

# Cranial Osteology of the Andean Lizard *Stenocercus guentheri* (Squamata: Tropicuridae) and Its Postembryonic Development

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**ABSTRACT** In spite of the great diversity of iguanian lizards, detailed descriptions of their osteocrania and postembryonic development are rare. Herein, the adult cranial osteology of the tropicurid lizard *Stenocercus guentheri* and its postembryonic development are described based on cleared and double-stained and dry skeletal specimens from a single Ecuadorian population. The amphikinetic skull of *S. guentheri* is short and elevated and bears teeth on the premaxilla, maxillae, and pterygoids. Mandibular teeth are present on the dentaries. Ossification of the articular from Meckel's cartilage and growth of the parietal (ossification and investment of the frontoparietal fontanelle) are the most significant ontogenetic changes of the splanchnocranium and dermatocranium, respectively. The ossification of the cartilage separating the bones of the braincase is the most relevant postembryonic ontogenetic event of the neurocranium. The number of teeth does not vary ontogenetically and replacement teeth are present throughout postembryonic life. This study includes a list of the osteocranial characters of *Stenocercus* that have been used in systematic studies, as well as a discussion of functional morphology and kinesis. *J. Morphol.* 255:94–113, 2003.

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**KEY WORDS:** Tropicuridae; *Stenocercus guentheri*; osteology; cranium; development

Most of the first studies on the morphology and development of the lizard skeleton are from the late 19th century (e.g., Parker, 1880, 1881; Gaupp, 1891; Cope, 1892; Siebenrock, 1892, 1893a,b, 1894, 1895; Versluys, 1898). Beginning with the description of the chondrocranium of *Lacerta agilis* (Gaupp, 1900), the embryonic cranium of the lizard attracted special attention in the early 20th century (e.g., Gaupp, 1906; Rice, 1920; Pearson, 1921; de Beer, 1930; Brock, 1932, 1940). Although literature on the osteocranium of adult lizards is quite extensive, comprehensive, detailed descriptions (e.g., Oelrich, 1956; Jollie, 1960) are scarce. Studies of the development of the cranium of lizards (e.g., Parker, 1880; Sewertzoff, 1900; de Beer, 1930, 1937; Rieppel, 1992a) focus mainly on the chondrocranium (Bellairs and Kamal, 1981). Thus, the morphology and development of the chondrocranium of lizards are

the best-studied among reptiles (Bellairs and Kamal, 1981). In contrast, the postembryonic development of the cranium (and postcranium) of lizards is poorly known (e.g., Hikida, 1978; Rieppel, 1984, 1987, 1992b). In an attempt to increase our knowledge of this facet of the osteology of lizards, I describe herein the postnatal development of the osteocranium of the tropicurid lizard *Stenocercus guentheri*.

The genus *Stenocercus*, comprising approximately 50 species, is endemic to South America and ranges from northern Colombia to central Argentina (Frost, 1992; Torres-Carvajal, 2000). Except for some general taxonomic studies (e.g., Fritts, 1974; Cadle, 1991; Torres et al., 2000; Torres-Carvajal, 2000), the systematics of *Stenocercus* has been poorly addressed; as a consequence, the phylogenetic relationships among species of *Stenocercus* have not been ascertained. Hallermann (1994) described the nasal capsules of *S. varius*, but there is no comprehensive description of the morphology and development of the skeleton of any species of *Stenocercus*. Nearly all osteological information on *Stenocercus* is contained in descriptions of characters in systematic studies (Etheridge, 1966; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Frost, 1992). Also, Cadle (1991) described briefly a few general features of the skull of five species of *Stenocercus* and discussed the pterygoid teeth in some species. The following account provides a detailed description of the adult osteocranium of *S. guentheri*, along with its postembryonic development. This study will facilitate identification of informative characters of cranial mor-

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TABLE 1. Specimens of *Stenocercus guentheri* examined

Specimen no.	SVL (mm)	Skull length (mm)	Sex
KU 147347	30	9.6	—
KU 147525	32	9.8	—
KU 147520	35	11.1	—
KU 147346	39	11.2	—
KU 147519	44	12.7	Female
KU 147534	49	13.4	Male
KU 147445	55	14.6	Female
KU 147477	60	15.1	Female
KU 147409	65	17.1	Male
KU 147326	66	15.8	Female
KU 147369	67	16.6	Female
KU 147382	68	16.6	Female
KU 147487	70	17.3	Male
KU 147482	74	18.0	Male
KU 147319	78.5	19.8	Male
KU 147421	79	18.8	Male
KU 147388	81	18.5	Male
KU 147412	88	20.3	Male

SVL = snout-vent length.

phology that can be used to infer the phylogenetic relationships among members of the genus *Stenocercus*.

## MATERIALS AND METHODS

Eighteen posthatching specimens of *Stenocercus guentheri*, snout-vent lengths (SVL) 30–88 mm, were examined (Table 1). Size is not an accurate estimate of age in reptiles (Andrews, 1982); nonetheless, size was the only available criterion for selecting the specimens. Although the neonatal size of *S. guentheri* is not known, the reported size of this species is 20–96 mm SVL (Torres-Carvajal, 2000). Thus, the description of the postnatal development of the osteocranium of *S. guentheri* presented here might not include neonates as defined by Morafka et al. (2000). Except for two dry skulls (KU 147319, 147326), all specimens were cleared and double-stained following the methodology of Taylor and van Dyke (1985) and Wassersug (1976). The sex of each specimen was determined by dissection; specimens smaller than 44 mm SVL had undifferentiated gonads. Descriptions and illustrations were prepared with the aid of a stereomicroscope equipped with a camera lucida.

The cranial osteology of adult *Stenocercus guentheri* is based on the description of the largest cleared-and-double-stained specimen (KU 147412, 88 mm SVL, male). Because of visual distortion of this specimen, several structures were drawn from dry skulls when appropriate (i.e., no major differences with the largest specimen). Because no serial sections were made, nasal and orbitotemporal cartilages are not described. Allometric analyses also were excluded from this study. The nomenclature proposed by Oelrich (1956) is followed unless otherwise mentioned; I follow Cope (1892) and Underwood (1970) for the nomenclature of the hyoid apparatus and scleral ossicles, respectively. To facilitate comparison with other studies of cranial osteology of lizards, synonyms and references are presented in parentheses after each term, as appropriate. For those anglicized names that are widely accepted, synonyms representing the Latin name (e.g., articulare instead of articular) are not included. Mandibular and maxillary teeth were counted from the anterior to the posterior ends of each side.

All specimens were collected in Ecuador (Mulaló; 00°47'S, 78°34'W; 2990 m; Provincia Cotopaxi) and are deposited in the herpetological collection of The University of Kansas Natural History Museum and Biodiversity Research Center.

## RESULTS

### Cranial Osteology of Mature Individual

The amphikinetic skull of *Stenocercus guentheri* (Fig. 1) is elevated (skull height = 46% of skull length) and short (skull width = 71% of skull length). Marginal teeth are present on the maxillary arcade (i.e., premaxilla and maxillae) and palatal teeth are present on the pterygoids. The opisthotics-exoccipitals and parasphenoid-basisphenoid are indistinguishably fused and, therefore, are described as single units—otoccipitals and parabasisphenoid, respectively. The only elements that bear ornamentation are the frontal and the parietal, which form the margins of the pineal foramen. The mandible is dentigerous and V-shaped in dorsal and ventral profiles and its greatest width is 87% of its total length (Fig. 2). Each mandibular ramus increases in height and width posteriorly. The rami meet anteriorly, forming the mandibular symphysis, the cartilaginous part of which represents the fused anterior ends of Meckel's cartilages.

### Dermatocranium

**Premaxilla.** This element forms the anteromedial margin of the snout and the medial margin of each fenestra exonarina (*apertura nasalis externa* Hallermann, 1994; *external naris* Rieppel, 1981; de Queiroz, 1987). The premaxilla (pm) bears a narrow posterodorsally oriented nasal process (*premaxillary spine* Cope, 1892; Frost and Etheridge, 1989; *pre-narial process*, *processus nasalis* Jollie, 1960), which extends between the nasals, and a broad anterior alveolar portion (Fig. 1A–C). The premaxilla articulates with the maxillae anterolaterally and nasals posteriorly. The short posterior end of the nasal process articulates with the anteromedial corners of the nasals. In ventral view (Fig. 1B), the premaxilla is separated from the vomers and bears a posteromedial incisive process (pip). This tongue-shaped process extends ventrally and is as wide as, but less than one-half the length of, a premaxillary tooth. The incisive process (*spina premaxillaris*, *prevomerine process* Jollie, 1960) lacks posterolateral extensions and is not pierced by foramina. Along its posteroventral edge, the premaxilla bears a crest that extends from its posterolateral corners to the base of the incisive process. Unlike other lizards, such as most iguanines (de Queiroz, 1987), the ventral surface of the premaxilla of *Stenocercus guentheri* lacks posteroventral extensions at its articulation with the maxilla. Anteroventrally, the alveolar portion of the premaxilla bears six teeth (Fig. 1B).

**Septomaxillae.** The septomaxillae (sm) are dorsoventrally compressed and lie anteromedially within the nasal capsules, lateral to the nasal septum (Fig. 1C). They form the floor of the anteromedial portion of the nasal cavity and the roof of the cavum containing the vomeronasal organ. Ventrally,

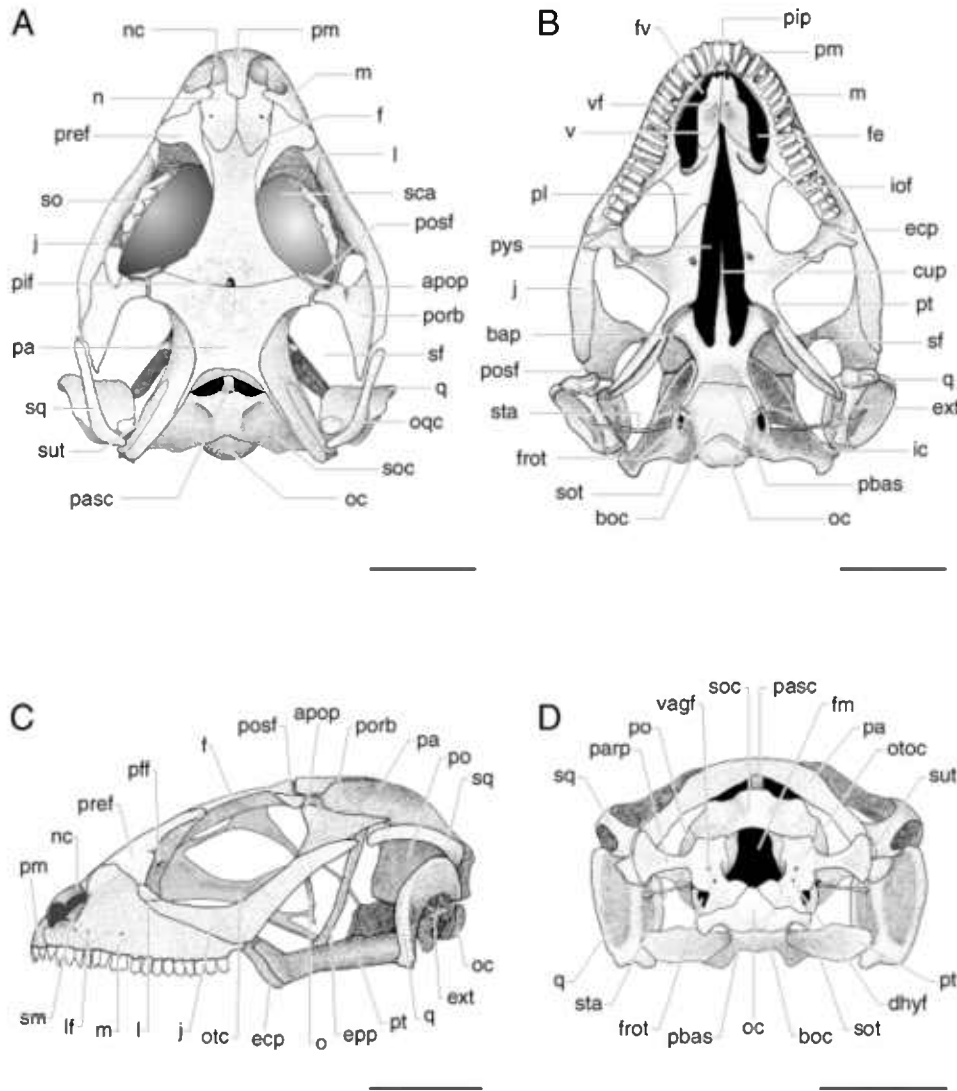


Fig. 1. *Stenocercus guentheri*. Skull of adult (A, B, C, KU 147412; D KU 147319) in dorsal (A), ventral (B), lateral (C) and posterior (D) views. apop, anterodorsal postorbital process; bap, basiptyergoid process; boc, basioccipital; cup, cultriform process; dhyf, dorsal hypoglossal foramen; ecp, ectopterygoid; epp, epipterygoid; ext, extracolumella; f, frontal; fe, fenestra exchoanal; fm, foramen magnum; frot, foramen rotundum; fv, fenestra vomeronasalis externa; ic, intercalary cartilage; iof, inferior orbital fenestra; j, jugal; l, lacrimal; lf, labial foramina; m, maxilla; n, nasal; nc, nasal capsules; o, orbitosphenoid; oc, occipital condyle; oqc, ossified quadrate cartilage; otc, orbitotemporal cartilages; otoc, otoccipital; pa, parietal; parp, paraoccipital process; pasc, processus ascendens; pbas, parabasisphenoid; pff, prefrontal foramen; pif, pineal foramen; pip, posteromedial incisive process; pl, palatine; pm, premaxilla; po, prootic; porb, postorbital; posf, postfrontal; pref, prefrontal; pt, pterygoid; pys, pyriform space; q, quadrate; sca, scleral cartilage; sf, supratemporal fossa; sm, septomaxilla; so, scleral ossicles; soc, supraoccipital; sot, sphenoccipital tubercle; sq, squamosal; sta, stapes; sut, supratemporal; v, vomer; vagf, vagal foramen; vf, vomerine foramen. Gray indicates cartilage; stippled gray denotes calcification. Scale bars = 5 mm.

the cavum is supported by the vomers. The septomaxillae are oriented anteroventrally and articulate with the maxillae anterolaterally and the vomers ventrally.

**Maxillae.** The maxillae (m) occupy most of the anterolateral aspects of the skull between the orbits and the snout (Fig. 1A–C). In lateral aspect, each maxilla extends approximately half the length of the skull. In an anterior-to-posterior sequence, the dorsal margin of the maxilla articulates with the premaxilla, septomaxilla, nasal, prefrontal, lacrimal, and jugal, respectively. The lateral surface of the preorbital facial process of the maxilla is concave and forms the ventral and posterodorsal rims of the fenestra exonarina. There are two (left) or three (right) anterior inferior alveolar foramina on the pars facialis of the maxilla. The anterodorsal margin of the facial process forms the posteromedial rim of the fenestra exonarina and overlaps the nasal anterolaterally. The posterior half of the pars facialis of the maxilla is flat; five labial foramina (lf) are

present on the lateral surface. The orientation of the labial foramina shifts from posterior (most posterior foramen) to anterior (most anterior foramen). These foramina are arranged in a nearly straight line that parallels the ventrolateral margin of each maxilla. The part of the maxilla bearing the last seven teeth forms part of the floor of the orbit (Fig. 3) and is dorsally overlapped by the palatine anteriorly, the jugal laterally, and the ectopterygoid posteriorly. This portion also constitutes the anteromedial rim of the inferior orbital fenestra (iof; *foramen suborbitale* Wellborn, 1933; *inferior orbital foramen* Oelrich, 1956; *palatine fontanelle* Jollie, 1960) and forms the floor of the maxillopalatine foramen (*infraorbital canal* Jollie, 1960; *infraorbital foramen* Kluge, 1962; de Queiroz, 1987) anteriorly. The maxillopalatine foramen is less than half the size of the lacrimal foramen (Fig. 3). Each maxilla bears 18 medially recurved and laterally compressed teeth on a well-developed alveolar shelf (Fig. 1B,C). Each maxillary alveolar shelf forms the lateral margin of each

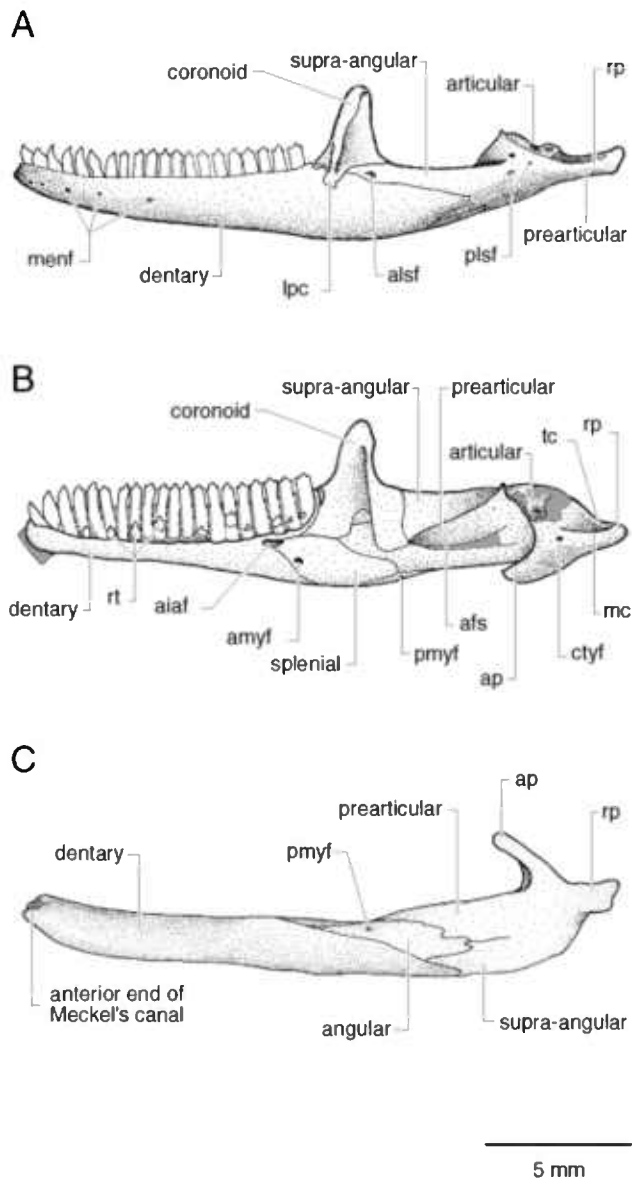


Fig. 2. *Stenocercus guentheri*. Mandible of adult (KU 147412) in lateral (A), medial (B), and ventral (C) views. afs, adductor fossa; aiaf, anterior inferior alveolar foramen; alsf, anterolateral supra-angular foramen; amyf, anterior mylohyoid foramen; ap, angular process; ctyf, chorda tympani foramen; lpc, labial process; mc, medial crest; menf, mental foramina; pls, posterolateral supra-angular foramina; pmyf, posterior mylohyoid foramen; rp, retroarticular process; rt, replacement teeth; tc, tympanic crest. Gray indicates Meckel's cartilage.

fenestra exochoanalis (*choana* or *internal nostril* Bellairs and Kamal, 1981; *internal choana* Kluge, 1962) posteriorly and each fenestra vomeronasalis externa (*foramen Jacobsoni* Wellborn, 1933) anteriorly. The latter two fenestrae are continuous (Fig. 1B)—i.e., palaeochoanate condition (Lakjer, 1927). The medial margin of the alveolar shelf bears a crest, which extends anteromedially to overlap the lateral portions of the posteroventral margin of the premaxilla.

**Nasals.** The nasals (n) articulate anteriorly with the nasal process of the premaxilla and posteriorly overlap the frontal, thereby forming most of the roof of the nasal capsules (Fig. 1A). The posterior halves of the nasals are ventrally concave and form a conspicuous depression of the skull table between the anterior margins of the orbits. Each nasal articulates with the premaxilla anterior to the internasal suture and is acuminate posteriorly. In an anterior-to-posterior sequence, the lateral margin of each nasal articulates with the maxilla, prefrontal, and frontal, respectively. The nasal–prefrontal articulation is interrupted posteriorly by the slender anterolateral processes of the frontal, which extend to a point anterior to the lacrimals; however, the nasals partially overlap these processes to meet the postfrontals. Anteriorly, the nasal forms the posterodorsal rim of the fenestra exoanarina. The dorsal surface of each nasal bears two (right) or three (left) small

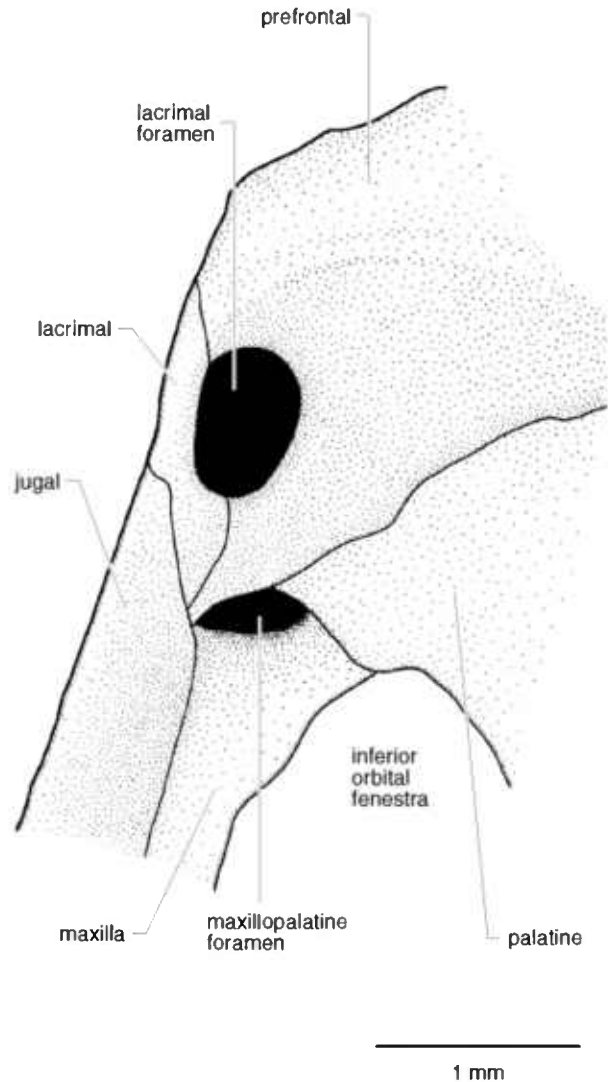


Fig. 3. *Stenocercus guentheri*. Anterior margin of orbit of adult (KU 147326) in posterior view.

foramina arranged on an oblique line parallel to the posterolateral margin of the bone. The posterolateral margin forms an angle of about 45° with the adjacent posteromedial margin.

**Prefrontals.** The prefrontals (pref) lie on the anterolateral aspects of the skull table and form the anterodorsal rims of the orbits and the posterior wall of the nasal capsules (Figs. 1, 3). Together with the frontal and palatines, the prefrontals border the orbitonasal fenestra, which communicates between the nasal and orbital cavities. Each prefrontal articulates with the frontal and nasal dorsomedially, the maxilla anterodorsally and anterolaterally, and the lacrimal ventrolaterally. The anterior part of the articulation between the prefrontals and the anterolateral processes of the frontal is overlapped by the nasals (Fig. 1A). In posterior view, each prefrontal articulates with the lacrimal laterally and is separated ventrally from the palatine by connective tissue. The ventrolateral portion of the posterior surface of each prefrontal is notched (*incisura lacrimalis* Wellborn, 1933) and forms the medial margin of the lacrimal foramen (Fig. 3). Ventral to this foramen, the ventrolateral end of each prefrontal is separated from the lacrimal by connective tissue. Ventral to the prefrontal–frontal suture, each prefrontal bears a foramen (Fig. 1C), herein termed the prefrontal foramen (pff).

**Lacrimal.** The lacrimals (*lachrymals* or *lacrymals* Bellairs and Kamal, 1981; Camp, 1923; de Beer, 1937) are small and laterally compressed bones, each of which completes the anterior orbit between the prefrontal and jugal (Fig. 1A,C). Each lacrimal (l) articulates with the maxilla anteriorly, jugal ventrolaterally and posteromedially, and prefrontal dorsolaterally and medially. Ventromedially, the lacrimals are separated from the prefrontals by connective tissue. The medial aspect of each lacrimal is notched to form the lateral wall of the lacrimal foramen (Fig. 3).

**Frontal.** The frontal (f) lies between the orbits and forms most of the dorsal orbital margin (Fig. 1A,C). It is longer than wide and bears ornamentation that more or less corresponds to the pattern of the scales closely adhered to its dorsal surface. Anteriorly, the frontal is W-shaped because of the presence of one anteromedial and two anterolateral processes, which are partially overlapped by the nasals. The anterolateral processes are thinner and longer than the anteromedial process and extend to a point anterior to the lacrimals. Each anterolateral process forms a conspicuous ridge that laterally borders the depression in the posterior portions of the nasals. The anterolateral processes articulate with the medial margin of the prefrontals; however, only the anterior and posterior portions of the anterolateral processes are dorsally exposed because of partial overlap by the nasals (Fig. 1A). The anteromedial process of the frontal articulates with the posteromedial margin of each nasal and meets the posterior

end of the internasal suture. The transverse posterior margin of the frontal lies anterior to the posterior margin of the orbits and articulates with the anterior margin of the parietal. Medially, the posterior margin of the frontal is notched (Fig. 1A) to form more than half of the margin of the pineal foramen (pif). Posterolaterally, the frontal articulates with the anteromedial margin of the postfrontal.

**Parietal.** The parietal (pa) forms most of the posterior surface of the skull table and has dorsal ornamentation that slightly corresponds to the pattern of the scales closely adhered to the surface (Fig. 1A,C). Laterally, the parietal is medially concave and forms the medial rim of the supratemporal fossae (sf). The corpus of the parietal bears a pair of short anterolateral processes, as well as a pair of long supratemporal processes (*lateroventral processes* Rieppel, 1981; *parietal processes* Wellborn, 1933; Jollie, 1960). A prominent, ventrolateral descending process connects the anterolateral and supratemporal processes and invests the lateral aspect of the taenia marginalis. The body of the parietal bears one medially concave longitudinal crest on each side. Each anterolateral process articulates with the posterior half of the medial margin of the postfrontal anteriorly and with the dorsal process of the postorbital laterally. The ventrally oriented supratemporal processes are laterally compressed and describe an angle of approximately 72°; the supratemporals overlap these processes ventrolaterally (Fig. 1A). The distal end of each supratemporal process articulates with the paraoccipital process (parp) of the otoccipital (Fig. 1D). The transverse anterior margin of the parietal articulates with the posterior margin of the frontal and encloses the pineal foramen medially. This foramen is mostly enclosed by a medial notch on the posterior margin of the frontal. Medially, the posteroventral surface of the parietal bears the parietal fossa, which receives the distal end of the cartilaginous processus ascendens of the supraoccipital.

**Supratemporals.** The supratemporals (sut) are laterally compressed, longitudinal bones with convex anterior margins (Fig. 1A). Each supratemporal (*squamosal* of many authors; *tabular* Camp, 1923; Broom, 1935; see Camp [1923], de Beer [1937], and Jollie [1960] for discussion on nomenclature) lies entirely on the posteroventral portion of the lateral surface of each supratemporal process of the parietal. The anterior end of each supratemporal extends halfway across the supratemporal fossa, whereas the posterior end articulates with the distal end of the paraoccipital process of the otoccipital, the cephalic condyle of the quadrate, the posterior end of squamosal, and the intercalary cartilage.

**Postfrontals.** The postfrontals (posf) are small, flat triangular bones that form part of the anterodorsal rims of the orbits (Fig. 1A,C). The medial margin of each postfrontal articulates with the anterolateral process of the parietal posteriorly and

the posterior end of the lateral margin of the frontal anteriorly. The posterior margin of each postfrontal articulates with the anterior margin of the dorsal process of each postorbital.

**Postorbitals.** These triradiate bones (porb; *quadratojugals* Reese, 1923) lie on the posterolateral aspects of the skull posterior to the orbits (Fig. 1A,C). The anterior margin of each postorbital forms the posteroventral rim of the orbit, whereas the posterior margin forms the anterolateral rim of the supratemporal fossa. Each postorbital forms the anterior half of the supratemporal arch. The posterodorsally oriented ventral margin of the postorbital articulates anteriorly with the jugal and is separated posteriorly from the squamosal by a flexible ligament. The dorsal process of each postorbital extends dorsomedially and articulates with the posterior margin of the postfrontal anteriorly and with the anterolateral process of the parietal medially. Lateral to the articulation with the postfrontal, the dorsal process bears a short, wide, anterodorsally oriented knob (Fig. 1A,C), herein termed the anterodorsal postorbital process (apop).

**Squamosals.** The squamosals (sq; *paraquadrates* Gaupp, 1906; *supratemporals* of many authors; nomenclature discussed by Camp [1923], de Beer [1937], and Jollie [1960]) are long and slender and form the posterolateral rims of the supratemporal fossae and the posterior halves of the supratemporal arches (Fig. 1A,C). The anterior portion of the dorsal margin of each squamosal is separated from the posteroventral margin of the postorbital by a flexible ligament. Posteriorly, the squamosal is expanded and articulates dorsally with the posterior end of the supratemporal and ventrally with the cephalic condyle of the quadrate.

**Jugals.** Jugals (j) are broadly V-shaped and form the ventral rims of the orbits (Fig. 1A–C). Each jugal (*zygomaticum* Gaupp, 1906) is composed of two elongate processes that enclose an angle of 120° with the vertex lying halfway between the anterior and posterior ends of the skull (Fig. 1C). The anterior, or maxillary, process articulates ventrally with the posterodorsal portion of the maxilla (Fig. 3), posteromedially with the distal margin of the anterolateral process of the ectopterygoid, and anteriorly with the lacrimal. The dorsal half of the anterior margin of the posterior or temporal process articulates with the anterior portion of the ventral margin of the postorbital (Fig. 1C). Medially, the temporal process bears the maxillary foramen, which lies immediately anterior to the anteroventral end of the postorbital.

**Vomers.** Vomers (v; *prevomers* Camp, 1923; Williston, 1925; de Beer, 1937; Kluge, 1962) are the most anterior elements of the palate and form the medial border of each fenestra vomeronasalis externa (fv) anterolaterally and about three-quarters of the length of the medial rim of each fenestra exochoanalis (fe) posterolaterally (Fig. 1B). The

vomers articulate with each other along the anterior two-thirds of their length and are separated from the posteroventral margin of the premaxilla and premaxillary process of the maxilla by connective tissue. Each vomer has a small groove anteriorly. The anterior half of each vomer bears a vomerine foramen (vf) and a lacrimal groove on its lateral aspect. There is a small notch anterior to the lacrimal groove that corresponds to the medial rim of the fenestra vomeronasalis externa. Posteriorly, the vomers are invested by the vomerine processes of the palatines. The posteromedial aspect of each vomer is dorsally concave.

**Palatines.** Palatines (pl) are medially separated by the anterior third of the pyriform space (pys; *pyriform recess* Oelrich, 1956). Each palatine bears three processes—the vomerine anteromedially, the pterygoid posteriorly, and the maxillary anterolaterally (Fig. 1B). The vomerine process overlaps the corresponding vomer dorsally, thereby lying in the most dorsal aspect of the palate. Together with the anterior margin of the maxillary process, the lateral margin of the vomerine process forms the posteriorly concave rim of the fenestra exochoanalis. The wide quadrangular pterygoid process descends posteroventrally and forms the medial margin of the inferior orbital fenestra. This process overlaps the dorsal surface of the palatine process of the pterygoid posteriorly and bears a series of small foramina on its ventral surface. The short maxillary process forms the medial half of the anterior rim of the inferior orbital fenestra posteriorly. The maxillary process overlaps the dorsal surface of the maxilla at the level of the anterior end of the orbit forming the roof of the maxillopalatine foramen (Fig. 3).

**Ectopterygoids.** The ectopterygoids (ecp) form the posterolateral rims of the inferior orbital fenestrae (Fig. 1B). Each ectopterygoid (*transpalatine* de Beer, 1937; *transversum* Beddard, 1905; Gaupp, 1906; Wellborn, 1933) bears three processes—anterolateral, posterolateral, and medial. The anterolateral process overlaps the dorsal surface of the posterior portion of the maxilla bearing the last four maxillary teeth. Laterally, this process articulates with the posterior portion of the ventromedial margin of the maxillary process of the jugal. The anterior aspect of the short posterolateral process overlaps (with a thin layer of connective tissue in between) the anteroventral end of the temporal process of the jugal dorsally and the posterior end of the maxilla ventrally. The medial process bifurcates into dorsal and ventral branches, which firmly brace the anterior aspect of the transverse process of the pterygoid. The vertical ventral branch is shorter than the dorsal one.

**Pterygoids.** The pterygoids (pt) are the largest and most posterior elements of the palate and bear one tooth each (Fig. 1B–D). They form the posteromedial rim of each inferior orbital fenestra and, together with the parabasisphenoid, the rim of the

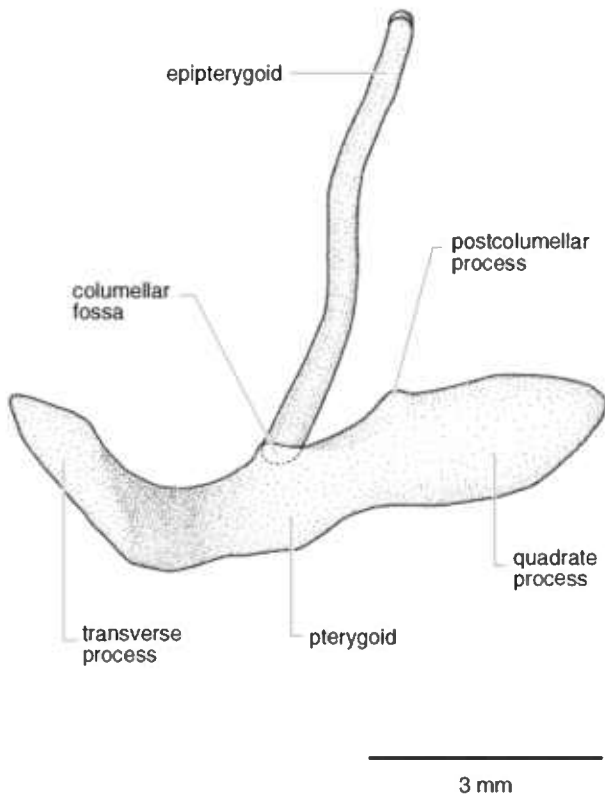


Fig. 4. *Stenocercus guentheri*. Left pterygoid and epipterygoid of adult (KU 147326) in lateral view. Gray denotes cartilage.

posterior two-thirds of the pyriform space. Anteriorly, each pterygoid bears two processes—the palatine medially and the transverse laterally. Each flat, triangular palatine process forms the posterior quarter of the roof of the mouth and, dorsally, is overlapped by the pterygoid process of each palatine. Each transverse process extends dorsolaterally; distally, the transverse process is expanded and anteriorly embraced by the dorsal and ventral branches of the medial process of the ectopterygoid. Posteriorly, each pterygoid bears the long, laterally compressed quadrate process, which constitutes half the length of the bone. The quadrate process is medially concave, laterally convex, and extends posterolaterally to articulate with the ventral portion of the medial aspect of the quadrate (Fig. 1D). The antero-medial aspect of each quadrate process bears the large pterygoid notch, which is fused with the overlying meniscus pterygoideus. The meniscus pterygoideus is partly ossified and receives the distal cartilaginous end of the basiptyergoid process (bap) of the parabasisphenoid (Fig. 1B). The proximal end of the dorsal border of each quadrate process bears the columellar fossa (*fossa pterygoidei* Jollie, 1960), which receives the ventral end of each epipterygoid; posterior to the columellar fossa, the quadrate process bears a small elevation, the postcolumnellar process (Fig. 4).

**Scleral ossicles.** The scleral ossicles (so) are thin plates of bone that lie in a circular depression (sulcus) that surrounds the cornea. The scleral ossicles maintain the concavity of the sulcus against the intraocular pressure (Underwood, 1970). There are 14 ossicles of similar size in each eye (Fig. 5). Each ossicle has a sigmoid flexure as it passes from the concavity of the sulcus to the convexity of the sclera (Underwood, 1970). Ossicles 1, 6, and 8 are plus (+) plates because they overlap both neighbors, whereas Ossicles 4, 7, and 10 are minus (−) plates because they are overlapped by both neighbors. This number and pattern of overlap of ossicles are fairly constant among iguanian lizards (Gugg, 1939; Underwood, 1970; de Queiroz, 1982) and, because all the ossicles contribute to the corneal margin of the ring, correspond with Pattern A (de Queiroz, 1982). Pattern A is widespread among iguanian lizards and, therefore, has been considered primitive for Iguania (de Queiroz, 1982).

**Dentary.** This anterolateral element is the largest of the mandibular bones and the only one that bears teeth (Fig. 2A–C). It is more than half the length of the lower jaw laterally and bears 20 (21 on left ramus) teeth on a well-defined alveolar shelf. The dentary (*dentale* Gaupp, 1906; Versluys, 1936) invests the anterior half of Meckel's cartilage; however, the anterior end of the cartilage exits the dentary anterolaterally through the anterior end of Meckel's canal, which lies ventral to the second

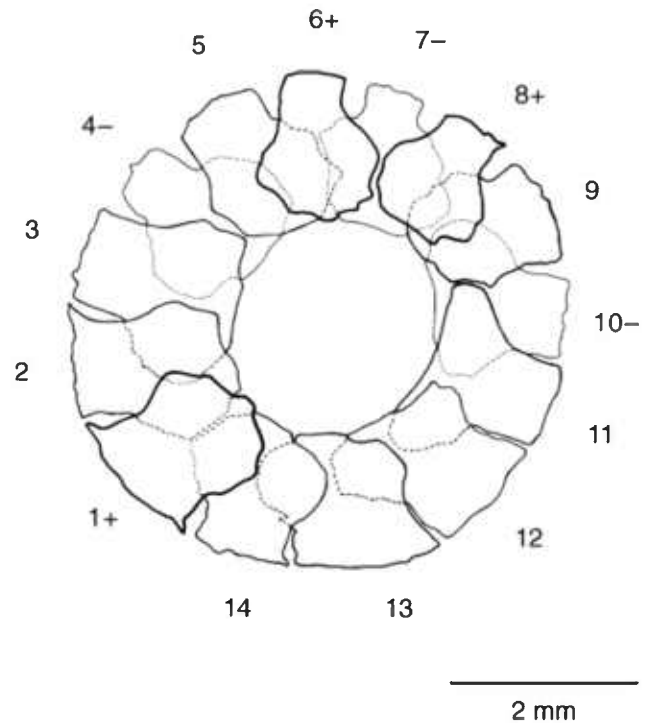


Fig. 5. *Stenocercus guentheri*. Right scleral ossicles of adult (KU 147412) in lateral view. "+" denotes ossicles overlapping both neighbors, "-" denotes ossicles overlapped by both neighbors.

tooth (Fig. 2B,C). Posteriorly, the dentary extends more than 50% the length from the apex of the coronoid to the anterior edge of the articular in lateral view. The posterior margin of the dentary articulates with several bones. Ventromedially, it is associated with the angular (Fig. 2C). Ventrolaterally and laterally, it articulates with the supra-angular and is overlapped dorsally by the labial process (lpc) of the coronoid (Fig. 2A). In lingual aspect, the dentary is bifurcate; the ventral splenial process and anteroventral portion of the dorsal coronoid process articulate with the splenial, whereas the posterior aspect of the dorsal coronoid process overlaps the anterior lingual process of the coronoid. Ventral to the third- and fourthmost posterior teeth, the dentary, splenial, and coronoid meet (Fig. 2B) to form the anterior inferior alveolar foramen (aiaf; *Meckelian foramen* Romer, 1956; Zalusky et al., 1980). The dorsolateral margin of the dentary, at its union with the coronoid, lies at the same level as the dorsal margin of the supra-angular. Laterally, the anterior half of the dentary bears five mental foramina (menf; *foramina dento-facialia* Versluys, 1936), which lie in a longitudinal series halfway between the ventral and dorsal margins (Fig. 2A).

**Coronoid.** The coronoid (*complementare* Gaupp, 1906) lies immediately behind the mandibular tooth row (Fig. 2A,B). It has a large dorsal process that extends above the rest of the dorsal margin of the mandible; the height of the dorsal process is nearly as high as the maximum height of the dentary. Anteriorly, the base of the dorsal process is separated from the tooth row by connective tissue. Ventrolaterally, the coronoid bears a small labial process, which overlaps the dentary; the length of the labial process is less than one-fourth the height of the mandible at that point (Fig. 2A). Posterior to the labial process, the coronoid articulates ventrolaterally with the dorsal margin of the anterolateral process of the supra-angular. In medial aspect, the coronoid bears two processes (Fig. 2B). The anterior lingual process articulates with the dentary anteriorly, splenial ventrally, prearticular posteroventrally, and supra-angular posterodorsally. The posterior lingual process overlaps the anteromedial portions of the supra-angular dorsally and prearticular ventrally. The base of the lingual bifurcation of the coronoid is dorsally concave and articulates with the anterior end of the supra-angular.

**Supra-angular.** The supra-angular (*surangular* Cope, 1892; Kingsley, 1905; Romer, 1956; Kluge, 1967; Zalusky et al., 1980; de Queiroz, 1987; Rieppel, 1993) occupies the posterior half of the mandible and forms the dorsal portion of the lower jaw between coronoid and articular (Fig. 2A–C). In order to make a clear distinction between lateral and medial supra-angular foramina, I propose the names anterolateral (alsf) and posterolateral (plsf) supra-angular foramina instead of only anterior and posterior, respectively (Fig. 2A). In lateral aspect, the

supra-angular is about one-third the length of the mandible and bears a narrow anterolateral process that extends between the coronoid dorsally and dentary ventrally. The dorsal margin of the distal portion of this process articulates with the ventrolateral border of the coronoid posterior to the labial process. The ventral margin of the anterior process articulates with the posterodorsal border of the dentary. The anterolateral supra-angular foramen pierces the anterior process at about one-fourth the distance from the end of the process to its base. The ventrolateral border of the supra-angular articulates anteriorly with the lateral border of the angular and posteriorly with part of the lateral border of the prearticular, posterior to which the supra-angular and prearticular are indistinguishably fused (Fig. 2C). Laterally, the posterodorsal portion of the supra-angular bears two posterolateral supra-angular foramina (*foramen nervi auriculo-temporalis* Versluys, 1936), medial to which lie three additional small foramina (one on left ramus). Lingually, the anterior portion of supra-angular is overlapped by the coronoid; as a consequence, a small portion of the supra-angular is exposed between the lingual processes of the coronoid (Fig. 2B). The ventromedial and posteromedial margins of the supra-angular are fused with the prearticular. The articulation between the supra-angular and prearticular lies mainly along the lateral wall of what Romer (1956) referred as the adductor fossa (afs; *mandibular foramen* Oelrich, 1956; *mandibular fossa* Jollie, 1960; *Meckel's fossa* Wellborn, 1933), which is delineated by these two bones (Fig. 2B). On the posterolateral wall of the adductor fossa, the supra-angular bears a foramen, herein termed the posteromedial supra-angular foramen. On the anterolateral wall of the adductor fossa, the supra-angular bears a second foramen, which I designate the anteromedial supra-angular foramen.

**Prearticular.** The prearticular (*articular* Parker, 1880, 1881; Cope, 1892; Wellborn, 1933; Kluge, 1962; Zalusky et al., 1980; Rieppel, 1993; *dermaticulare* Kingsley, 1905; *goniale* Versluys, 1936; Stimie, 1966; *postoperculare* Gaupp, 1906) forms the posterior end of each mandibular ramus and lies mostly on the ventral and lingual aspects of the mandible (Fig. 2A–C). Posteriorly, the prearticular bears two triangular processes—the retroarticular process (rp) posteriorly and angular process (ap; *processus subarticularis* Siebenrock, 1895) medially. In dorsal view, the retroarticular process is defined by two rounded crests that converge posteriorly (Fig. 2B)—the tympanic crest (tc) laterally and the medial crest (mc) medially (de Queiroz, 1987). The medial crest bears the chorda tympani foramen (ctyf) at the medial side of its proximal end (Fig. 2B). A small foramen, herein designated the angular foramen, is present on the dorsal aspect of the angular process halfway between its posteromedial margin and the medial crest. Anterior to the angular and retroar-



ticular processes, the dorsal aspect of the prearticular is fused with the overlying articular. The anteromedial portion of the prearticular is overlapped by the posterior lingual process of the coronoid and articulates with the supra-angular dorsally and the splenial ventrally. The anteromedial end of the prearticular also meets the posteroventral portion of the anterior lingual process of the coronoid. The dorsal margin of the remaining prearticular articulates with the ventromedial border of the supra-angular and forms the ventral wall of the adductor fossa (Fig 2B). The prearticular articulates anteroventrally with the angular and posteroventrally with the supra-angular; only the anterior portion of the prearticular-supra-angular suture is distinguishable (Fig. 2C).

**Angular.** As seen in ventral view (Fig. 2C), the angular comprises less than one-fourth the length of the mandible and lies along the ventral surface of each ramus. Its posterior margin is irregular and articulates laterally with the supra-angular and medially with the prearticular. Anteromedially, each angular bears a thin medial process that articulates laterally with the dentary, anteromedially with the splenial, and posteromedially with the prearticular. Ventromedially, each angular is pierced by a small, posteriorly directed posterior mylohyoid foramen (pmyf; *foramen nervi mylohyoid* Versluys, 1936) at the level of the anterior end of the adductor fossa (Fig. 2B,C).

**Splenial.** The small splenial (*operculare* Wellborn, 1933; *praeoperculare* Gaupp, 1906) is the only bone that is exposed solely on the medial aspect of the mandible (Fig. 2B). The anterior half of its dorsal margin articulates with the lingual coronoid process of the dentary anteriorly and the ventral border of the anterior lingual process of the coronoid posteriorly, whereas the posterior half articulates with the prearticular. The posterior half of the ventral border articulates with the lingual margin of the medial process of the angular. The anterior half of the ventral margin articulates with the dorsal border of the lingual splenial process of the dentary. The anterior end of the splenial forms the posterior rim of the anterior inferior alveolar foramen. The anterior portion of the splenial bears the anterior mylohyoid foramen (amyf), which is located at the same vertical level of the ventral rim of the adductor fossa (Fig. 2B). The anterior mylohyoid foramen is located posteroventral to the anterior inferior alveolar foramen.

## Neurocranium

**Basioccipital.** The basioccipital (boc) lies between the otic capsules and forms the posterior floor of the braincase and the medial portion of the occipital condyle (oc; Fig. 1B,D). It articulates broadly with the parabasisphenoid anteriorly and is ventrally invested by the posterolateral processes of the

parabasisphenoid. The basioccipital articulates with the inferior process of the prootic anterolaterally and the cristae interfenestralis and tuberalis of the otoccipital posterolaterally. On each side the basioccipital has a short ventrolateral process (*basioccipital process* Jollie, 1960) that projects ventrally as the spheno-occipital tubercle (sot; *basal tubera* Zalusky et al., 1980). Dorsally, the ventrolateral process bears a large occipital recess, which forms an antrum to the foramen rotundum (frot; Fig. 1D) with the otoccipital. The occipital recess described by Oelrich (1956) does not correspond to the recessus scalae tympani, as argued by Rieppel (1985).

**Supraoccipital.** The anterodorsally oriented supraoccipital (soc) is a saddle-like bone that lies posteroventral to the parietal and forms the posterior roof of the braincase (Fig. 1A,D). The medial portion of its posteroventral margin forms the dorsal rim of the foramen magnum (fm; *foramen occipitale* Wellborn, 1933). The ventrolateral margin of the supraoccipital articulates with the dorsolateral margin of the alar process of the prootic anteriorly and the posterodorsal margin of the body of the otoccipital posteriorly. Its ventromedial margin articulates with the dorsomedial margin of the body of the otoccipital posteriorly and the posteromedial margin of the alar process of the prootic anteriorly. The anterodorsal margin of the supraoccipital is separated from the parietal by a gap of connective tissue except for the medial cartilaginous processus ascendens (pasc), which extends anteriorly into the parietal fossa of the parietal (Fig. 1A,D). Posterior to this process, the dorsal surface of the supraoccipital bears a shallow depression on each side. A small process on each lateral end of the anterodorsal margin of the supraoccipital is fused to the posterior end of the taenia marginalis. The inner surfaces of the posteroventral and posterodorsal portions of the supraoccipital bear a deep, concave recess that is anteromedially oriented and that constitutes the anterior half of the auditory bulla; the posterior half is formed by the otoccipital. The auditory bulla is pierced on the posteroventral aspect of the supraoccipital by the endolymphatic foramen.

**Parabasisphenoid.** Except for its long anteromedial cultriform process (cup), the dermal parabasisphenoid is indistinguishably fused with the basisphenoid, which has both cartilaginous and membranous origins (Patterson, 1977; Rieppel, 1993). Therefore, these bones are described as a single parabasisphenoid (pbas; Fig. 1B,D). The parabasisphenoid (*sphenoid* Gaupp, 1906; de Beer, 1937; Kluge, 1962; Stimie, 1966) forms the anterior floor of the braincase. It articulates with the basioccipital posteriorly and the prootic dorsally. Its ventrolateral edges are formed by the cristae ventrolaterales and its anterodorsal edge is formed by the transverse crista sellaris. The parabasisphenoid bears three pairs of processes in addition to the cultriform process (*rostromparasphenoid* Jollie, 1960). Two thin, flat

posterolateral processes overlap the basioccipital anterolaterally and extend to the anterodorsal aspect of its sphenoccipital tubercles. Between the proximal ends of these processes, the ventral surface of the parabasisphenoid bears a recess. Anteriorly, two ventrolaterally oriented basipterygoid processes (*basitrabecular processes* Säve-Söderbergh, 1947; Kluge, 1962), which have expanded distal ends covered with articular cartilage, articulate with the partly ossified meniscus pterygoideus lying on the pterygoid notch of the quadrate processes of each pterygoid. Dorsal to each basipterygoid process the parabasisphenoid bears a short dorsolateral alar process (*clinoid process* Jollie, 1960). The distal end of this process and the anterior end of the anteroventral process of the prootic provide attachment for the pila antotica. Ventral to each alar process the anterior surface of the parabasisphenoid bears the abducens canal. Laterally, the parabasisphenoid is pierced at the base of each posterolateral process by the entrance to the Vidian canal (*carotid or parabasal canal* Jollie, 1960), which exits through the ventrolateral portion of its anterior surface. Between these exits the parabasisphenoid bears a short anteromedial process that overlaps the proximal end of the cultriform process (parasphenoid) and provides attachment for the bifurcate posterior end of the trabecula communis. This bifurcation corresponds to the posterior ends of the two trabeculae cranii, which fuse from front to back to form the trabecula communis in early developmental stages (tropibasic or tropitrabic skull, de Beer, 1937). The thin, triangular cultriform process underlies the trabecula communis and extends anterodorsally to a point corresponding to the posterior limit of the maxillary arcade along the posterior half of the pyiform space.

**Otoccipitals.** Early in development, the exoccipital fuses with the opisthotic (*paroccipital* Williston, 1925) on each side of the braincase of most species of lizards (Gaupp, 1906; de Beer, 1937; Oelrich, 1956). These elements are herein described as a single unit—otoccipital (otoc). The otoccipitals (*pleuro occipitale* Gaupp, 1906; Wellborn, 1933) form the posterolateral walls of the braincase and meet the prootics anterolaterally, the supraoccipital dorsomedially, and the basioccipital ventromedially (Fig. 1D). They form the lateral margins of the foramen magnum and lateral portions of the occipital condyle. Each otoccipital bears a lateral paraoccipital process (parp; *processus paroticus* Versluys, 1898; Wellborn, 1933; Säve-Söderbergh, 1947). The inner surface of the otoccipital has a deeply concave recess that forms the posterior half of the auditory bulla; the anterior half is formed by the supraoccipital. Two foramina pierce the posterior surface of each otoccipital between the most posterior portion of the auditory bulla (*ampulla canalis semicircularis frontalis* Wellborn, 1933; *internal semicircular canal* Cope, 1892) and the foramen magnum; these are the

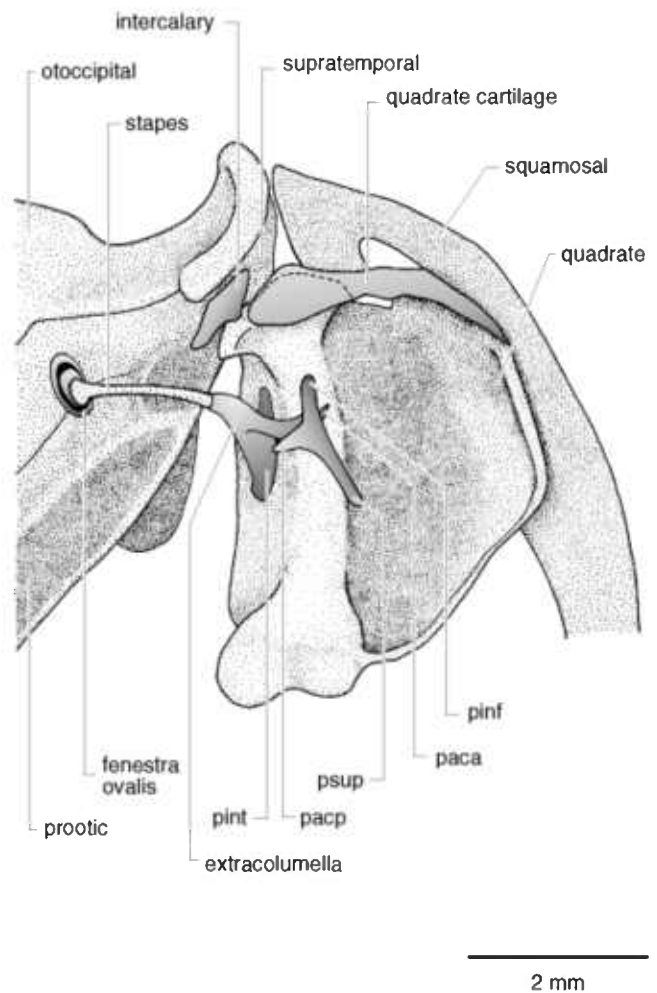


Fig. 6. *Stenocercus guentheri*. Right middle ear of adult (KU 147412) in posteroventral view. paca, processus accessorius anterior; pacp, processus accessorius posterior; pinf, pars inferior; pint, processus internus; psup, pars superior. Gray represents cartilage.

dorsal hypoglossal foramen (dhyf) ventrally and the vagal foramen (vagf) dorsally (Fig. 1D). The paraoccipital processes extend posterolaterally and have expanded distal ends that are laterally compressed. A lateral extension of the auditory bulla forms a horizontal ridge that divides the posterior surface of each paraoccipital process into dorsal and ventral recesses. The distal end of each paraoccipital process is overlapped by the posterior end of the supratemporal anteriorly, the supratemporal process of the parietal dorsally, and the intercalary cartilage ventrally. The quadrate and squamosal also participate in this contact zone; however, they are separated from the paraoccipital process by the intercalary cartilage and the posterior end of the supratemporal, respectively (Fig. 6). Anterior to the paraoccipital process, each otoccipital bears ventrally the posterior half of the posterior jugular recess; the anterior half of the jugular recess is formed by the prootic. The fenestra ovalis (*fenestra vestibuli*

Gaupp, 1906; Jollie, 1960; Rieppel, 1992a), which lies mostly in the otoccipital and receives the footplate of the stapes, is located between the jugular recess and the foramen rotundum (*fenestra cochleae* Jollie, 1960; *fenestra rotunda* Versluys, 1936; Säve-Söderbergh, 1947). The anterior margin of the fenestra ovalis is formed by the medial margin of the posteroventral process of the prootic (Fig. 6). The medial wall of the jugular recess extends ventrally, forming the crista interfenestralis, which separates the fenestra ovalis from the foramen rotundum. Posterior to this crista lies the anteroventrally oriented crista tuberalis, which bears laterally the ventral hypoglossal foramen on its proximal end. Together with the occipital recess of the basioccipital, the cristae interfenestralis and tuberalis form a large antrum to the foramen rotundum, which opens into the recessus scalae tympani. The medial and dorsal surfaces of the recessus scalae tympani are pierced by the foramen perilymphaticus (*foramen metotica, aqueductus cochleae* Jollie, 1960) and fenestra cochlea (*foramen perilymphaticum* Rao and Ramaswami, 1952; Rieppel, 1985), respectively. The foramen perilymphaticus opens into the cranial cavity through the anteroventral portion of the medial surface of each otoccipital. This part of the otoccipital also bears three posterodorsally directed hypoglossal foramina on the posteroventral portion, along with the vagal foramen (*jugular foramen* Jollie, 1960; Rieppel, 1985) on the posterodorsal portion. Dorsal to the foramen perilymphaticus, each otoccipital forms the medial wall of the posterior auditory foramen; the lateral wall is formed by the prootic.

**Prootics.** The prootics (po; *otosphenoids* Siebenrock, 1895; Wellborn, 1933; *petrosals* Baur, 1889; Cope 1892) form the anterolateral walls of the braincase (Fig. 1C,D). Each bone bears three processes—the alar (*superior anterior process* Jollie, 1960), anteroventral (*inferior process* Oelrich, 1956), and posterodorsal (*posterior process* Oelrich, 1956). The short, anterodorsally oriented alar process articulates with the lateral margin of the supraoccipital posteriorly. The anterior margin of the alar process forms the crista alaris, ventral to which the prootic bears a lateral bulge that corresponds to the acoustic recess medially. This bulge forms the posterior portion of the trigeminal notch (*incisura prootica* Säve-Söderbergh, 1947; Jollie, 1960). The anteroventral process articulates with the parabasisphenoid anteriorly and the basioccipital ventrally. The pila antotica attaches to the anterior end of the suture between the prootic and the parabasisphenoid. The suture between the prootic and the basioccipital lies dorsal and parallel to the posterolateral process of the parabasisphenoid. The anteroventral process bears ventrally a large anteromedially oriented cavity, the anterior half of the anterior vena jugularis recess, which is pierced posteromedially by the facial foramen. The lateral margin of the anteroventral

process forms the anterior half of the crista prootica (*crista otosphenoidica* Wellborn, 1933; Jollie, 1960), a longitudinal crest that runs from the posterodorsal to the anteroventral process forming the lateral wall of the anterior vena jugularis recess. The dorsal margin of the anteroventral process forms the ventral portion of the trigeminal notch. The posterodorsal process of the prootic overlaps the anterior surface of the paraoccipital process of the otoccipital and its medial margin forms the anterior margin of the fenestra ovalis (Fig. 6). Medial to the crista prootica, the posterodorsal process forms both the posterior half of the anterior vena jugularis recess and the anterior half of the posterior vena jugularis recess. The vena jugularis recesses form the roof and medial wall of the tympanic cavity. Along its ventromedial margin, the prootic bears a crest that forms the short supratrigeminal process anteriorly. The deeply concave acoustic recess lies posteroventral to this process on the medial aspect of the prootic. The acoustic recess bears three foramina—two anterior auditory foramina dorsally and the facial foramen ventrally. Posterior to this recess, the prootic forms the lateral wall of the posterior auditory foramen; the medial wall is formed by the otoccipital.

**Orbitosphenoids.** Anteromedial to the epipterygoids, the anteroposteriorly compressed orbitosphenoids (*laterosphenoids* Romer, 1956; Zalusky et al., 1980; *postoptics* Cope, 1892) lie along the posterior limit of the orbits (Figs. 1C, 7). The orbitosphenoids form the anterior aspect of the braincase and the lateral margins of the optic foramen (*optic fenestra* Zalusky et al., 1980). Each orbitosphenoid (o) is anterodorsally and posterolaterally oriented and continuous with the taenia parietalis media (*planum suprasedale* Oelrich, 1956; de Queiroz, 1987) anterodorsally, the pila accesoria and pila antotica posterodorsally, and the ventral portion of the pila metoptica (*taenia metoptica* Gaupp, 1906) ventrally. The dorsal portion of the pila metoptica is ossified as the orbitosphenoid.

### Splanchnocranium

**Quadrates.** The quadrates (q), which are located at the posterolateral corners of the skull, articulate with and support the lower jaw (Figs. 1, 6). Ventrally, each quadrate bears a large condyle, which articulates with the medial and lateral portions of the glenoid fossa of the articular. A prominent crest extends posterodorsally from the transverse condyle to the dorsally convex cephalic condyle that lies on the posterodorsal end of each quadrate. The cephalic condyle articulates with the intercalary cartilage ventromedially, the distal end of the supratemporal dorsomedially, and the distal end of squamosal dorsolaterally. The intercalary cartilage separates the cephalic condyle from the paraoccipital process of the otoccipital (Fig. 6). The posterior crest divides each quadrate into a wide, anterolaterally concave

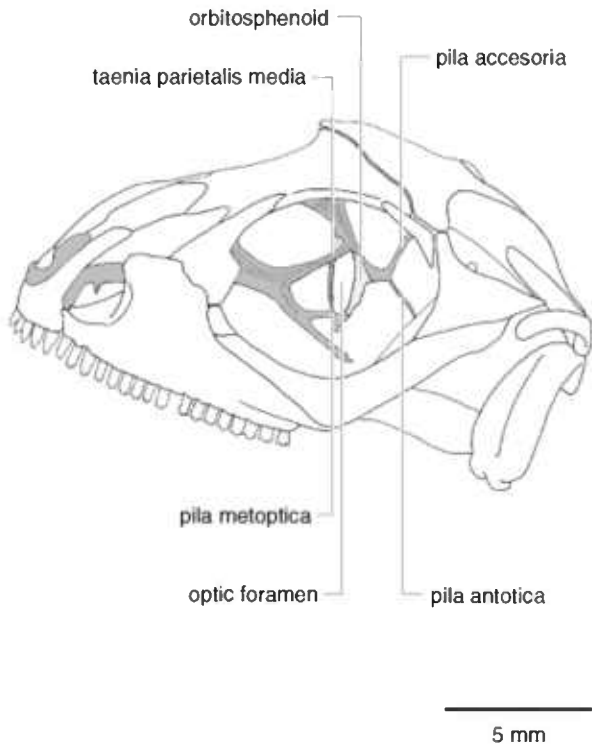


Fig. 7. *Stenocercus guentheri*. Orbitotemporal region of adult (KU 147412). Gray and stippled gray denote cartilage and calcified cartilage, respectively.

lateral half with the tympanic crest along its lateral margin and a short medial half with the medial crest along its medial margin. The dorsolateral aspect of the lateral half is laterally notched (superior fossa) and attached to a small cartilage (quadrate cartilage) that extends along the dorsolateral margin of each quadrate from the dorsal end of the tympanic crest to the cephalic condyle (Fig. 6). The anterior portion of this cartilage is ossified as a thin plate of bone (oqc; Fig. 1A). The medial half of each quadrate articulates with the quadrate process of the pterygoid ventromedially (Fig. 1D) and provides attachment for the processus internus of the extracolumella posterodorsally. The lateral half bears the anterior quadrate foramen on its anteroventral surface dorsal to the transverse condyle, whereas the medial half bears the posterior quadrate foramen on its posteroventral surface dorsal to the articulation with the pterygoid.

**Epipterygoids.** The rod-shaped epipterygoids (epp) form a pair of vertical braces between the palate and the skull table (Fig. 1C). They are posterodorsally tilted and their dorsal halves laterally bowed, extending dorsally as far as the same vertical plane of the ventrolateral border of the parietal, from which they are separated by connective tissue. The dorsal end of each epipterygoid (*columella cranii* Wellborn, 1933; *columella, antipterygoid* Gaupp, 1906) is capped with partly ossified cartilage and the ventral end inserts into the columellar fossa of the

quadrate process of the corresponding pterygoid (Fig. 4).

**Meniscus pterygoideus.** The meniscus pterygoideus (*cartilago articularis ossis pterygoidei* Gaupp, 1900) lies on each pterygoid notch, forming part of the synovial joint between the basiptyergoid processes and the pterygoids. Except for its dorsal border, each meniscus pterygoideus is ossified as a small ossicle inserted in the pterygoid notch.

**Middle ear.** In addition to the tympanic membrane, the middle ear is composed of the bony stapes (sta) proximally and the cartilaginous extracolumella (ext) distally (Figs. 1, 6), which together form the columella auris (de Beer, 1937; Jollie, 1960; Stimie, 1966). Both the stapes and the extracolumella are about the same length. Each thin cylindrical stapes (*columella* Cope, 1892; Wever, 1978; *columella auris* Oelrich, 1956; Romer, 1956; Kluge, 1962; Bellairs and Kamal, 1981; Rieppel, 1993) lies anteroventral to the paraoccipital process of the otoccipital and extends anteromedially between the extracolumella and the fenestra ovalis. The cartilaginous, expanded proximal end of the stapes forms an elongated footplate that attaches to the membrane covering the fenestra ovalis, the perimeter of which is only slightly larger than the perimeter of the footplate. The cartilaginous extracolumellae (*epistapedial cartilages* Cope, 1892; *extrastapes* Bellairs and Kamal, 1981; Rieppel, 1993) articulate with the distal ends of the stapes. *Stenocercus guentheri* has an iguanid type of middle ear (Wever, 1978)—the proximal portion of each extracolumella bears a laterally compressed processus internus (pint), which extends anteriorly to attach through its expanded anterior margin to the medial half of the quadrate. The distal end of each extracolumella is cruciform, bearing four elongate processes—the pars inferior (pinf) anteroventrally, the pars superior (psup) posterodorsally, the processus accessorius anterior anterodorsally (paca), and the processus accessorius posterior (pacp) posteroventrally (Fig. 6).

**Intercalary cartilages.** A small intercalary cartilage (ic) separates the cephalic condyle of the quadrate from the paraoccipital process of the otoccipital (Figs. 1, 6) on each side. The intercalary cartilage (*processus paroticus* Bellairs and Kamal, 1981; *second supratemporal* Beddard, 1905) derives from the dorsal process of the columella auris early in development (Bellairs and Kamal, 1981; Rieppel, 1993) and has been reported as a separate element only for a few taxa, such as *Varanus* (Bahl, 1937; Varanidae) and *Uromastix* (Jollie, 1960; Agamidae).

**Articular bone and Meckel's cartilage.** The triradiate articular bone (*articular condyle* Parker, 1880; *prearticular* Oelrich, 1956) lies on the dorsal aspect of the posterior portion of each mandibular ramus (Fig. 2A,B). The articular is located between the proximal portions of both the retroarticular and angular processes of the prearticular, with which it is fused. It is also fused anteriorly with the supra-

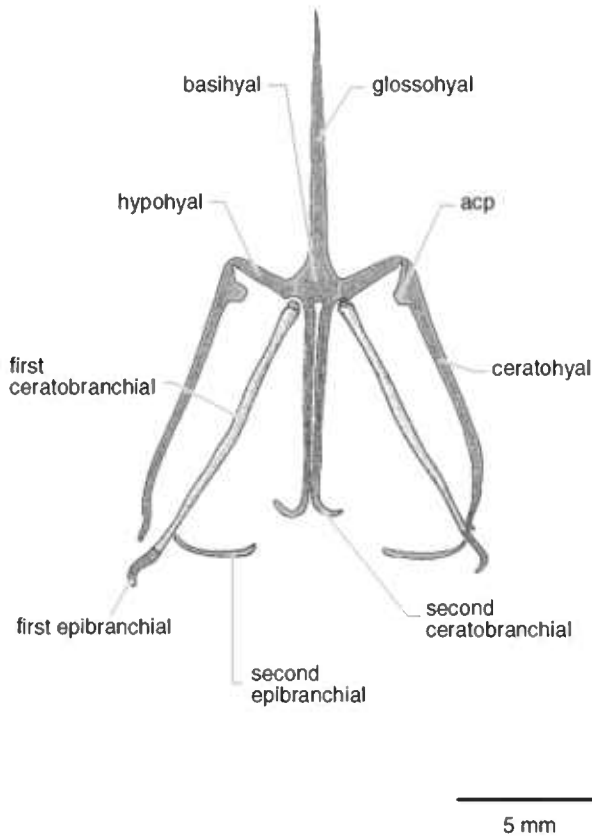


Fig. 8. *Stenocercus guentheri*. Hyoid apparatus of adult (KU 147412) in ventral view. acp, anteromedial ceratohyal process. Gray and stippled gray denote cartilage and calcified cartilage, respectively.

angular. The articular has three processes—anterodorsal, posterolateral, and posteromedial. It also bears a pair of dorsal concavities, the medial and lateral portions of the glenoid fossa, which form the articular facet of the lower jaw. More than half of the articular is ossified. Meckel's cartilage is represented by three short, discrete segments; one lies in the adductor fossa, another at the level of the anterior inferior alveolar foramen, and the third exits the anterior end of Meckel's canal (Fig. 2B). The latter segment meets its counterpart to form the cartilaginous portion of the mandibular symphysis.

**Hyoid apparatus.** The hyoid lies beneath the lower jaw and supports the tongue, throat muscles, and anterior portion of the trachea. It is composed of the basihyal (*body* Oelrich, 1956; Romer, 1956; Bellairs and Kamal, 1981; de Queiroz, 1987; *copula* Romer, 1956; Jollie, 1960; *corpus hyoideum* Romer, 1956), which forms the body of the hyoid apparatus, and three pairs of visceral arches (Fig. 8). Anteriorly, the basihyal bears a long and thin medial process, the glossohyal (*hypohyal* Oelrich, 1956; de Queiroz, 1987; *lingual process* Oelrich, 1956; Romer, 1956; Jollie, 1960; Bellairs and Kamal, 1981; *processus entoglossus* Gaupp, 1906). The first pair of visceral arches is attached to the anterolateral portions

of the basihyal and each arch is composed of an anterolaterally oriented short hypohyal (*basihyal* de Queiroz, 1987; *hyoid cornu*, *hyoid horn* Romer, 1956) and a long, posterolaterally oriented ceratohyal (*cornu principale* Gaupp, 1906; *epihyal* Romer, 1956). The proximal end of each ceratohyal bears a medial dorsoventrally compressed process, herein termed the anteromedial ceratohyal process (acp). The second pair of visceral arches is attached to the posterolateral portions of the basihyal. Each arch is formed by the long, posterolaterally oriented first ceratobranchial (*Cornu Branchiale I*, Gaupp, 1906) anteriorly and the short first epibranchial (*cartilaginous dorsal process*, Romer, 1956) posteriorly. The third pair of visceral arches corresponds to the second pair of ceratobranchials (*Cornu Branchiale II*, Gaupp, 1906) and is continuous with the posterior portion of the basihyal. The posterior portions of all the visceral arches are dorsally oriented; a pair of short, posterodorsally oriented second epibranchials, which do not articulate with any structure, lies medial to the first ceratobranchials. The posterior end of each second epibranchial is expanded and lies medial to the anterior end. The cornua branchiale prima are the only completely ossified elements of the hyoid apparatus and the second epibranchials are the only unossified cartilaginous elements. All other elements are heavily calcified with only a thin cartilaginous sheath remaining.

## Teeth

**Marginal teeth.** The premaxilla, maxillae, and dentaries bear 6, 18 (each), and 20 (21 on left ramus) marginal teeth, respectively (Figs. 1, 2). Premaxillary teeth are recurved posteriorly, laterally compressed, and similar in size to the maxillary teeth. Maxillary dentition is heterodont; Teeth 1–7 are conical or tricuspid with nearly inconspicuous lateral cusps, whereas Teeth 8–18 are tricuspid with the lateral cusps much smaller than the medial one. Maxillary tooth positions 5, 7, 10, 12, 14, and 17, and premaxillary tooth positions 2 and 4, bear replacement teeth. Mandibular dentition also is heterodont; teeth on the anterior third are conical or tricuspid and teeth on the posterior two thirds are tricuspid with the lateral cusps smaller than the medial one. A replacement tooth (rt) is located on the medial side of each of Teeth 2, 4, 6, 8, 10, 13, 15, 16, 18, 19, and 20 on the right dentary (Fig. 2B) and Teeth 2, 4, 6, 9, 11, 14, 16, and 19 on the left dentary. The first and last two teeth are lower than the others, but because the portion of the shelf where the last two teeth are located is elevated, only the tips of Teeth 1 and 2 are lower than those of the other teeth. The position of the replacement teeth (i.e., lingual to the corresponding functional teeth) and the presence of resorption pits in the pulp cavity of some functional teeth indicate a typical iguanid pattern of tooth replacement (Edmund, 1960, 1969; Rieppel, 1978a).

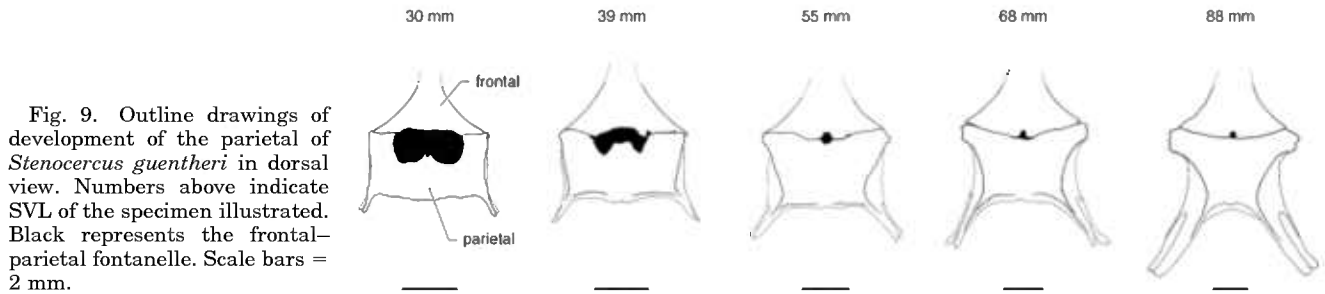


Fig. 9. Outline drawings of development of the parietal of *Stenocercus guentheri* in dorsal view. Numbers above indicate SVL of the specimen illustrated. Black represents the frontal-parietal fontanelle. Scale bars = 2 mm.

**Palatal teeth.** Pterygoids are the only tooth-bearing bones of the palate. Each pterygoid bears one, non-recurved, conical tooth on its ventral surface at the level of the posterior end of the inferior orbital fenestra (Fig. 1B).

### Postembryonic Development

**Dermatocranium.** Of all the dermal bones of the cranium of *Stenocercus guentheri*, the parietals undergo the greatest postnatal ontogenetic change (Fig. 9). At 30 mm SVL, only the posterior halves of the parietals are fused, leaving a large, prominent frontoparietal fontanelle. The anterolateral portion of each parietal overlaps the posterolateral margin of the frontal; the anteromedial aspect of each parietal is overlapped by the frontal. The parietals continue ossifying anteromedially and they are completely fused at 55 mm SVL (Fig. 9). Nevertheless, a small circular portion of the frontoparietal fontanelle remains unossified to form the pineal foramen. The proportional contribution of the parietal (i.e., fused parietals) and frontal (i.e., fused frontals) to the pineal foramen is variable and not related to size. In 58% of the specimens, the frontal forms only half of the pineal foramen, whereas in 42% of the specimens it forms more than half of this foramen. At an SVL of 30 mm, the portion of the parietals corresponding to the corpus of the adult single parietal is wider than long and the longitudinal lateral crests are nearly straight. Thus, the dorsal surface of the parietal corpus is about equal to the ventral surface. With increasing age and size the anterolateral and posterolateral portions of the parietal grow faster than the corpus to reach the condition described for the largest specimen. Similar ontogenetic changes in the shape of the parietal roof have been described for other iguanian lizards, such as anolines (Etheridge, 1959), iguanines (de Queiroz, 1987), and leiocephalines (Etheridge, 1966; Pregill, 1992). Because of this change in shape, the anterolateral processes (as described for the largest specimen) cannot be distinguished in specimens smaller than 55 mm SVL. The distal ends of the supratemporal processes are short in small specimens, lying anterior to the posteroventral margin of the supraoccipital in specimens less than 60 mm SVL. The anterolateral processes gradually overlap the pos-

terolateral ends of the frontal until they articulate (through a thin layer of connective tissue) with 50% or more the length of the medial margin of the postfrontal in specimens larger than 74 mm SVL.

Other components of the skull table that vary ontogenetically are the frontal and postorbital. The anterolateral processes of the frontal are only slightly longer than the anteromedial process at 30 mm SVL; they become much longer than the anteromedial process with increasing age and size. The anteromedial process does not meet the posterior end of the internasal suture in specimens less than 39 mm SVL; thus, a gap of connective tissue (i.e., frontonasal fontanelle) remains. Regarding the postorbital, the anterodorsally oriented knob of its dorsal process is nearly inconspicuous in specimens smaller than 35 mm SVL.

In a 30-mm individual, the ventrolateral margin of the coronoid is located dorsal to the dorsolateral margin of the dentary; these margins meet in a 35-mm specimen. In larger individuals, the coronoid develops a labial process that extends ventrally with age until it reaches the condition described for the largest specimen.

**Neurocranium.** Except for the medial portion of the basioccipital-parabasisphenoid articulation (i.e., basicranial fontanelle), all elements of the braincase are widely separated from one another by cartilage in a 30-mm lizard (Fig. 10). However, the bones of the braincase approach each other as ossification replaces the intervening cartilages in larger lizards. Thus, the cartilages separating the otoccipital from the basioccipital, and the prootic from the supraoccipital, are almost completely ossified in a 68-mm lizard. At 81 mm SVL, only the cartilage surrounding the parabasisphenoid and that between each prootic and each otoccipital remain unossified; all other bones are fused. The medial portion of the occipital condyle, which corresponds to the posterior end of the basioccipital, lies ventral to the lateral portions (formed by the otoccipitals) in a 30-mm individual (Fig. 10A). These medial and lateral portions are connected with cartilage that ossifies with age; in a 49-mm specimen, the basioccipital portion of the condyle lies at the same dorsal level as the otoccipital portions. The spheno-occipital tubercles and occipital recesses of the basioccipital are poorly

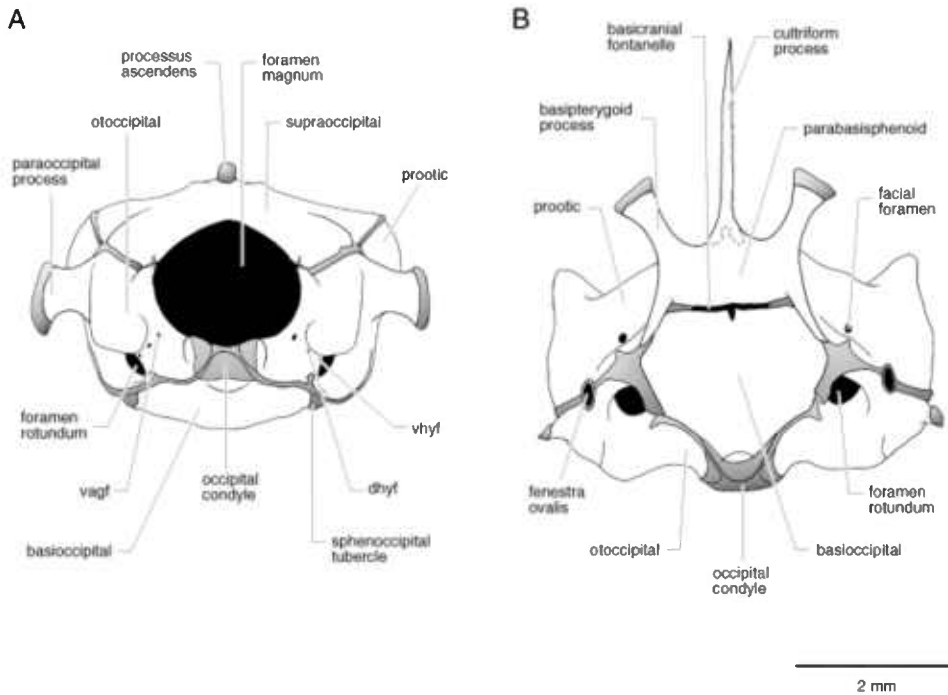


Fig. 10. *Stenocercus guentheri*. Neurocranium of juvenile (KU 147347) in posterior (A) and ventral (B) views. dhyf, dorsal hypoglossal foramen; vagf, vagal foramen; vhyf, ventral hypoglossal foramen. Gray indicates cartilage.

developed in specimens smaller than 35 mm SVL and 49 mm SVL, respectively. The cristae interfenestralis and tuberalis of the otoccipitals appear at 39 mm SVL, whereas the cristae prooticae of the prootics, along with the vena jugularis recesses, can be distinguished at 44 mm SVL. The length of each paraoccipital process of the otoccipitals is smaller than the distance between the base of the process and the foramen magnum in specimens smaller than 60 mm SVL. In a 30-mm individual, the distal end of each paraoccipital process is embraced by a thick layer of cartilage, which is almost completely ossified in an 88-mm specimen. Unlike other lizards, such as large iguanines (de Queiroz, 1987), the orbitosphenoid does not vary ontogenetically.

**Splanchnocranium.** In specimens smaller than 44 mm, the medial halves of the quadrates as seen in adults are absent and the processus internus of each extracolumella is attached to the base of the cephalic condyle of each quadrate. The latter attachment moves medially with the growth of the medial half of each quadrate. A small cartilage overlies the dorsal end of the anterolateral aspect of each quadrate in the 30-mm individual. The medial aspect of this cartilage ossifies with age and has been erroneously described as the quadratojugal by several authors (Jollie, 1960); the lateral aspect does not change (see description of largest specimen, Fig. 6). I was not able to determine the ossification pattern of this cartilage by simple observation through the microscope because of visual distortion.

In a 30-mm-SVL individual, Meckel's cartilage is represented by a long longitudinal bar, a short posterodorsal bar, and a posterodorsal facet; the latter

emerges through the posterodorsal portion of the prearticular to form the articular (Figs. 11, 12A). The flat longitudinal bar extends from the anterior end of the mandible, where it meets its counterpart through the mandibular symphysis, to the posterior end of the adductor fossa. At this level it bears a posterodorsal bar that meets the anteroventral aspect of the articular. The longitudinal bar of Meckel's cartilage is exposed through the anteromedial groove of the dentary, the anterior inferior alveolar foramen, and the adductor fossa. In specimens smaller than 79 mm SVL the posterodorsal bar is exposed lingually, because the prearticular does not articulate with the supra-angular at this level. In addition, the posterodorsal bar ossifies with age and it is completely ossified in a lizard 81 mm long. The degree to which Meckel's cartilage is exposed anteriorly varies with the position of the anterior end of Meckel's canal—it lies ventral to the fourth mandib-

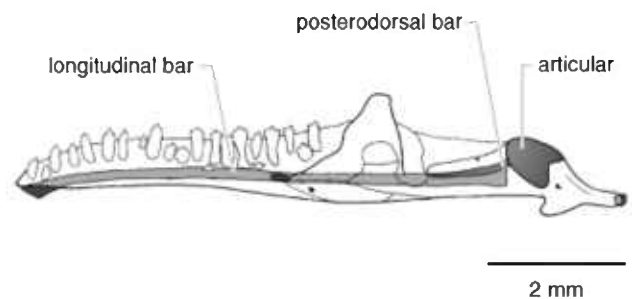


Fig. 11. *Stenocercus guentheri*. Meckel's cartilage of juvenile (KU 147347) in medial view. Exposed areas are shown in dark gray.

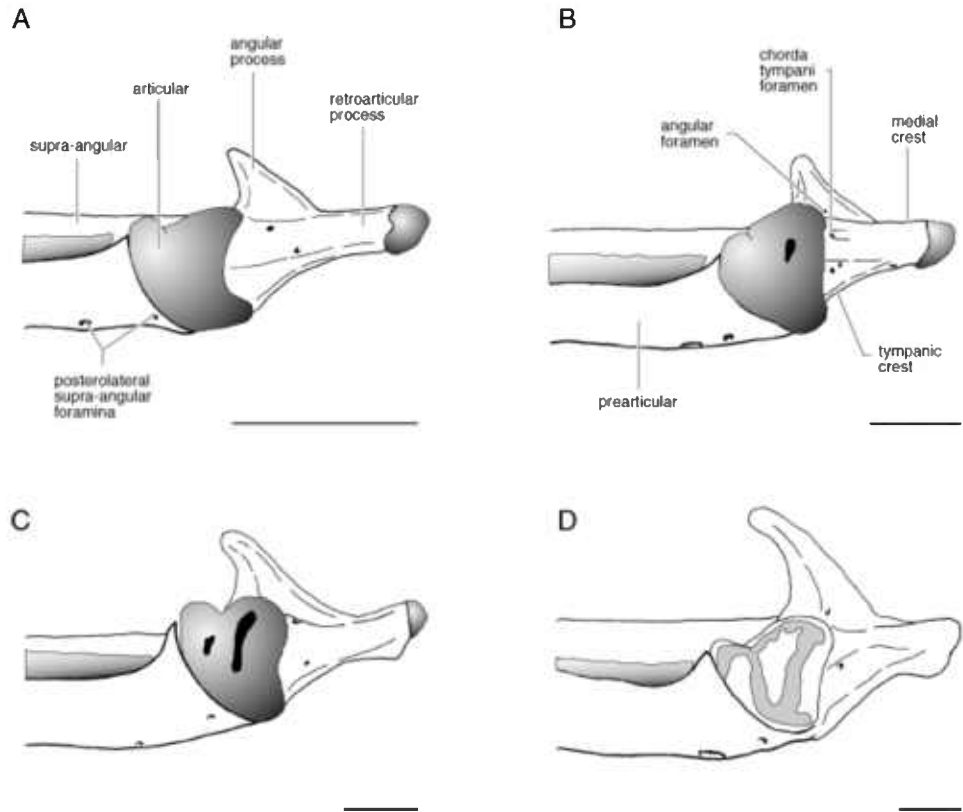


Fig. 12. *Stenocercus guentheri*. Dorsal view of the posterior aspect of the mandible of four specimens: KU 147347, 30 mm SVL (A); KU 147445, 55 mm SVL (B); KU 147409, 65 mm SVL (C); KU 147412, 88 mm SVL (D). Stippling indicates calcified cartilage, gray represents cartilage, and black denotes centers of ossification of articular. Scale bars = 2 mm.

ular tooth in specimens less than 44 mm long, ventral to the third tooth in specimens between 44 and 79 mm long, and ventral to the second tooth in larger specimens. However, Meckel's canal opens ventral to the fourth tooth and second tooth in two individuals 74 mm long (KU 147482) and 60 mm long (KU 147477), respectively. Whether the anterior ends of both Meckel's cartilages remain fused during postnatal life of lizards is unknown for most species (Bellairs and Kamal, 1981). This fusion was observed in all specimens of *Stenocercus guentheri* examined. A second center of ossification appears in the longitudinal bar at a level between the first and last mandibular teeth in individuals 39 mm long. Ossification progresses anteriorly and posteriorly with age and, together with a third center of ossification that appears at 44 mm SVL at the level of the coronoid, produces the condition described for the largest adult specimen. A small cartilage lies in the distal end of the retroarticular process of the prearticular in specimens smaller than 67 mm. This cartilage probably is a remnant of Meckel's cartilage that is isolated with the growth of the retroarticular process in earlier developmental stages.

Ossification of the articular was first evident in a 44-mm individual. The bone forms at the base of the anterodorsal process from a small, circular ossification center that is elongated through the posteromedial process in a 55-mm individual (Fig. 12B). In a lizard 65 mm long, the ossification center is ex-

panded across the posterolateral process and another small ossification center has appeared in the anterodorsal process (Fig. 12C). Both ossification centers are present in larger specimens, except for KU 147369 (67 mm SVL) and KU 147482 (74 mm SVL), both of which lack the anterior center. These centers of ossification expand irregularly with age to reach the condition described for the largest adult specimen (Fig. 12D).

The posterior portion of the meniscus pterygoideus starts ossifying at 79 mm SVL and at 88 mm SVL only its dorsal border remains cartilaginous.

The only completely ossified elements of the hyoid apparatus in a 30-mm lizard are the cornua branchiale prima (first ceratobranchials) and the only fully cartilaginous elements are the second epibranchials, which do not ossify throughout ontogeny. All other elements show some ossification in the 30-mm individual; ossification progresses with age and size until all parts of the hyoid are heavily mineralized at 88 mm SVL except for the second epibranchials (Fig. 8). A small cartilage is attached to the proximal end of each first ceratobranchial at 30 mm SVL; this epiphysis is barely ossified in its center and ossifies gradually with age until no cartilage remains at 88 mm SVL. However, the fully ossified epiphysis at 88 mm SVL can be distinguished from the first ceratobranchial (Fig. 8).

**Teeth.** Unlike most lizards, the number of marginal and palatal teeth in *Stenocercus guentheri*



does not increase with size of the skull (Torres-Carvajal, 2001). Similarly, intrapopulational variation in the number of pterygoid teeth in two other species of *Stenocercus* (*S. imitator* and *S. percultus*) cannot be explained by ontogenetic or sexual factors (Cadle, 1991). Replacement teeth are present in the premaxilla, maxillae, and dentaries in all specimens examined.

## DISCUSSION

### Comparative Osteology and Systematics

Despite the application of osteocranial characters to elucidate the phylogenetic relationships among members of Iguania, only a few detailed descriptions of the osteocrania of iguanian lizards have been published (e.g., Oelrich, 1956; Stimie, 1966; de Queiroz, 1987), and none of them includes species of *Stenocercus*. Therefore, a comprehensive, comparative discussion of the osteological and systematic relevance of these data is not possible. However, herein I use information available in previous studies of lizard systematics (Etheridge, 1966; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Cadle, 1991; Frost, 1992; Pregill, 1992) to compare cranial characters between *Stenocercus* and several closely related taxa. The following list includes only those osteological characters that differ between *Stenocercus guentheri* and related taxa, as revealed by the literature. These include: 1) nasal process of premaxilla overlapping nasal bones (nasal bones overlapping nasal process in *Leiocephalus*); 2) nasal process of premaxilla narrow (broad in *Plica*, *Strobilurus*, *Uracentron*, and *Uranoscodon*); 3) six premaxillary teeth (four or five in *Uracentron*, *Strobilurus*, *Tapinurus*, *Uranoscodon*, *Plica plica*, and *Plica lumaria*); 4) no ontogenetic upward tilting of ventral margin of premaxilla (ontogenetic elevation of premaxilla in some species of Tropicurini, *Leiocephalus*, and *Stenocercus*); 5) prefrontal not in contact with margin of fenestra exorarina (in contact in *Tapinurus*); 6) supratemporal lying mostly on lateral surface of supratemporal process of parietal (supratemporal lying within groove in ventral margin of supratemporal process of parietal in *Liolaemus* and *Ctenoblepharys*); 7) labial foramina of maxillae small (large in Tropicurini east of the Andes); 8) anterior maxillary teeth not enlarged in older adults (enlarged in some members of Tropicurini); 9) posterior maxillary teeth extending above edge of maxillae more than the width of a tooth (teeth not extending far above edge of maxillae in *Tropicurus nanuzae*, *Uracentron flaviceps*, and *Plica*); 10) dentary extending posteriorly well beyond level of superior apex of coronoid (not extended in *Ctenoblepharys* and some members of Tropicurini); 11) coronoid process of dentary slightly overlapping anterior lingual process of coronoid (great overlap in Tropicurini except *Uranoscodon*); 12) dentary extending posteriorly more than 50% the length from apex of

coronoid to anterior edge of articular (less than 50% extension in *Stenocercus* fide Frost [1992]); 13) alveolar shelf of dentary well defined (not well defined in Tropicurini); 14) coronoid labial process small (large in *Leiocephalus*, *Liolaemus*, and *Ctenoblepharys*); 15) Meckel's groove fused (unfused in *Ctenoblepharys*, *Liolaemus*, and some species of *Phymaturus*); 16) anterior surangular foramen not captured by contact of coronoid and dentary posterior to the foramen (captured in Tropicurini east of the Andes except *Uranoscodon* and *Tropicurus bogerti*); 17) posterior mylohyoid foramen pierces angular (not in Tropicurini east of the Andes except *Uranoscodon*, *Tropicurus spinulosus*, and *Uracentron*); 18) splenial not extending anteriorly more than one-sixth length of tooth row (variable in *Liolaemus* and extending more than one-sixth length of tooth row in *Ctenoblepharys*); 19) angular articulating with splenial on lingual surface of mandible (on ventral or labial surfaces in *Phymaturus*, *Ctenoblepharys*, *Liolaemus*, *Leiocephalus*, *Tropicurus*, and *Uranoscodon*); 20) posterior mylohyoid foramen at the level of anterior end of adductor fossa (foramen located anterior [*Phymaturus*, *Ctenoblepharys*, *Liolaemus*] or posterior [*Uracentron*, *Tapinurus*] to this point; foramen located posterior to the anterior end of adductor fossa in *Stenocercus* fide Frost and Etheridge, 1989); 21) maxillopalatine foramen much smaller than lacrimal foramen (maxillopalatine foramen subequal in size to lacrimal foramen in *Plica*, *Uracentron*, and *Strobilurus*; lacrimal foramen not much larger than maxillopalatine foramen in *Stenocercus* fide Frost and Etheridge, 1989); and 22) pterygoid teeth present (absent in *T. bogerti*, *Plica umbra*, *Strobilurus torquatus*, *Tapinurus semitaeniatus*, *Uracentron azureum*, and some species of *Leiocephalus*; intraspecific variation in some species of *Stenocercus*).

### Functional Morphology and Kinesis

Traditionally, the cranial bones of lizards are grouped into three units: dermal skull roof, palate, and braincase. This approach is based on the function of the homologous bones in primitive tetrapods, such as the labyrinthodont *Palaeogyrinus* or the seymouriamorphans *Seymouria* and *Kotlassia* (Romer, 1956). However, the traditional classification is inconsistent with the actual function of some of the elements of the skull in lizards. This problem is reflected in the confusing way in which some elements have been classified. For example, the quadrate has been considered an element of both the palate (e.g., Romer, 1956; Hikida, 1978) and the skull roof (e.g., de Queiroz, 1987). There are several bones in the skull of *Stenocercus guentheri* (and most lizards) that have different functions than do their homologs in primitive tetrapods. The squamosal, postorbital, and jugal do not form part of the solid shield of bone protecting the top and sides of

the head known as the dermal skull roof. Instead, these three bones, together with the quadrate, epipterygoid, ectopterygoid, and pterygoid, are mainly components of the suspensorium. They also contribute significantly to the kinesis of the skull by constituting a site of mobility in the lateral postorbital region, which is characteristic of iguanian lizards (Arnold, 1998). Because the squamosal and postorbital (temporal arch) are not firmly articulated with any other bone (Fig. 1), the temporal region of the skull has considerable flexibility. The postorbital can rotate around its articulation with the parietal and, at the same time, its posterior process can lift away from the squamosal (Arnold, 1998). On the other hand, the anterior half of the jugal is firmly attached to, and supports, the maxillary arcade. The posterodorsal portion of the premaxilla and the dorsal aspect of the maxillae that overlap the nasals are other primary sites of support of the maxillary arcade. The supratemporal is another element that has lost its function of roofing the skull; it provides a point of attachment for the quadrate, along with the parietal, squamosal, and otoccipital. Thus, the function of a solid shield of bones protecting the head dorsally is limited to the nasals, prefrontals, frontal, postfrontals (although they are very small), and parietal (Fig. 1). In addition, the sides of the head are fenestrate; the rostrum is the only region that is completely covered with bones (maxillae, prefrontals, and lacrimals). The palates of lizards also differ from those of primitive tetrapods. As mentioned above, the ectopterygoids are components of the suspensorium rather than elements of the palate, which is the case in primitive tetrapods. They are attached to the posterior ends of the maxillary arcade and provide support for the highly movable pterygoids by bracing them firmly. Similar to the skulls of most other lizards (Frazetta, 1962; Rieppel, 1978b, c), the skull of *Stenocercus guentheri* is amphikinetic and the quadrate can rotate around its dorsal suspension (streptostyly). The skull of this species has all the joints described by Bellairs and Kamal (1981) that are involved in mesokinesis and metakinesis (Versluys, 1912). Streptostyly is greatly facilitated by the presence of the intercalary cartilage, which provides more flexibility to the complex dorsal suspension of the quadrate (Fig. 6). Apparently, mesokinesis in young individuals of *S. guentheri* is greatly enhanced by the incomplete frontoparietal suture and the high flexibility provided by the frontoparietal fontanelle.

### Postembryonic Ossification of the Skull Roof in Lizards

Although information on the postembryonic development of the cranium in lizards is scarce, some differences in patterns of ossification of the skull roof can be described. Herein, I comment on the postembryonic ossification of the parietals in *Stenoc-*

*ercus guentheri* and eight other taxa—*Acontias meleagris* (Scincidae), *Anniella* (Anguillidae), *Calotes versicolor* (Agamidae), *Cyrtodactylus pubisulcus* (Gekkonidae), *Eumeces latiscutatus* (Scincidae), *Lacerta vivipara*, *Podarcis muralis*, and *P. sicula* (Lacertidae). On one hand, from the descriptions of late embryos of the small fossorial lizards *Acontias* and *Anniella* (Brock, 1941; Bellairs, 1950, respectively), it can be deduced that neonates of these species have fused parietals. Rieppel (1984) proposed that one reason for this pattern might be that the dermatocranium and neurocranium serve as a suspensorium for the jaws and their muscles in hatchlings of these fossorial lizards. On the other hand, neonates of most lizards have incomplete skull roofs (i.e., unfused frontals and/or parietals). This condition has been reported for many iguanians (Haller- mann, 1992). The degree to which the frontals and parietals are fused in neonates and, consequently, the size of the frontoparietal fontanelles, vary interspecifically. For example, similar to *S. guentheri*, neonates of *P. muralis*, *P. sicula*, *L. vivipara*, and *C. versicolor* have large frontoparietal fontanelles (Rieppel, 1984, 1987, 1992a; Ramaswami, 1946, respectively), whereas in hatchlings of *C. pubisulcus* and *E. latiscutatus* the frontoparietal fontanelles are almost closed (Rieppel, 1992b; Hikida, 1978, respectively). In addition, the pattern of postembryonic ossification of the parietals also varies among these species. Even though a neonate of *S. guentheri* was not included in the present work, it can be deduced from the smallest specimen examined (KU 147347, 30 mm SVL) that the parietals of the hatchling are widely separated and ossify in two directions (i.e., posterior–anterior and lateral–medial, Fig. 9). This pattern has been reported for species like *L. vivipara* (Rieppel, 1992a) and *E. latiscutatus* (Hikida, 1978), although the parietals in newborn hatchlings of the latter species are almost completely fused. However, *S. guentheri* differs from *L. vivipara* and *E. latiscutatus* in that the parietals ossify without leaving a narrow longitudinal parietal fontanelle that extends from the frontoparietal suture to the position of the pineal foramen (i.e., halfway between the anterior and posterior margins of the parietal), as is the case in *L. vivipara* and *E. latiscutatus*. This difference is clearly related to the position of the pineal foramen, which is located in the frontoparietal suture in *S. guentheri*. The gekkonid *C. pubisulcus* exhibits a different pattern of postembryonic development of the parietals. This species is unique in having a cruciform fontanelle formed by a longitudinal opening between the parietals and a short, transverse slit that intersects this longitudinal opening posterior to the point halfway between the anterior and posterior margins of the parietals (Rieppel, 1992b); the parietals ossify in a lateromedial direction until they fuse in later developmental stages.

The morphology and postembryonic development of the osteocranium of *Stenocercus guentheri* was described in this study. Although the results presented here contribute to our knowledge of the cranial morphology in lizards, we still lack information to gain a better understanding of the patterns of morphological and developmental diversity of the cranium (and postcranium) in lizards. Even general information of all extant saurian families is unavailable; this indicates clearly that basic research on the osteology of lizards is needed. An additional purpose of this study was to identify new cranial osteological characters that could be used for phylogenetic analyses of *Stenocercus*. The utility of these will only become apparent once the cranial osteology of other species of *Stenocercus* (and other iguanian lizards) has been investigated and the characters examined in a phylogenetic context.

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