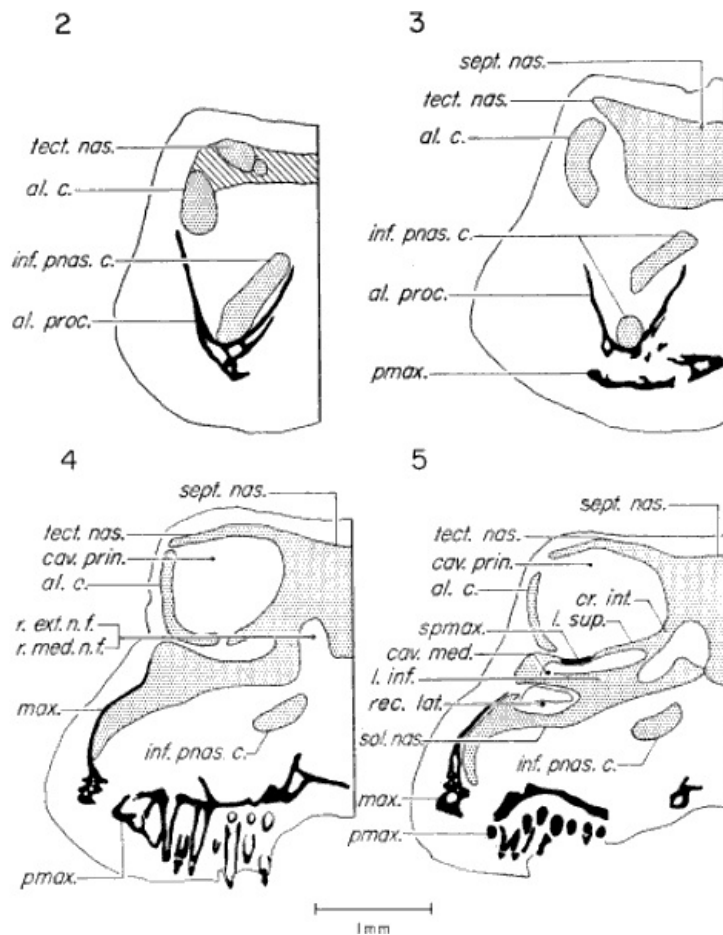
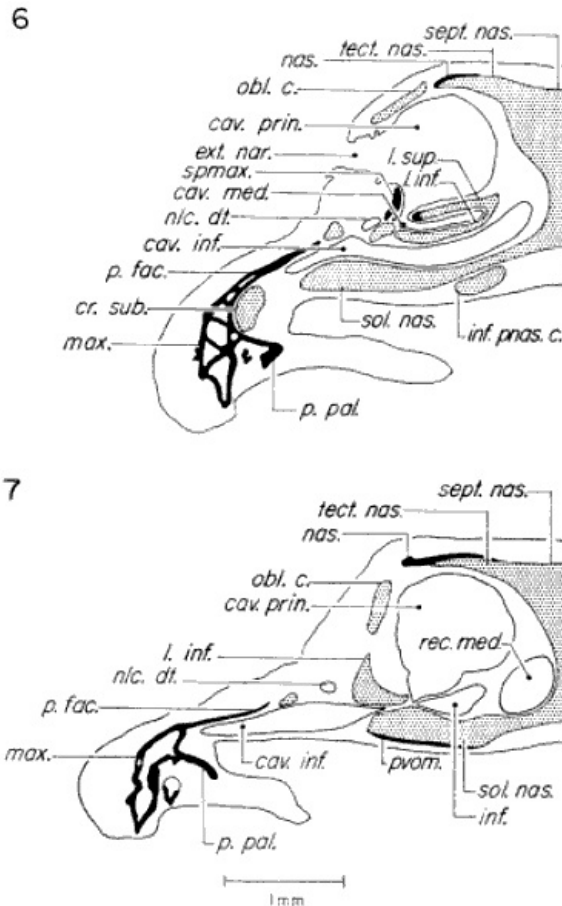


FIG. 1. Partially disarticulated skull (left frontoparietal and nasal removed) of *Smilisca baudini*, KU 68183, ♀ × 4. Abbreviations: *al. proc.*, alary process of premaxillary; *ant. sq.*, anterior arm of squamosal; *epi. em.*, epiotic eminence; *exocc.*, exoccipital; *fpar.*, frontoparietal; *fpar. fon.*, frontoparietal fontanelle; *max.*, maxillary; *nas.*, nasal; *pal.*, palatine; *pal. proc.*, palatine process; *pasph.*, parasphenoid; *pmax.*, premaxillary; *pvom.*, prevomer; *post. sq.*, posterior arm of squamosal; *pro.*, prootic; *pter.*, pterygoid; *qj.*, quadratojugal; *spmax.*, septomaxillary; *sept. nas.*, septum nasi; *spheth.*, spnenethmoid; *vent. sq.*, ventral arm of squamosal.



FIGS. 2-5. Transverse sections through anterior end of skull: 2) anterior level of inferior prenasal

cartilage; 3) anterior level of internasal septum; 4) olfactory capsule at anterior level of cavum principale; 5) olfactory capsule at anterior level of cavum inferius. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *cr. int.*, crista intermedia; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *max.*, maxillary; *pmax.*, premaxillary; *r. etx. n. f.*, ramus externus narium foramen; *r. med. n. f.*, ramus medialis narium foramen; *rec. lat.*, recessus lateralis; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spx.*, septomaxilla; *tect. nas.*, tectum nasi.



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FIGS. 6-7. Transverse sections through olfactory capsule: 6) posterior level of cavum medium; 7) anterior level of prevomer. Abbreviations: *cav. inf.*, cavum inferius; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *cr. sub.*, crista subnasalis; *ext. nar.*, external nares; *inf.*, infundibulum; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *max.*, maxillary; *nas.*, nasal; *ncl. dt.*, nasolacrima duct; *obl. c.*, oblique cartilage; *p. fac.*, pars facialis; *p. pal.*, pars palatina; *pvom.*, prevomer; *rec. med.*, recessus medialis; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spx.*, septomaxillary; *tect. nas.*, tectum nasi.

*Nasal cavities and associated structures.*—The cavum principale (*cav. prin.*, Fig. 4) is the most anterior of the nasal cavities. It first appears within the capsule bordered dorsally by the tectum nasi, medially and ventrally by the septum nasi, and laterally by the alary cartilage. The cavity extends posteriorly within recesses of the sphenethmoid to the level at which the septum nasi terminates.

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The cavum medium (*cav. med.*, Fig. 5) lies ventral and slightly posterior to the anterior end of the cavum principale. It appears slightly anterior to the septomaxillary at the level of the foramen ramus externus narium and ramus medialis narium. The appearance of the cavum medium within the ventrolateral extension of the septum nasi divides the latter into an upper component, the lamina superior (*l. sup.*) lying between the cavum principale and cavum medium, and a lower part, the lamina inferior (*l. inf.*) lying ventral to the cavum medium. As the cavum medium increases in width in posterior sections, the lamina superior and lamina inferior lose their lateral connection. The lateral part of the cavum medium diverges in the region of the external nares as the nasolacrima duct (*ncl. dt.*) and the cavum medium becomes confluent with the cavum principale (Fig. 6). The posterior end of the cavum medium lies at the level of the posterior terminus of the septomaxillary.

Slightly posterior to the anterior end of the cavum medium the foramen for the ramus externus narium (*r. ext. n. f.*) and ramus medialis narium (*r. med. n. f.*) opens ventromedially into the floor of the septum nasi (Fig. 4). The ventral closure of the floor of the foramen completes the solum nasi, marks the anterior end of the recessus medialis of the cavum inferior, and differentiates the roof of the recess, the crista intermedia (*cr. int.*), from the solum (Fig. 5). The crista intermedia joins the laminae superior and inferior and joins them for a short distance to the septum nasi medially. The anterolateral part of the cavum inferior (*cav. inf.*) lies ventrolateral to the cavum medium, and extends medially to join the medial recess. The fusion of the two recesses of the cavum inferior completely separates the lamina inferior from the solum nasi (Fig. 6).

Near the level of the union of the recessus lateralis and recessus medialis of the cavum inferior, the crista intermedia separates from the septum nasi, and the lamina superior diverges at its mid-width to accommodate the septomaxillary (*spmax.*) (Figs. 5 6). The lateral remnant of the lamina superior and transition zone between the lamina superior and lamina inferior is short and is quickly replaced by connective tissue. Slightly posterior, the distal edge of the lamina inferior diverges laterally as a small process, which lies dorsal to the pars facialis (*p. fac.*) of the maxillary. This part of the lamina inferior terminates posteriorly at the level of confluence between the cavum principale and lateral recess of the cavum inferior.

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Slightly posterior to the divergence of the crista intermedia from the septum nasi, the crista terminates, thereby separating the lamina superior and the lamina inferior from one another (Figs. 6 and 8). The lamina superior terminates at the level of the infundibulum (*inf.*, Fig. 7), whereas the lamina inferior extends posterolaterally, increases greatly in depth and joins the laterally ascending oblique cartilage (*obl. c.*) to form the planum terminale (*pla. ter.*, Fig. 10).

The crista subnasalis (*cr. sub.*, Fig. 6) differentiates from the lateral edge of solum nasi adjacent to the maxillary in sections just posterior to the confluence of the recessus medialis and the recessus lateralis. The crista persists as a rod of cartilage which gradually diminishes in size and terminates at the posterior level of the septomaxillary.

*The septomaxillary.*—The septomaxillary (*spmax.*, Fig. 9a-c) is a triradiate bone. The anterior terminus is a thin sliver of bone oriented horizontally between the cavum principale and cavum medium and lateral to the lamina superior (Figs. 5 and 8a). This anterior ramus of the septomaxillary increases in size posteriorly and diverges medially into a medial ramus (*med. r. spmax.*) and lateral ramus (*lat. r. spmax.*, Fig. 9a-b) to accommodate the confluence of the cavum principale and cavum medium (Figs. 6 and 8b-c). The small medial ramus is associated with the distal end of the lamina superior whereas the lateral ramus lies dorsal to the lateral margin of the cavum medium. Just anterior to the anterior end of the nasolacrimal duct, the ventral ramus of the septomaxillary (*vent. r. spmax.*, Fig. 9c) is present in cross-sections ventral to the cavum medium. The ventral ramus joins the horizontal and dorsal rami of the septomaxillary at the anterior end of the nasolacrimal duct. The medial branch terminates posteriorly at the level at which the cavum principale joins the cavum inferior. The lateral ramus of the septomaxillary terminates posteriorly at the level at which the recessus medialis diverges from the recessus lateralis posteriorly and cavum principale and recessus lateralis are confluent.

*Planum terminale.*—Posterior to the infundibulum the lamina inferior and oblique cartilage join to form the planum terminale (*pla. term.*) which lies lateral to the cavum principale (Fig. 10). The lamina inferior diverges ventrally from the planum terminale anterior to the olfactory eminence. The planum terminale is restricted ventrally and terminates at the level of the olfactory eminence (*olf. em.*, Fig. 11).

[Pg 20]

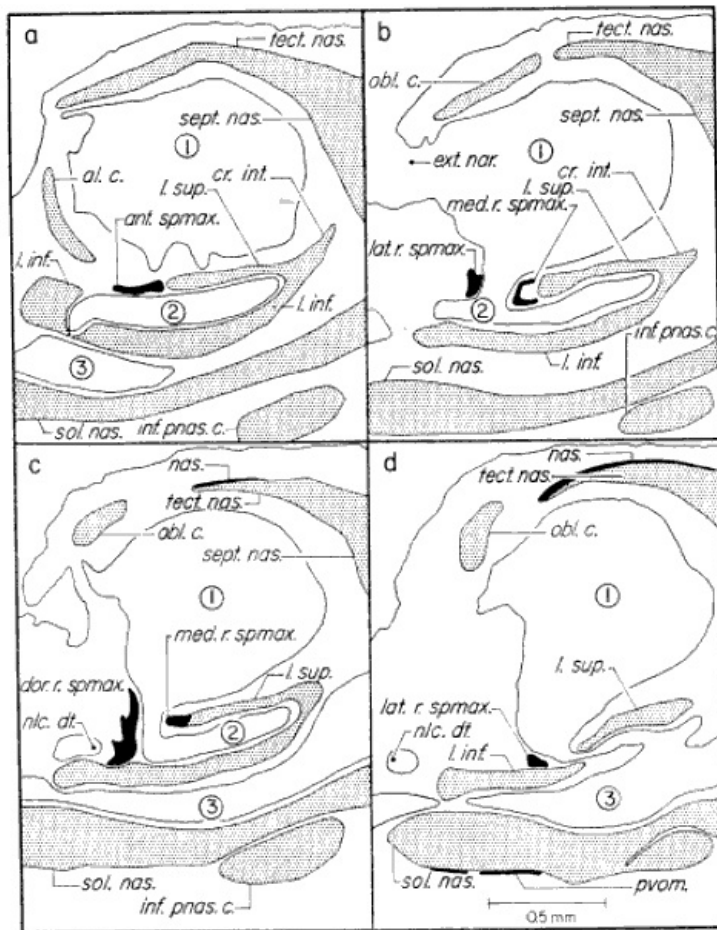


FIG. 8. Transverse sections through olfactory capsule in region of septomaxillary: a) anterior terminus of septomaxillary; b) medial divergence of septomaxillary; c) dorsal ramus of septomaxillary; d) posterolateral terminus of septomaxillary. Encircled numbers represent the nasal cavities as follows: 1) cavum principale; 2) cavum medium; and 3) cavum inferius. Abbreviations: *al. c.*, alary cartilage; *ant. spmax.*, anterior end of septomaxillary; *cr. int.*, crista intermedia; *dor. r. spmax.*, dorsal ramus of septomaxillary; *ext. nar.*, external nares; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *lat. r. spmax.*, lateral ramus of septomaxillary; *med. r. spmax.*, medial ramus of septomaxillary; *nas.*, nasal; *nlc. dt.*, nasolacrimal duct; *obl. c.*, oblique cartilage; *pvom.*, prevomer; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spmax.*, septomaxillary; *tect. nas.*, tectum nasi.

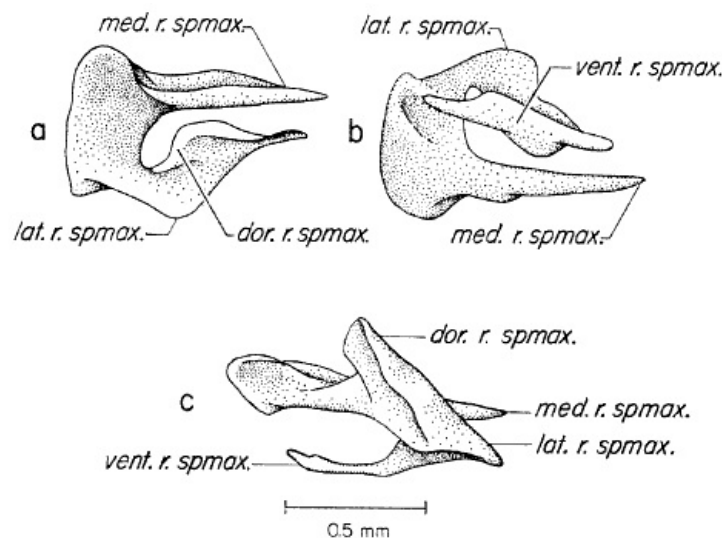
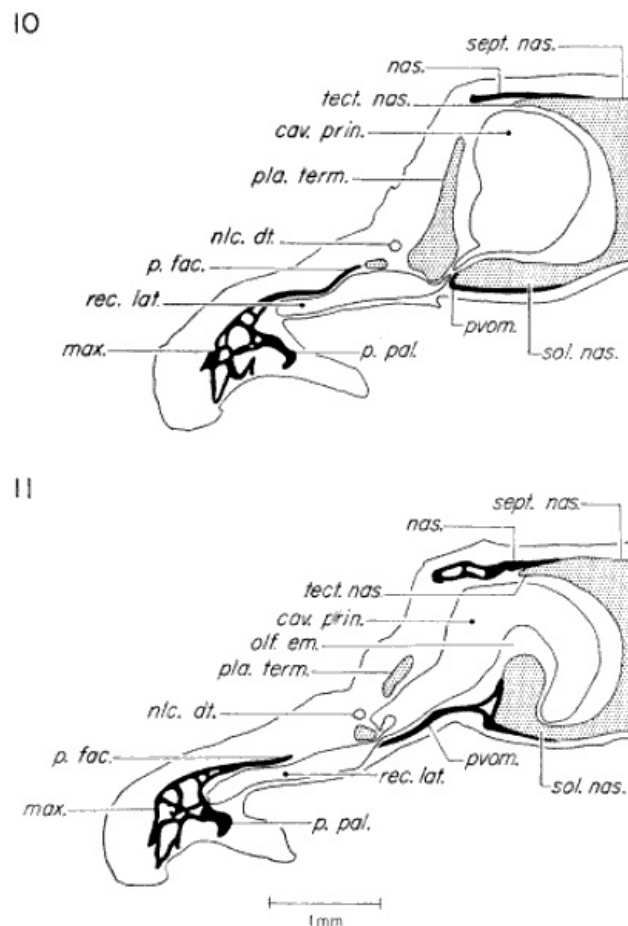


FIG. 9. Septomaxillary drawn from cleared and stained specimen of *Smilisca baudini*, KU 55614: a) dorsal; b) ventral; c) lateral. In each example, the anterior end lies to the left. Abbreviations: *dor. r. spmax.*, dorsal ramus of septomaxillary; *lat. r. spmax.*, lateral ramus of septomaxillary; *med. r. spmax.*, medial ramus of septomaxillary; *vent. r. spmax.*, ventral ramus of septomaxillary.

*Anterior and posterior maxillary processes.*—The anterior end of the anterior maxillary process (*ant. max. proc.*) lies within the maxillary at the level of the posterior terminus of the planum terminale. The anterior maxillary process diverges medially from the maxillary (Fig. 13) and expands dorsally along the medial face of the pars facialis to meet the planum antorbitale just anterior to the transition zone between the latter and the solum nasi. Posterior to the transition zone, the planum antorbitale disappears and the posterior maxillary process is restricted ventrally along the pars facialis of the maxillary. Posteriorly the cartilage is associated with the pterygoid, where it is known as the pterygoid process (*pter. proc.*, Fig. 14).

*Planum antorbitale.*—The anterior terminus of the planum antorbitale (*pla. ant.*) lies medial to the ventrolateral part of the nasal and lateral to the internal nares (Fig. 12). It abruptly expands dorsally along the medial face of the nasal to join the tectum nasi dorsolaterally; somewhat posteriorly the planum antorbitale joins the anterior maxillary process ventrally at the posterior margin of the internal nares.

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FIGS. 10-11. Transverse sections through posterior part of olfactory capsule: 10) region of planum terminale; 11) anterior region of olfactory eminence. Abbreviations: *cav. p.*, cavum principale; *max.*, maxillary; *nas.*, nasal; *nlc. dt.*, nasolacrimal duct; *olf. em.*, olfactory eminence; *p. fac.*, pars facialis; *p. pal.*, pars palatina; *pla. ter.*, planum terminale; *pvom.*, prevomer; *rec. lat.*, recessus lateralis; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *tect. nas.*, tectum nasi.

*External dermal bones associated with the olfactory region.*—The association of the premaxillary (*pmax.*) to the nasal cartilages is described in preceding sections. The premaxillaries are separated from each other medially and from the maxillaries laterally by dense connective tissue. Anteriorly, the maxillary (*max.*) bears a small palatine process (*pal. proc.*, Fig. 1) and a long, delicate pars facialis (*p. fac.*, Fig. 6), which terminates dorsally at the level of the lamina inferior. Posterior to the transition zone between the planum antorbitale and solum nasi the pars facialis is greatly reduced. The pars palatina (*p. pal.*, Fig. 6) persists to the posterior part of the orbit.

[Pg 23]



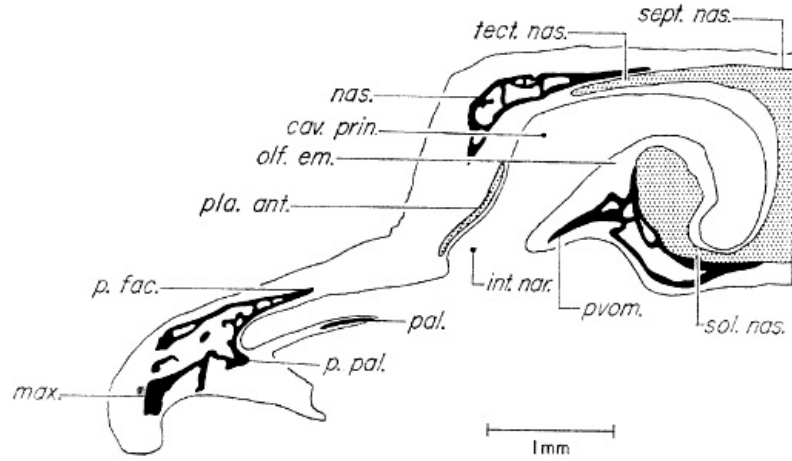


FIG. 12. Transverse section through the olfactory capsule in region of planum antorbitale. Abbreviations: *cav. prin.*, cavum principale; *int. nar.*, internal nares; *max.*, maxillary; *nas.*, nasal; *olf. em.*, olfactory eminence; *p. fac.*, pars facialis; *p. pal.*, pars palatina; *pal.*, palatine; *pla. ant.*, planum antorbitale; *pvom.*, prevomer; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *tect. nas.*, tectum nasi.

The anterior end of the prevomer (*pvom.*, Fig. 1) is associated with the venter of the solum nasi at the level of the infundibulum just posterior to the incorporation of the inferior prenasal cartilage into the solum (Fig. 7). The prevomer expands dorsally around the distal end of the solum to provide a bony lateral support for the olfactory eminence (Figs. 10 and 11). A distal wing of the prevomer forms the bony anterior and medial margins of the internal nares.

The palatine (*pal.*, Figs. 1 and 12) lies in connective tissue medial and adjacent to the pars facialis. At its maximum size the palatine forms the bony posterior margin of the internal nares and extends dorsomedially from the pars palatina to the distal part of the solum nasi.

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The nasal (*nas.*, Fig. 1) is a thin bone overlying the tectum nasi anteriorly (Fig. 7). It expands laterally to form a complete roof over the cavum principale (Fig. 10). In the region of the internal nares, the nasal forms the lateral wall of the cavum principale (Fig. 12).

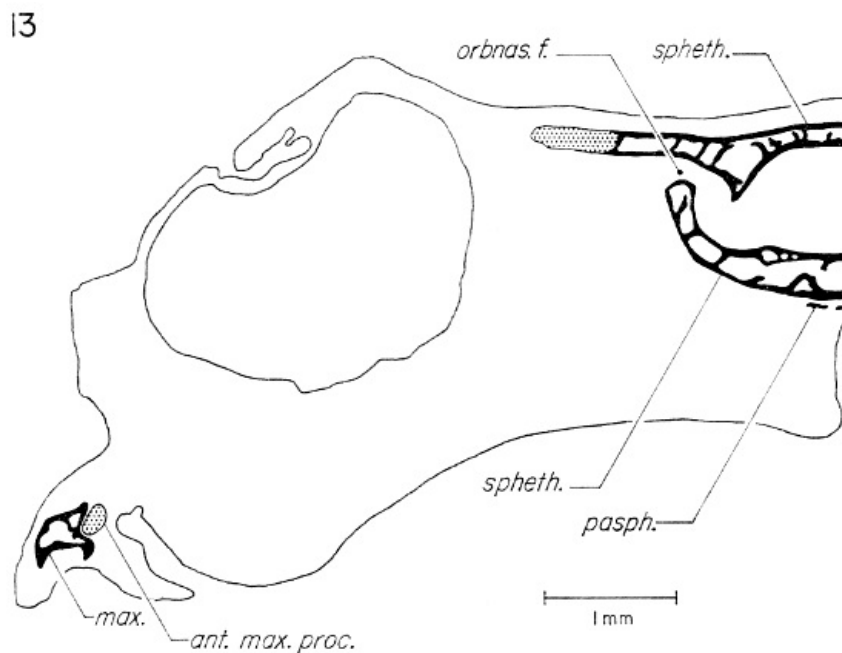


FIG. 13. Transverse section through sphenethmoid region at level of orbitonasal foramen. Abbreviations: *ant. max. proc.*, anterior maxillary process; *max.*, maxillary; *orbnas. f.*, orbitonasal foramen; *pasph.*, parasphenoid; *spheth.*, sphenethmoid.

## Sphenethmoid Region

Posterior to the transition zone between the planum antorbitale and solum nasi, the sphenethmoid (*spheth.*, [Fig. 1](#)) is fully ossified medially, the lateral parts of the bone at this level are only ossified perichondrally. The septum nasi persists at the anterior level of the orbit and terminates just anterior to the orbitonasal foramen (*orbnas. f.*) and the anterior end of the parasphenoid (*pasph.*, [Fig. 13](#)). The orbitonasal foramen is moderately large, has a complete bony margin, and is located at the dorsolateral corner of the braincase.

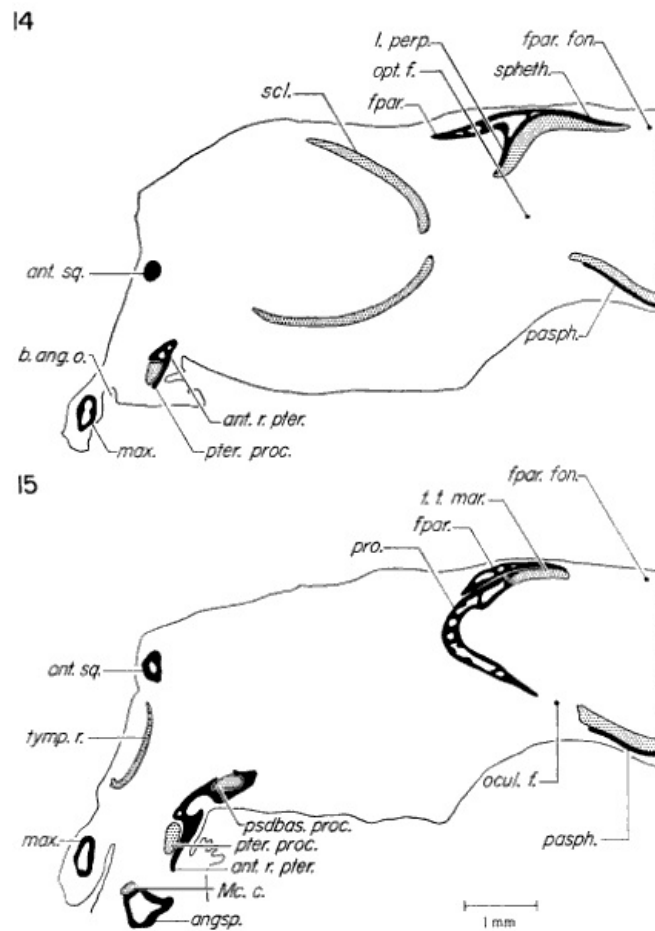
At the level of the orbitonasal foramen, the sphenethmoid is entirely ossified except for a small dorsolateral extension. This distal extension expands laterally in posterior sections as the braincase is increased to its maximum width at the mid-length of the orbit; the cartilaginous margin is retained throughout the length of the sphenethmoid. [Pg 25]

The bony dorsomedial part of the sphenethmoid diverges, forming the anterior border of the frontoparietal fontanelle (*fpar. fon.*, [Figs. 1 and 14](#)). The entire fontanelle is covered with a layer of dense connective tissue continuous with that in which marginal bones and cartilage of the sphenethmoid lie, and which is discrete from the lower dermal layer of the overlying skin. At this level the braincase is U-shaped in cross-section. Ossification terminates first in the ventrolateral corners, followed by the lateral and dorsolateral areas. The bony support of the latter area is furnished by the lamina perpendicularis (*lam. perp.*) of the frontoparietal (*fpar.*, [Fig. 14](#)). Cartilage appears in the ventral part of the sphenethmoid in posteromost sections; at the posterior levels of the orbit the sphenethmoid is entirely cartilaginous.

## Orbital, Otic, and Occipital Regions

*Orbital region.*—The sclera (*scl.*, [Fig. 14](#)) of the eye is cartilaginous. The optic foramen (*opt. f.*) is large and lies in connective tissue at the posterior limits of the orbit and sphenethmoid. At the posterior levels of the foramen the dorsolateral cranial roof cartilages, taeniatecti marginales (*t. t. mar.*) converge medially to form the posterior margin of the frontoparietal fontanelle and the tectum synoticum (*tect. syn.*) of the occipital region. At the posterior levels of the orbit the bursa angularis oris (*b. ang. o.*, [Fig. 14](#)) is present adjacent to the maxillary.

*Nerve foramina of otic and occipital regions.*—The trochlear foramen lies within the bony margins of the optic foramen. The trochlear nerve is located posterodorsal to the optic tract, and separated from the latter by connective tissue. The oculomotor foramen (*ocul. f.*) lies in connective tissue posterior and ventral to the optic foramen ([Fig. 15](#)). Anteriorly, dorsally, and ventrally the foramen has a bony margin formed by the prootic (*pro.*); posteriorly, only a thin layer of connective tissue separates the oculomotor from the large prootic foramen (*pro. f.*). The latter is bordered by bone dorsally and by cartilage ventrally ([Fig. 16](#)). Posteriorly, bone separates the prootic foramen from the anterior acoustic foramen (*ant. acus. f.*), through which the ramus acusticus anterior and medius pass ([Fig. 17](#)). An extremely narrow bridge of cartilage separates the anterior acoustic foramen from the larger posterior acoustic foramen (*post. acus. f.*). The latter has a bony posterior margin and is widely separated from the bony jugular foramen (*jug. f.*) posteriorly ([Fig. 19](#)).



FIGS. 14-15. Transverse sections through skull: 14) at level of optic foramen; 15) at level of oculomotor foramen. Abbreviations: *angspl.* angulosplenic; *ant. r. pter.*, anterior ramus of pterygoid; *ant. sq.*, anterior arm of squamosal; *b. ang. o.*, bursa angularis oris; *fpar.*, frontoparietal; *fpar. fon.*, frontoparietal fontanelle; *l. perp.*, lamina perpendicularis of frontoparietale; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *pasph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *pter. proc.*, pterygoid process; *scl.*, sclera; *t. t. mar.*, taenia tecti marginalis; *tym. r.*, tympanic ring.

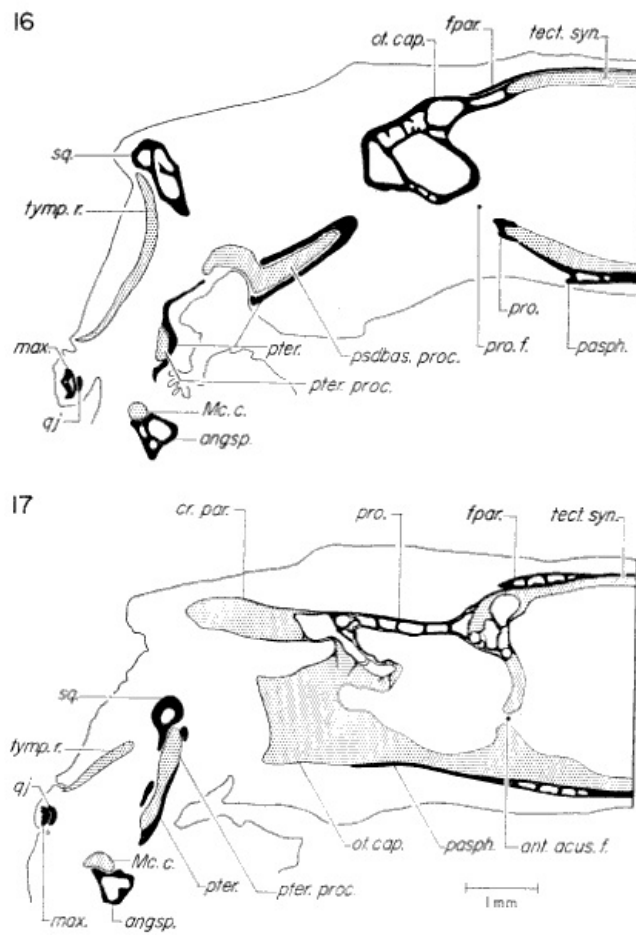
*Pterygoid.*—The anterior terminus of the pterygoid (*pter.*, Fig. 1) appears at approximately the mid-length of the orbit as a small arcuate bone closely applied to the posterior maxillary process. Farther posteriorly the maxillary decreases in size, and the pterygoid and posterior maxillary process diverge medially from it. Posterior to this point of divergence, the posterior maxillary process is known as the pterygoid process (*pter. proc.*). The anterior terminus of the quadratojugal (*qj.*) lies medial to the maxillary at the level of the oculomotor foramen (Fig. 14).

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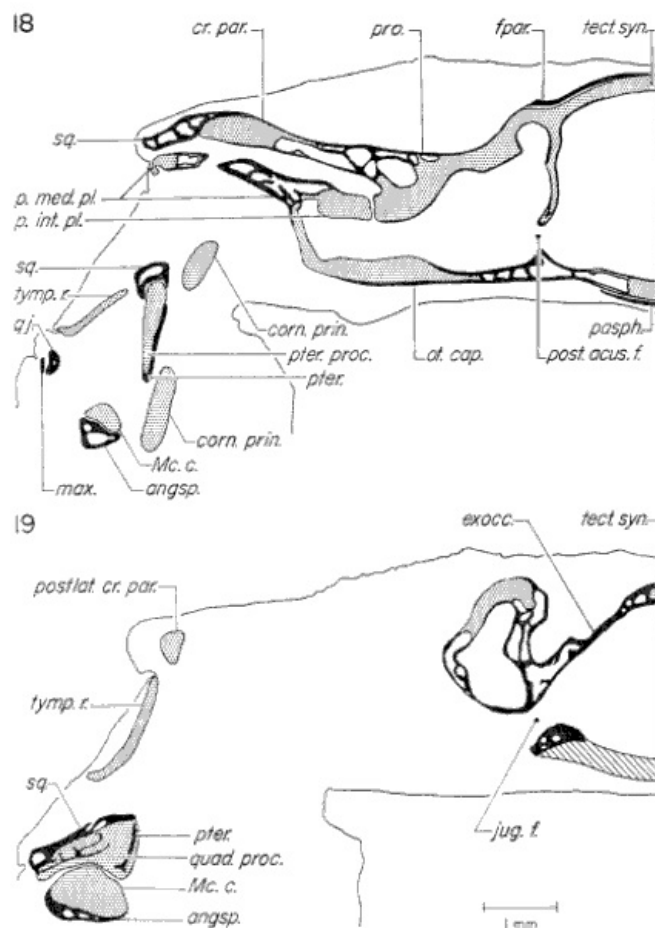
*Otic region.*—The anterior end of the otic capsule (*ot. cap.*) is present at the anterior level of the oculomotor foramen. The anterior terminus of the pseudobasal process (*psdbas. proc.*) lies within the medial portion of the pterygoid at the posterior border of the oculomotor foramen (Fig. 15). The pseudobasal process abruptly increases in size. At the level of the prootic foramen (Fig. 16) the medial branch of the pterygoid diverges from the posterior ramus and is closely applied to the medial surface of the pseudobasal process. The otic process extends along the medial surface of the squamosal from the dorsolateral edge of the pseudobasal process, and then expands medially to meet the bony edge of the otic capsule and form the crista parotica. Posterior to the formation of the crista parotica, the ventral part of the otic process splits. The medial part forms the ventrolateral ledge of the otic capsule (*vl. l. ot. c.*, Fig. 20a-f), whereas the lateral part moves ventrad in association with the ventral arm of the squamosal and fuses with the pterygoid process posteriorly.

Posterior to the bony closure of the prootic foramen, the ventromedial part of the pseudobasal process joins the prootic and forms the ventrolateral edge of the otic capsule. The posterior terminus of the medial branch of the pterygoid lies ventral to the lateral part of the otic capsule. The posterior branch of the otic process merges with the pterygoid process ventrally.

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FIGS. 16-17. Transverse sections through otic region: 16) at level of prootic foramen; 17) at level of anterior acoustic foramen. Abbreviations: *angspl.*, angulosplenic; *ant. acus. f.*, anterior acoustic foramen; *cr. par.*, crista parotica; *fpar.*, frontoparietal; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *ot. cap.*, otic capsule; *pasph.*, parasphenoid; *pro.*, prootic; *psdbas. proc.*, pseudobasal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.



FIGS. 18-19. Transverse sections through otic capsule: 18) at level of posterior acoustic foramen; 19) at level of jugular foramen. Abbreviations: *angspl.*, angulosplenic; *corn. prin.*, cornu principalis; *cr. par.*, crista parotica; *exocc.*, exoccipital; *fpar.*, frontoparietal; *jug. f.*, jugular foramen; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *ot. cap.*, otic capsule; *p. ext. pl.*, pars externa plectri; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *pasph.*, parasphenoid; *post. acus. f.*, posterior acoustic foramen; *postlat. cr. par.*, posterolateral edge of crista parotica; *pro.*, prootic; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *quad. proc.*, quadrato process; *qj.* quadratojugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

At the level of the anterior acoustic foramen the cornu principalis of the hyale (*corn. prin.*) appears as a lateral ledge at the ventrolateral corner of the otic capsule (Fig. 20a-b). The cornu principalis diverges from the ledge at the level of the abbreviated bridge between the anterior and posterior acoustic foramina. In posterior sections the cornu lies medial to the squamosal-ptyerygoid process-ptyerygoid complex (Fig. 18). The posterior terminus of the cornu lies at a level with that of the posterior acoustic foramen.

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The pars externa plectri (*p. ext. pl.*, Fig. 20a-b) is cartilaginous and first appears dorsal to the ventral arm of the squamosal in association with the tympanic membrane. The pars externa plectri expands dorsomedially and is fused briefly to the crista parotica by the pars ascendens plectri (*p. asc. pl.*, Fig. 20b). The pars interna plectri (*p. int. pl.*, Fig. 20b-f) is cartilaginous and appears medial to the pars media plectri and the ventrolateral ledge of the otic capsule at the level of the anterior acoustic foramen. The pars media plectri (*p. med. pl.*, Fig. 20b-f), a cartilage and bone element, appears proximally at the dorsolateral edge of the otic capsule and distally, ventral to the squamosal at a level between the anterior and posterior acoustic foramina. At the level of the posterior acoustic foramina the pars media plectri is bony, greatly expanded in size, and joined to the pars interna plectri medially.

The operculum (*op.*, Fig. 20d-h) is cartilaginous and lies medial to the lateral edge of the otic capsule between the pars interna plectri and pars media plectri. The anterior end of the operculum (Fig. 20d) lies at a level corresponding to the posterior part of the posterior acoustic foramen. Posteriorly the operculum increases in size, and the pars interna plectri and pars media plectri are reduced (Fig. 20e-f). At a level corresponding to the posterior border of the posterior acoustic foramen the medial portion of the pars interna plectri disappears and leaves a small lateral rod of cartilage surrounded on all but the ventral side by the operculum (Fig. 20f). The operculum expands medially to merge with the main part of the otic capsule (Fig. 20g). The lateral edge of the operculum expands ventrally and then dorsomedially to form a complete tube. Slightly more posteriorly the cartilaginous lateral edge of the otic capsule, lateral to the

operculum, dissipates into connective tissue and finally disappears, leaving the posterior end of the operculum as the most distal element of the otic capsule ([Fig. 20h](#)).

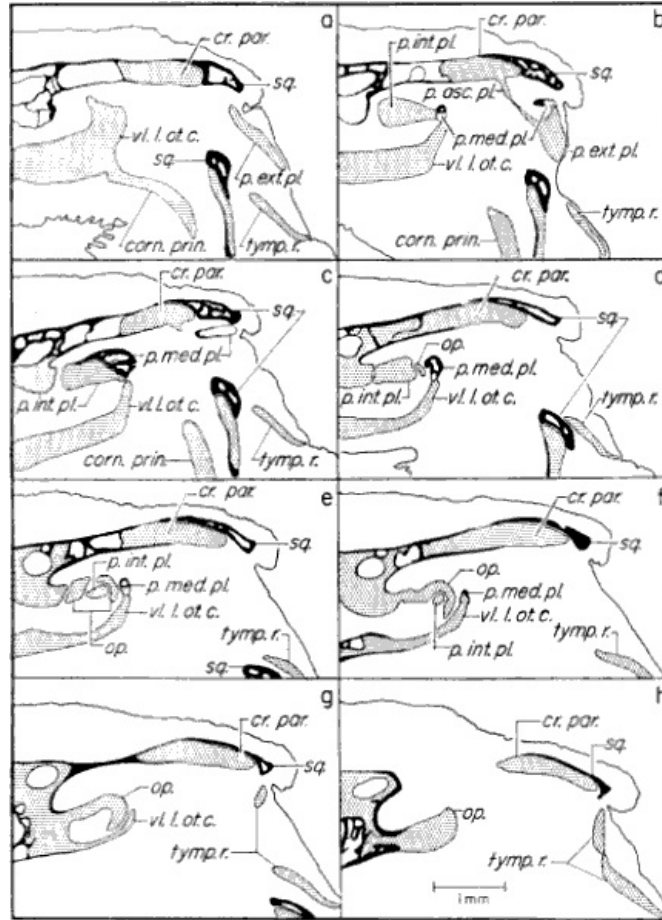


FIG. 20. Transverse sections through otic capsule: a) level of anterior ledge of otic capsule; b) anterior level of pars interna plectri and pars ascendens plectri; c) level of pars media plectri; d-f) successive levels of operculum and pars media plectri; g-h) posterior levels of operculum. Abbreviations: *corn. prin.*, cornu principalis; *cr. par.*, crista parotica; *op.*, operculum; *p. asc. pl.*, pars ascendens plectri; *p. ext. pl.*, pars externa plectri; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *sq.*, squamosal; *tym. r.*, tympanic ring; *vl. l. ot. c.*, ventrolateral ledge of otic capsule.

*Ossification in otic and occipital regions.*—The otic region of the cranium is largely unossified. At the level of the optic foramen ([Fig. 14](#)) the floor of the neurocranium is cartilaginous but completely underlaid by the bony parasphenoid. The taenia tecti marginales and the tectum synoticum are covered dorsally and laterally by the frontoparietals. Perichondral ossification representing the prootic bone occurs at the margin of the optic foramen and somewhat posteriorly over part of the floor of the neurocranium. Perichondral and endochondral ossification occurs in the sides of the neurocranium ventral to the lamina perpendicularis. This ossification expands laterally until it meets the crista parotica dorsolaterally and forms the dorsal part of the prootic bone. The anteroventral edge of the otic capsule remains cartilaginous. Posteriorly, at the level of the anterior acoustic foramen, endochondral ossification is meager and restricted to the dorsomedial parts of the otic capsule, plus a small amount in the neurocranial floor; perichondral ossification is restricted to the peripheral areas showing endochondral ossification. Posteriorly, endochondral ossification is restricted in the dorsal part of the otic capsule but somewhat increased in the floor of the capsule. The lateral part of the otic capsule posterior to the terminus of the operculum and the ventromedial and dorsomedial parts of the neurocranium remain unossified.

### Articular Region

In the anterior sections (at the level of the oculomotor foramen) the angulosplenic (*angspl.*) is

a moderate-sized bone (Fig. 15). Meckel's cartilage (*Mc. c.*) is present as a small ovoid cartilage lying dorsolateral to the angulosplenic. Posteriorly, Meckel's cartilage is dorsal to the angulosplenic. The cartilage increases in size at the level of the posterior acoustic foramen, and the angulosplenic decreases in size posteriorly. At the level of the posterior border of the posterior acoustic foramen, the maxillary terminates and is replaced by the quadratojugal. The quadratojugal, ventral arm of the squamosal, pterygoid process, pterygoid, and Meckel's cartilage converge. At the level of the jugular foramen (*jug. f.*) (Fig. 19) the quadratojugal is incorporated into the squamosal-ptyerygoid process-ptyerygoid complex. The complex is narrowly separated by connective tissue from Meckel's cartilage ventrally. The quadrate process (*quad. proc.*) is represented by the cartilage bordered dorsally by the pterygoid process and the ventral arm of the squamosal, and ventrally by Meckel's cartilage. At the posterior terminus of the skull all bony elements of the articular region terminate, except for a small terminal part of the angulosplenic underlying Meckel's cartilage.

## SUMMARY

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Since no accounts comparable to the preceding for *Smilisca baudini* are available for other hylid frogs, it is meaningless to attempt any discussion dealing with character significance or variation within the Hylidae. There is considerable literature treating bufonids, leptodactylids, ranids, and various Old World genera (see Baldauf, 1955, for a review of these works). Likewise, a comparison at the familial level based on the study of a single species seems inadequate and premature. By way of summary and synoptic description a list of cranial osteological characters of *Smilisca baudini* is presented. The items selected enable comparison with similar compilations by other workers, and are based in part on my unpublished observations of other hylids.

1. Compared to hylids not having integumentary-cranial co-ossification, the dermal roofing bones of *Smilisca baudini* are extensive, and the skull is well-ossified internally. In contrast to most casque-headed hylids (those having integumentary-cranial co-ossification), the dermal roofing bones are much less extensive, the dermal sphenethmoid (see Trueb, 1966, p. 563) is absent, and internal ossification is less extensive.
2. The solum nasi is not ossified; the septum nasi is ossified only posteriorly, and the olfactory eminence is supported by the cartilaginous solum nasi and the bony prevomer.
3. The lingual process is absent. There is no palatal cartilage isolated between the premaxillaries.
4. The anterior end of the cavum medium lies anterior to the cavum inferius.
5. The septomaxillary is basically a U-shaped structure and has a dorsal, anteriorly curved, ramus on the lateral branch and a longitudinal loop of bone ventrally.
6. A distinct pars nasalis is absent on the maxillary.
7. A cartilaginous sclera is present.
8. The taenia tecta marginalis and the tectum synoticum are the only roofing cartilages present.
9. The external part of the plectral apparatus (columella) is directed anterolaterally. The pars ascendens plectri is fused with the crista parotica.
10. The pseudobasal process is fused to the otic capsule.
11. The cornu principalis of the hyale fuses with the pseudobasal process.
12. Two acoustic foramina are present.
13. The sphenethmoid and prootic are synchondrotically united.
14. The frontoparietal is separate from the prootic and exoccipital.
15. The prootic and exoccipital are fused.
16. A bursa angularis oris is present.

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