

Original article

Cranial osteology of the African gerrhosaurid *Angolosaurus skoogi* (Squamata; Gerrhosauridae)

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Abstract.—Phylogenetic relationships both within and between the scincomorph families Gerrhosauridae and Cordylidae are in need of re-examination. Currently the basal gerrhosaurid is unknown, although *Angolosaurus skoogi* previously was proposed as the sister taxon to mainland African gerrhosaurids. Many details of the cranial osteology of *A. skoogi* are also unknown because of the rarity in museum collections and elusive lifestyle of this dune-dwelling lizard, endemic to the Namib Desert. In this study, High-Resolution X-ray Computed Tomography (HRXCT) was used to study in detail the cranial osteology of *A. skoogi*. Results of this study enabled completion of the first anatomical description of the skull and mandible of *A. skoogi*. Throughout the description, reference is made to a fully labeled cross-sectional HRXCT data set, available online as supplementary material. Detailed information on cranial osteology obtained from these data can help resolve the contentious placement of *A. skoogi* within Gerrhosauridae. Unlike other Cordyliformes (Gerrhosauridae + Cordylidae), the post-frontal in *A. skoogi* is not extensive and does not extend posteriorly beyond the orbital margin. The squamosal is not bifurcated anteriorly in *A. skoogi*, unlike other gerrhosaurids. In the braincase of *A. skoogi*, there is no separate foramen for passage of the glossopharyngeal nerve (cranial nerve IX). This morphological study emphasizes the utility of both HRXCT scans and disarticulated skeletal material as valuable sources of phylogenetically-informative data.

Key words.—*Angolosaurus skoogi*; Cordyliformes; Namib Desert; anatomy; skull, mandible

The acquisition and subsequent study of rare, extant species, such as the coelacanth or the tuatara, have provided many insights pertaining to both the phylogenetic relationships of related taxa and their morphological character states. However, there are inherent challenges associated with studying the morphology of fauna that are poorly represented in museum collections. Among these are small taxon sample sizes (of particular concern to systematists), and obtaining data on detailed anatomy while maintaining the integrity of the limited number of specimens available for research. Both of these challenges are encountered by squamate morphologists and systematists who study the enigmatic *Angolosaurus skoogi*, a gerrhosaurid lizard endemic to the Namib Desert in southern Angola and northern Namibia (Fig. 1) and known to spend up to 24 hours a day buried beneath the sand dunes

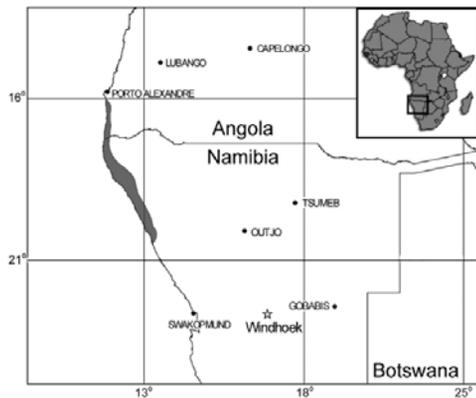


Figure 1. Geographic range of *Angolosaurus skoogi*, shaded in grey on the map.

(Steyn 1963; Mouton & van Wyk 1997). Such a limited geographic range and elusive life style make *A. skoogi* a difficult animal to study (FitzSimons 1955). While the biology and ecology of this dune-dwelling gerrhosaurid have been examined (Hamilton & Coetzee 1969; Pietruszka *et al.* 1986; Mitchell *et al.* 1987; Pietruszka 1988; Seely *et al.* 1988; Nagy *et al.* 1991), information regarding its detailed cranial osteology is minimal (Lang 1991; Locketto 2002). This is due in part to the extremely limited number of skeletal specimens available for study. Of these few specimens, most are whole-body preparations preserved in alcohol, making detailed study of the cranial osteology, and particularly the braincase, impossible. Data pertaining to its anatomy are important because the phylogenetic position of *A. skoogi* within Gerrhosauridae, a family of lizards endemic to sub-Saharan Africa and Madagascar, has historically been problematic.

Angolosaurus skoogi previously was hypothesised to be the sister taxon to mainland African gerrhosaurids (Lang 1991) (Fig. 2), although more recent analyses suggested *A. skoogi* is nested within *Gerrhosaurus* (Locketto 2002; Lamb *et al.* 2003). Its potential basal position within African Gerrhosauridae renders

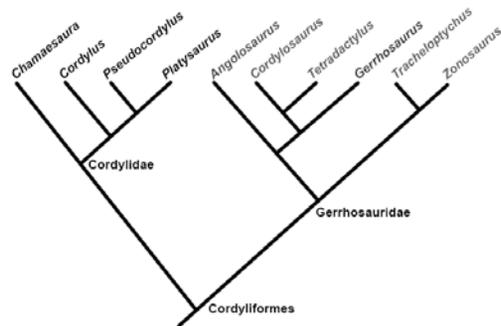


Figure 2. Preferred generic relationships among Cordyliformes (Cordylidae + Gerrhosauridae) from Lang (1991).

A. skoogi is a key taxon in addressing the larger question regarding relationships among the scincoid families Gerrhosauridae, Cordylidae, and Scincidae. However, attaining morphological data necessary to clarify the phylogenetic position of this gerrhosaurid is difficult for two reasons. First, as previously mentioned, detailed anatomy of *A. skoogi* is known from relatively few specimens due to the rarity of this extant gerrhosaurid in museum collections. Second, a lack of detailed cranial osteological data on *A. skoogi* results from the layer of osteoderms present in all gerrhosaurids and cordylids. In the cranial region, these ossifications often fuse to the bones of the skull, rendering osteological features like bone-to-bone contacts and sutures difficult, if not impossible to see in articulated specimens (Fig. 3). Although these ossifications are less numerous in *A. skoogi* than in other cordyliforms (e.g., *Gerrhosaurus* and *Cordylus*), their presence obstructs a clear view of the cranial anatomy. To circumvent these two problems, I utilized HRXCT (see Methods) to digitally remove the osteoderms from scanned images of the skull of this rare lizard and study its anatomy in detail.

Cranial osteology has been recognized as an important source of taxonomically significant data for over 150 years (e.g., Cope 1864, 1871,



Figure 3. Three-dimensional HRXCT volumetric reconstruction of the skull depicting lateral view of *A. skoogi* (CAS 206978) with osteoderms present.

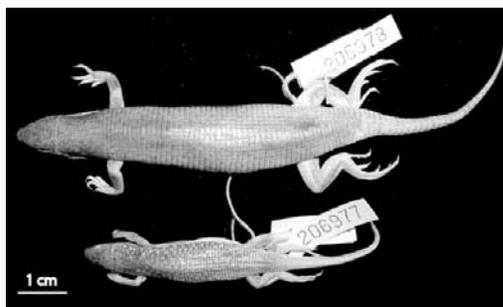


Figure 4. Specimens of *A. skoogi*: top, adult (CAS 206978); bottom, juvenile (CAS 206977).

1892). Among gerrhosaurids, many studies devoted to cranial osteology focused on the genus *Gerrhosaurus* (e.g., Siebenrock 1892; Brock 1935; Broom 1935; Malan 1941). The following anatomical description is the first detailed cranial osteological study of *A. skoogi*, which can be used to help resolve its phylogenetic position within Gerrhosauridae.

MATERIALS AND METHODS

Biological material.—Two formalin-fixed and alcohol-preserved specimens of *Angolosaurus skoogi* (Fig. 4), an adult (California Academy of Sciences [CAS] 206978) and a juvenile (CAS 206977) were scanned at The University of Texas High Resolution X-ray Computed Tomography Facility (UTCT). Both specimens were captured near the Odondujengo River in Namibia on July 27, 1998 by A. M. Bauer, A. C. Lamb, W. R. Branch, and J. L. Wright.

Scanning parameters.—Both specimens of *A. skoogi* were scanned using the ultra-high resolution subsystem at the UTCT. High resolution X-ray computed tomography uses the differential attenuation of X-rays as they pass through materials of different density and composition (such as scales, flesh, cartilage, and bone) to generate a series of digital images or ‘slices,’ in which grayscale values correspond to density and elemental contrast. Series of these two-

dimensional images are stacked to render a three-dimensional image of the object and its internal structure (Rowe *et al.* 1999; Ketcham & Carlson 2001). This technique enables digital serial-sectioning of an object at a slice resolution of 20 microns or less (Rowe *et al.* 1999), and offers a non-destructive means to study the interior of an object (e.g., Rowe *et al.* 1997; Rowe *et al.* 1999; Maisey 2001; Polcyn *et al.* 2002; Tykoski *et al.* 2002; and Brochu 2003). The specimens were mounted in a plastic cylinder, and positioned to acquire a series of slices along the transverse (= coronal) plane. The adult specimen is nearly twice as large as the juvenile, so different scanning parameters were used. The adult specimen was scanned using an X-ray energy set to 100 kV and 0.24 mA, with a slice thickness and inter-slice spacing of 0.53 mm. The image field of reconstruction was 18 mm. The image was reconstructed as a 512 x 512 16-bit TIFF file, resulting in an in-plane pixel resolution (i.e., the distance between each pixel) of 0.035 mm. A total of 402 transverse slices through the head and neck were obtained. The juvenile specimen was scanned with an X-ray energy set to 120 kV and 0.27 mA. The slice thickness and inter-slice spacing was 0.05 mm, and the field of reconstruction was 10 mm. The image of the juvenile was reconstructed using the same parameters as the adult, except with an in-plane pixel resolution of 0.02 mm.

Image processing.—To create serial cross-sectional slices of the cranium and mandible of *A. skoogi*, the transverse stack was digitally resliced in both the frontal (= horizontal) and sagittal planes. Three digit file names for each stack were drawn into the upper left-hand corner of each image using Slicorama®. The transverse stack was sequentially numbered from the tip of the snout to the posterior base of the skull, the frontal stack was numbered from the dorsal surface of the skull to the ventral surface, and the sagittal stack was numbered from the right side of the skull to the left side. Tonal range, or brightness, contrast, and color, of the HRXCT images were adjusted in Adobe Photoshop® to optimize visibility of anatomical detail.

QuickTime Pro® was used to create cut-away movies of each anatomical plane. For these movies, the HRXCT images were imported and exported at a speed of 15 frames per second. The parameters ‘graphics compression,’ ‘grayscale depth,’ and ‘best quality’ were used to reduce file size while maintaining the quality of the images in the movies.

Adobe Illustrator® was used to label the data set of the adult specimen, adopting the UTCT convention of labeling bones red, and processes and foramina yellow. Teeth are labelled blue and additional structures are green. Every fifth slice in the transverse plane is labelled, as well as additional slices in the transverse, frontal, and sagittal planes when necessary to depict morphological details. Abbreviations used in labeling the HRXCT data are listed in Table 1. Labeled figures in the text are black and white, with bones written in all uppercase letters and processes and foramina in lowercase.

Osteological description.—Several previous studies on squamate anatomy were referenced, including those by Cope (1892), Siebenrock (1892), Malan (1941), van Pletzen (1946), Säve-Söderbergh (1946, 1947), Oelrich (1956),

Table 1. Abbreviations used in HRXCT data set.

Abbreviation	Full terminology
ant.	anterior
dent.	dentary
f.	fenestra, foramen, fossa
hor.	horizontal
inf.	inferior
max.	maxilla, maxillary
p.	process
post.	posterior
premax.	premaxilla, premaxillary

Baird (1960), Kamal (1965, 1966a,b, 1969), Edmund (1969), Wever (1978), Bellairs & Kamal (1981), de Queiroz (1987), and Evans (in press). Unless otherwise noted, the terminology used here was adopted by Evans (in press) for both the labelled HRXCT dataset and the anatomical description. Structures named by Evans (in press) with a cardinal direction (e.g., ‘posterior process’) were referred to by their previously published names or a new name if none existed. Although the HRXCT images only show detailed osteology (and not soft anatomy), reference to some soft anatomical features was made in the description of *A. skoogi*. While tentative, these references (e.g., passage of nerves or blood vessels through foramina) were made based on descriptions of the closely related *Gerrhosaurus* (Malan 1941) and *Cordylus* (van Pletzen 1946), and the more distantly related iguanids *Ctenosaura* (Oelrich 1956) and *Iguana* (de Queiroz 1987). However, these soft anatomical features were not visible in the HRXCT images of *A. skoogi*.

When applicable, character states discussed in the phylogenetic analyses of Estes *et al.* (1988) and Lang (1991) were referenced. The character numbers used in this description are the same as those used by the original authors, preceded by a ‘C’ (for ‘character’) if Estes *et al.* (1988), and preceded by a ‘CC’ if

Lang (1991). The additional ‘C’ in the latter case reflects the designation of ‘cranial’ characters by Lang (1991). The polarity for the character state given corresponds to that used by those authors.

The cranial description is based on the adult specimen of *A. skoogi* (CAS 206978). Individual elements of the skull are described starting with bones located at the tip of the snout and working towards the back of the skull. Individual elements comprising the osseus braincase and the mandible are then described, followed by the dentition. In the osteological description, reference is made to the appropriate labeled HRXCT slices in which structures can be seen. These slices can be viewed as QuickTime movies at the Herpetological Association of Africa’s homepage (<http://www.wits.ac.za/haa/>). These references are made parenthetically, indicating in which anatomical plane and on which numbered slices the structures appear. The following abbreviations were used: transverse plane = Tra, frontal plane = Fro, and sagittal plane = Sag.

Despite having only two specimens available to study, preliminary observations of ontogenetic variation in *A. skoogi* were made by comparing the HRXCT images of the adult and the juvenile. Designation of the larger of the two specimens as an adult was based on development of the frontals and parietals, fusion between the prootic and basisphenoid, and fusion between the prootic and supraoccipital being to the extent of that found in most mature squamates (Maisano 2001, 2002). To compare the two specimens of *A. skoogi*, previous work related to squamate ontogenetic variation was referenced, including studies by de Queiroz (1987), Barahona and Barbadillo (1998), Barahona *et al.* (1998, 2000), and Evans (in press). Characters known to vary between adult and juvenile iguanids, as well as those that differ between the two specimens of *A. skoogi*, are

discussed. Additional variation between the two specimens regarding the stapes and dentition was also observed and discussed here.

RESULTS

GENERAL SKULL ARCHITECTURE

The overall shape of the skull of *Angolosaurus skoogi* reflects its dune-dwelling lifestyle. The anterior end of the snout is depressed, causing the entire skull to be shovel-shaped in lateral view (Fig. 3). In dorsal view, the snout appears depressed laterally, widening more posteriorly (Fig. 5). At the level of the coronoid process of the coronoid, the skull reaches its widest breadth, which it maintains toward the posterior end of the skull in dorsal view.

The skull can be divided into six regions based on their relative positions; the snout, palate, orbital region, temporal region, osseus braincase, and the mandible. The snout is bound by the median premaxilla anteriorly, and the paired maxilla anterolaterally, nasal dorsally, and vomer ventrally. The paired septomaxilla lies within the cartilaginous portion of the nasal chamber. The palate includes the paired vomer, palatine, pterygoid, and ectopterygoid. The orbital region consists of the paired prefrontal, lacrimal, jugal, frontal, postfrontal, and postorbital. The temporal region of the skull houses



Figure 5. Dorsal view of the skull of *A. skoogi* (CAS 206978) with osteoderms removed.

large temporal muscles (Oelrich 1956), and hence requires large fenestrae into which these muscles can expand as the jaw is adducted. These openings are discussed below with the other openings in the skull. The bones comprising the temporal region and forming the margins of these fenestrae are the unpaired, median parietal, and the paired squamosal, supratemporal, and quadrate. The osseous braincase is located in the posterior region of the skull and includes the paired prootic and otooccipital, and the median sphenoid, basioccipital, and supraoccipital. The mandible, or lower jaw, lies ventral to the lateral margins of the palate and consists of six paired elements: the dentary, splenial, coronoid, angular, surangular, and articular.

OPENINGS IN THE SKULL

At the anterior end of the snout is the paired external naris (fenestra exonarina of Oelrich (1956)). This fenestra is oval-shaped in lateral view in *A. skoogi* (Fig. 6), and is bordered anteriorly by the premaxilla, laterally by the maxilla, posteriorly by the nasal, and ventrally by the vomer. More posterior is the large, paired orbit (Fig. 6). Each large, nearly circular opening is covered dorsally by osteoderms, and has palpebral ossifications confined to the anterior margin (Tra 108-133; Estes *et al.* 1988: C36 (1)). The orbit is bordered by the prefrontal and lacrimal anteriorly, the frontal medially, the maxilla and jugal ventrally, and the postorbital and postfrontal posteriorly. In *A. skoogi*, the anteroventral border is formed by the maxilla in lateral view, because the anterior portion of the jugal is confined to the medial surface of the maxilla (Estes *et al.* 1988: C31 (0); Lang 1991: CC4 (1)). Medial to each orbit is a bony ring of individual scleral ossicles surrounding the eye (Tra 134-238). The number of individual ossicles comprising each scleral ring and their imbrication pattern varies within Squamata (Gugg 1939; Underwood 1970, 1984; de Queiroz 1987; Estes *et al.* 1988). The

resolution of the scanned images is inadequate to determine the number and pattern of scleral ossicles present in *A. skoogi*.

Posterior to the orbit, in the temporal region, is the paired upper temporal fenestra (supratemporal fossa of Oelrich (1956)). This fenestra is closed in other gerrhosaurids (Malan 1941), but is present as a slit bordered by the postorbital, parietal, supratemporal, and squamosal in *A. skoogi* (Lang 1991: CC8 (0)). Each fenestra is covered dorsally by osteoderms, and bounded by the postorbital anteriorly, the parietal medially, and the supratemporal and squamosal posteriorly (Fig. 7). The paired lower temporal fenestra (infratemporal fossa of Oelrich (1956)) is bound anterodorsally by the jugal, posterodorsally by the squamosal, and posteriorly by the quadrate and supratemporal (Fig. 6). Each fenestra is open ventrally in *A. skoogi*, as in all squamates (Evans, in press). The paired post-temporal fenestra (posterior temporal fossa of Oelrich (1956)) is situated more posteriorly. This narrow opening is between the parietal and ossified braincase (Fig. 8). The median, posterior opening of the osseous braincase, where the spinal cord exits the skull, is the foramen magnum (Fig. 8). Its margins are formed by the supraoccipital dorsally, the paired exoccipital components of the otooccipital laterally, and the basioccipital ventrally.

The paired choana (fenestra exochoanalis of Oelrich (1956)) is located ventrally within the palate. The choana is an oval-shaped opening bordered anteromedially by the vomer, anterolaterally by the maxilla, and posterolaterally by the maxillary process of the palatine (Fig. 9). The paired suborbital fenestra (inferior orbital fenestra of Oelrich (1956)) is located more posteriorly. Each fenestra is bordered anterolaterally by the maxilla, posterolaterally by the ectopterygoid, and medially by the palatine and pterygoid (Fig. 9). This fenestra transmits the superior alveolar nerve and artery (Oelrich 1956). Posterior to the suborbital fenestra is the

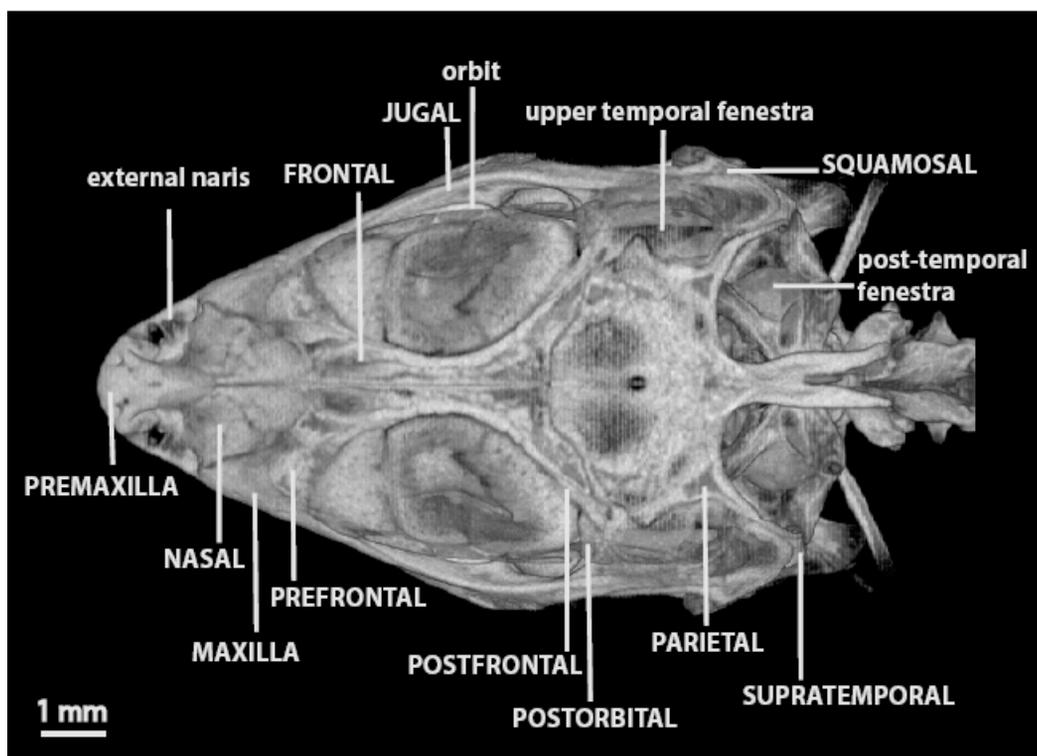


Figure 6. Labeled lateral view of the skull of *A. skoogi* (CAS 206978) with osteoderms removed.

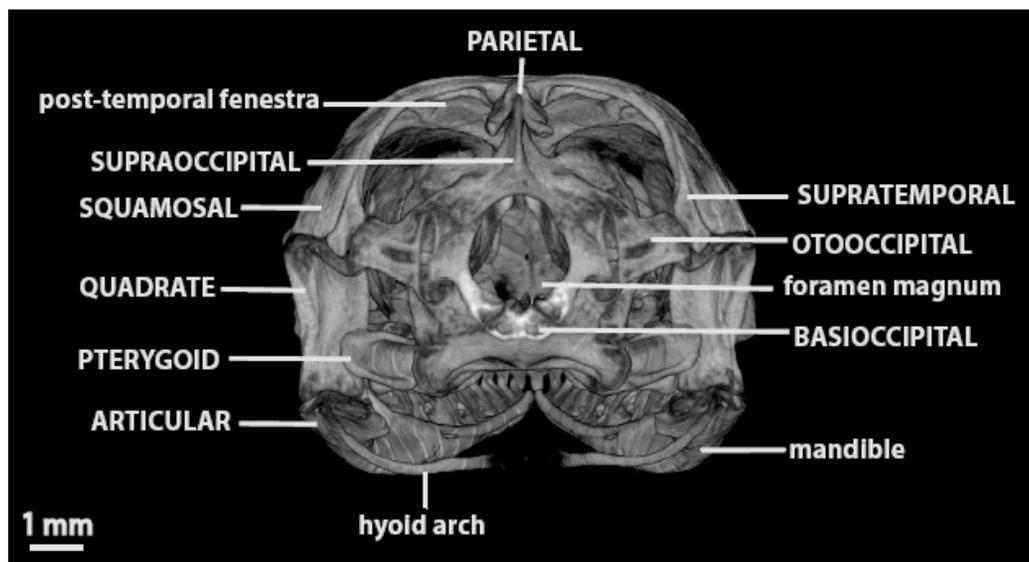


Figure 7. Labeled dorsal view of the skull of *A. skoogi* (CAS 206978) with osteoderms removed.

paired subtemporal fenestra. This fenestra is bound anteriorly by the ectopterygoid, medially by the pterygoid, and posteriorly by the quadrate (Fig. 9). The lateral margin of the subtemporal fenestra is open, and this fenestra provides room for the mandibular adductor muscles (Evans, in press).

The paired coronoid recess is more of a hollow space than an opening or fenestra (Fig. 9). This space is bound laterally by the jugal, medially by the ectopterygoid and pterygoid, and receives the coronoid process of the coronoid bone when the mandible is adducted (Evans, in press).

The interpterygoid vacuity (palatal sinus and pyriform recess of Oelrich (1956); pyriform recess of Estes *et al.* (1988)) is located at the ventral midline of the skull. This elongated opening (Fig. 9) is narrow at its anterior-most point, where it separates the posterior ends of the paired vomers medially (referred to as the palatal sinus by Oelrich (1956)). It continues posteriorly, widening between the palatines and the pterygoids (referred to as the pyriform recess by Oelrich (1956)). The posterior margin of the vacuity is formed laterally by the paired basiptyergoid process of the sphenoid, and medially by the sphenoid bone.

INDIVIDUAL ELEMENTS

Premaxilla.—The premaxilla is a median, unpaired, bilaterally symmetrical bone (Tra 15-60, Figs. 6-8), and forms the anteriormost element of the snout. The premaxilla laterally contacts both maxillae, posterodorsally meets the anteromedial edges of the nasals, and posteroventrally meets the anterior margins in the vomers. The premaxilla has a pair of lateral processes, called the palatal processes, which border the external nares and meet the anteromedial margin of the maxillae laterally. The nasal process of the premaxilla lies medially between the external nares, is wide laterally, and extends posteriorly, tapering to a point just

posterior to where it meets the nasals. This process is smooth dorsally, and appears flattened dorsoventrally in transversal view. The incisive process on the ventral side of the premaxilla is a small, anteriorly-rounded projection extending anteriorly toward the posterior margins of the premaxillary teeth. The premaxilla is broad and curved anteriorly, tapering posteriorly to form an anchor-shaped bone (Oelrich 1956).

The anteroventral surface of the premaxilla bears a row of seven unicuspid teeth; one tooth lies along the midline and both the right and left sides bear three teeth each. The anterodorsal surface (anterior, rostral body of Oelrich (1956)) is pierced by a pair of foramina (Tra 20-27). These foramina transmit the medial ethmoid nerves (cranial nerve V [CN V]) (Oelrich 1956). At the base of the nasal process, located on the midline of the premaxilla, is a single oblong foramen piercing the dorsal surface (Tra 30-41). This foramen does not penetrate the ventral surface, nor does it continue either anteriorly or posteriorly as a canal in the bone.

Septomaxilla.—The paired septomaxilla in *A. skoogi* is a short and narrow bone, lying near the midline of the skull between the premaxilla and the vomer (Tra 41-92, Fig. 7). It is located just posterior to the posteroventral border of the premaxilla, and meets the medial edge of the vomerine process of the maxilla anteriorly, and the pointed anterior tip of the vomer posteriorly. There is no contact between the septomaxilla and the premaxilla in *A. skoogi*. Medially, the septomaxilla nearly meets its twin on the midline, forming a raised crest (Estes *et al.* 1988: C40 (1)). The septomaxilla extends within the nasal vestibule, and is mainly supported by surrounding cartilage in other lizards (Malan 1941; van Pletzen 1946; Oelrich 1956).

The septomaxilla is broad anteriorly and has a ventral, posteriorly-projecting septal process

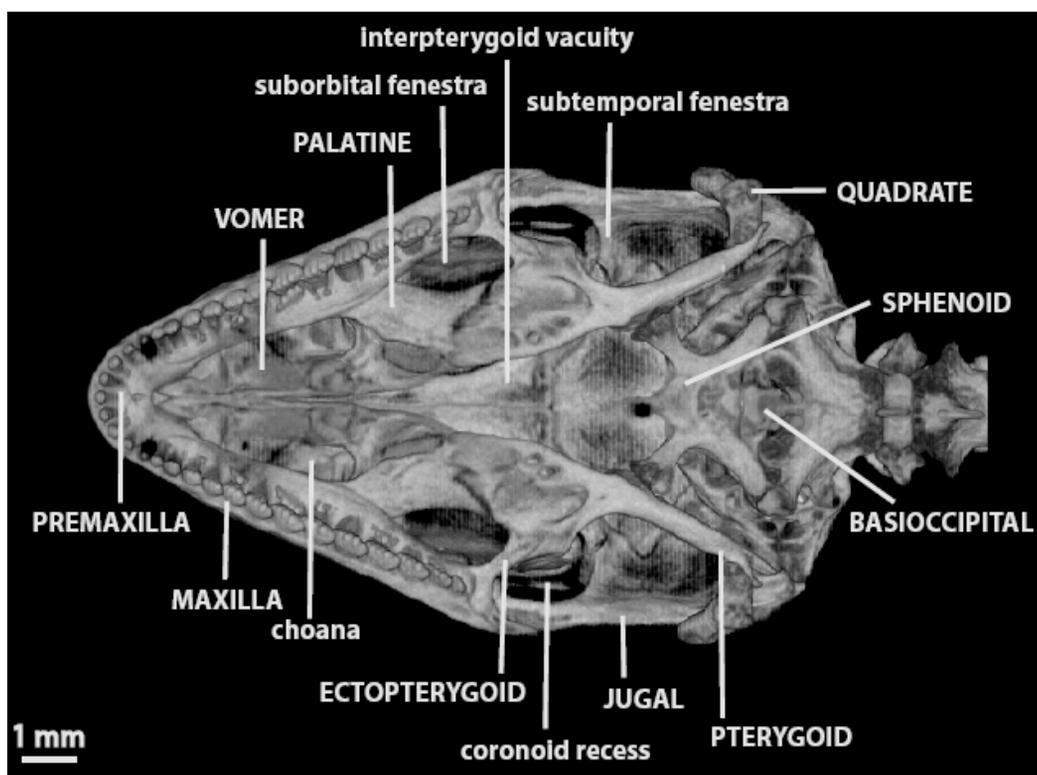


Figure 8. Labeled posterior view of the skull of *A. skoogi* (CAS 206978) with osteoderms and cervical vertebrae removed.

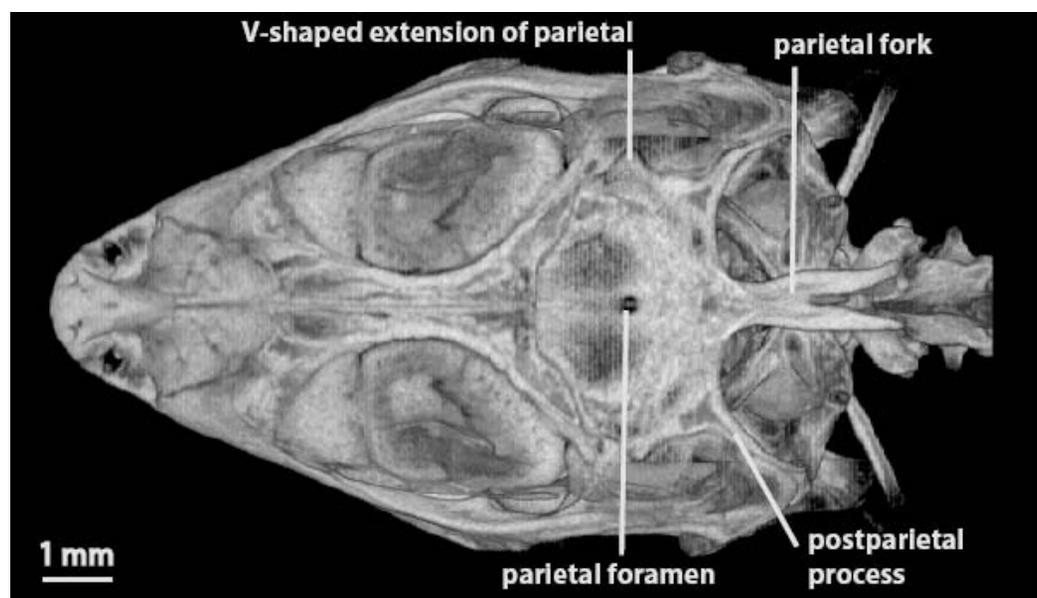


Figure 9. Labeled palatal view of the skull of *A. skoogi* (CAS 206978) with jaw disarticulated.

that nearly meets its opposite medially as it tapers to a point between the vomers posteriorly. Anterior to this septal process is the vomeronasal organ. The dorsal surface of the septomaxilla is expanded and convex (Estes *et al.* 1988: C41 (1)), but its ventral surface is concave dorsally, allowing the bone to both roof the vomeronasal organ and floor the anterior nasal vestibule (Malan 1941; van Pletzen 1946; Oelrich 1956). The function of the septomaxilla is thought to be for protection of the cartilages between the anterior chamber of the nasal capsule and the vomeronasal organ (Oelrich 1956).

Maxilla.—The large, mediolaterally-flattened maxilla (Tra 30-175, Fig. 9, 10, 11) forms the lateral side of the snout. Each maxilla has three processes: the premaxillary, the orbital (Oelrich 1956), and the facial. The maxilla meets the premaxilla anteromedially, and the jugal and lacrimal posteriorly. Along the posteromedial side of the maxilla, just dorsal to the tooth row, this bone meets the anteriormost tip of the ectopterygoid and the lateral margin of the maxillary process of the palatine. The facial process of the maxilla, located on its dorsal surface, contacts the lateral edge of the nasal anteriorly. Posteriorly, it meets the ventral margin of the prefrontal. The ventral surface of the maxilla bears a single row of pleurodont (Estes *et al.* 1988: C84 (0)), moncuspid and polycuspid teeth (described in detail below). The orbital process of the maxilla extends posteriorly to contribute to the anterior half of the ventral margin of the orbit in lateral view (Estes *et al.* 1988: C27 (0), C31 (0); Lang 1991: CC4 (1)). This same condition was scored in other cordyliforms by Estes *et al.* (1988; their 'Cordylidae' included both gerrhosaurids and cordylids as used in my study). The condition scored by Lang (1991) differed in that the jugal was said to form the anteroventral margin of the orbit, although that description does not specify from which view the character was scored.

The dorsal side of the premaxillary process (Tra 24-55) is flattened and slightly concave. The premaxillary process lies dorsal to the palatal process of the premaxilla and meets the anterior margin of the vomer medially.

The orbital process of the maxilla (Tra 180-200) contacts the jugal and lacrimal posteriorly, and the ectopterygoid medially. This process extends posteriorly beneath the orbit in *A. skoogi*, forming the anteroventral margin of the orbit. The medial side of this process forms the lateral margin of the wide suborbital fenestra. The lateral part of this process contributes to the rim of the suborbital fenestra and serves as attachment for the inferior orbital membrane in other lizards (Oelrich 1956).

The facial process, located between the premaxillary and orbital processes of the maxilla (Tra 62-107), is a wide dorsal extension of the maxilla forming the lateral wall of the nasal chamber. This process tapers to a point dorsally, separating the nasal and the prefrontal. Just ventral to the facial process, the maxilla is pierced by five of seven foramina located along its inferior lateral border (Tra 59-132). These foramina transmit cutaneous branches of the superior alveolar nerve (maxillary branch of CN V) and the maxillary artery (Oelrich 1956). Anterodorsal to this row of foramina are three to four small foramina piercing the medial wall of the maxilla (the precise number is difficult to discern from the scanned images). These foramina transmit cutaneous branches of the lateral ethmoidal nerve (CN V) (Oelrich 1956). A large, single foramen, called the anterior inferior alveolar foramen (Oelrich 1956), is present at the anterior base of the facial process (Tra 88-95). This anteriorly-directed foramen transmits the terminal branches of the maxillary artery and superior alveolar nerve to the nasal chamber (Oelrich 1956). The medial side of the facial process meets the lateral side of the cartilaginous nasal chamber (Oelrich 1956).

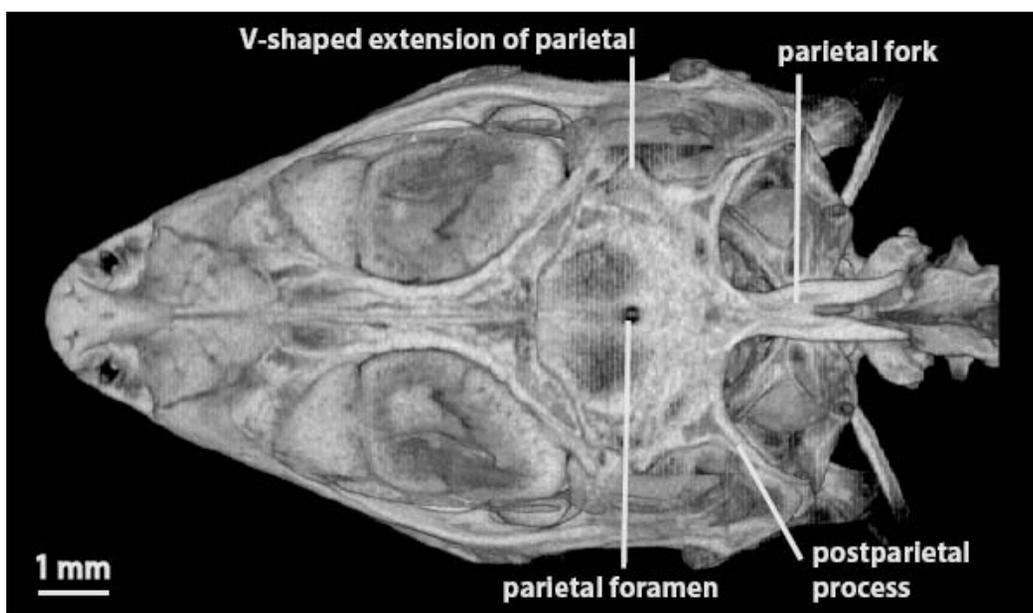


Figure 10. Dorsal view of the skull of *A. skoogi* (CAS 206978) detailing parietal morphology.

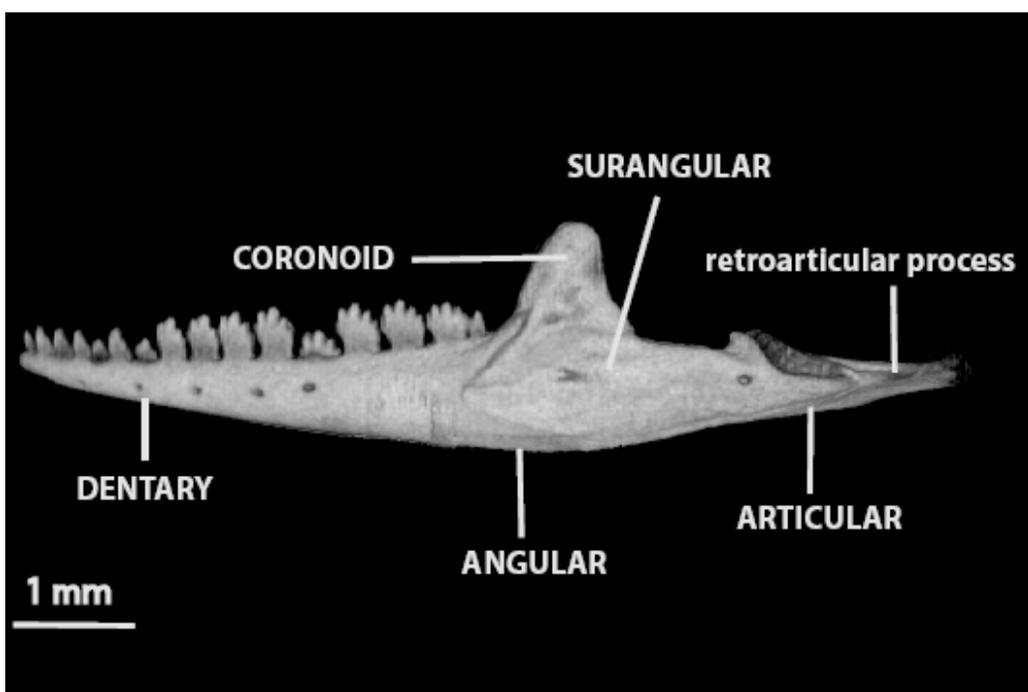


Figure 11. Labeled lateral view of the left mandible of *A. skoogi* (CAS 206978).

In contrast to the smooth, lateral side of the maxilla, the medial side has a shallow, medially-extending palatal shelf (Lang 1991: CC19 (0)) running along its length. This shelf floors the nasal chamber (Oelrich 1956), and dorsally bears 14 tooth positions, each with a functional tooth or replacement tooth coming in (Tra 34-180). Along the labial margin of these teeth are large resorption pits (Estes *et al.* 1988: C85 (0)), which mark the development of replacement teeth. These teeth have no basal infolding, and do not appear striated in *A. skoogi* (Estes *et al.* 1988: C86 (0)). There is no offset in the tooth margin of the maxilla (Estes *et al.* 1988: C87 (0)). The portion of the palatal shelf posterior to the palatine/maxilla suture forms the lateral margin of the choana, while the portion of the palatal shelf anterior to this suture forms the lateral margin of the fenestra vomeronasalis externa (Oelrich 1956). Dorsal to this shelf is the hollow superior alveolar canal, which transmits the maxillary artery and the superior alveolar nerve (Oelrich 1956). Both the nerve and the artery enter through the posterior alveolar foramen, which pierces the anteroventral margin of the facial process. Many small dental foramina that transmit both dental nerves and arteries (Oelrich 1956) pierce the ventral surface of this hollow tube in the palatal shelf.

Nasal.—The nasal is a flat bone overlying the anterior part of the cartilaginous nasal chamber (Malan 1941; Oelrich 1956). The paired nasal bone (Tra 45-100, Fig. 7) lies midway between the premaxilla and frontal. The right and left nasals are medially sutured to each other for about half of their entire length posteriorly. Each nasal meets the nasal process of the premaxilla anteromedially, the facial process of the maxilla anterolaterally, the prefrontal posterolaterally (Estes *et al.* 1988: C4 (0)), and the frontal posteriorly. The nasal process of the premaxilla separates the nasals anteriorly, while the anteromedially projecting process of the frontal separates the posterior extremities of the nasals, forming a V-shaped notch along the

midline of the pair, with the pointed tip of the V directed anteriorly. The posterior edge of the nasal overlies a thin, short shelf located at the anteriormost edge of the frontal. Each nasal is somewhat triangular-shaped, with the anterior border of the nasal perpendicular to the sagittal plane, while both lateral and medial borders taper posteriorly to a point near the frontal. Along the anterior margin of the nasal, there is an anteriorly-concave excavation made by the external naris. This concavity results in antero-medial and anterolateral extensions of the nasal. The more medial of the two is referred to here as the premaxillary process and the more lateral of the two as the maxillary process. In *A. skoogi*, the maxillary process is the longer of the two. The anterior border of the nasal contributes to the posterior margin of the external naris.

About two-thirds of the way toward the posterior end of the bone, lying along the midline of each nasal in dorsal view, is a foramen (Tra 77-80). In other lizards, this foramen transmits cutaneous branches of the lateral ethmoidal nerve (CN V1) and venous tributaries of the orbital sinus (Oelrich 1956). The remaining dorsal surface of the nasal is smooth.

Vomer.—Each vomer (Tra 75-127, Fig. 9) has a convex ventral surface and concave dorsal surface. The posterior end of the vomer meets the dorsal surface of the vomerine process of the palatine, while the anterior end meets the medial surface of the premaxilla. The anterior two-thirds of the vomer contact its twin medially, while the posterior third is separated by the anterior extension of the interpterygoid vacuity (median palatal sinus of Oelrich (1956)), a space running anteroposteriorly between the two bones. There is no contact between the vomer and the maxilla in *A. skoogi*, thus the posterior border of Jacobson's organ is not closed by bone, representing the 'paleochoanate' condition (Estes *et al.* 1988: C42 (0); Evans, in press). Each vomer is relatively large,

exceeding half the length of the maxillary tooth row in *A. skoogi* (Estes *et al.* 1988: C39 (1)). In dorsal view, the anterior-most portion of the vomer is narrow and triangular, and contacts the other vomer medially (Fro 185-190). Posterior to this triangular portion, the vomer narrows laterally, while maintaining contact with the other vomer medially. These paired palatal bones are not inseparably fused in the adult *A. skoogi* (Estes *et al.* 1988: C38 (0)). For the remaining two-thirds of its length, the vomer broadens laterally while the space between the two vomers, the interpterygoid vacuity, broadens as well. The lateral border of the vomer is not constricted anteriorly, and does not form a laterally-concave margin in *A. skoogi*.

A large portion of the posterolateral border of the vomer contributes to the medial margin of the choana. In the iguanid lizard, *Ctenosaura pectinata*, the groove for the lacrimal duct runs along the anterolateral border of each vomer (Oelrich 1956); however, a groove is not visible in the scanned images of *A. skoogi*. This duct opens into and supplies fluid to the vomeronasal organ in lizards (van Pletzen 1946). The median border of the fenestra vomeronasalis externus (Oelrich 1956) is positioned where the anterior end of the lacrimal groove should be in *A. skoogi*. Running between the anterolateral borders of each vomer is a groove for the paired ramus medialis (palatine branch) of CN VII (Oelrich 1956). There is no heart-shaped depression along the midline of the two vomers posteriorly (Lang 1991: CC14 (0)).

Palatine.—The palatine (Tra 110-197, Fig. 9) contacts the palatine process of the pterygoid posteriorly, the palatine process of the maxilla laterally, and the posterior end of the vomer anteriorly. There is no contact between the palatine and the ectopterygoid (Estes *et al.* 1988: C45 (0)), or the jugal (Lang 1991: CC3 (0)). The palatine has three processes: the ante-

rior vomerine process, the posterior pterygoid process, and the lateral maxillary process (Oelrich 1956). There is no medial extension from the ventrolateral edge of the palatine contributing to a bony secondary palate (Estes *et al.* 1988: C43 (0)), and there is no medial extension from the anteromedial margin of the palatine. The palatine forms a large portion of the palate, the floor of the orbit, and the floor of the posterior nasal chamber (Oelrich 1956). There are no teeth on the surface of the palatine in *A. skoogi* (Estes *et al.* 1988: C82 (1)).

The thin vomerine process (Tra 108-127) tapers slightly anteriorly, is concave dorsally, and forms the floor of the posterior nasal chamber. The anterior-most end of the process slightly overlaps the dorsal surface of the posterior end of the vomer (Tra 108-126). The lateral border of the vomerine process forms the posteromedial border of the choana. This opening is relatively prominent in relation to the size of the palatine bone in *A. skoogi* (Estes *et al.* 1988: C44 (1)). In other lizards, the medial palatine nerve runs along the midline of the dorsal surface of this process (Oelrich 1956).

The large, quadrangular pterygoid process of the palatine meets the palatine process of the pterygoid posteriorly, forming an interdigitating suture (Tra 170-197). This process extends posteroventrally from the main body of the palatine. The concave dorsal surface forms the floor of the orbit and anteriorly contains a groove running anteroposteriorly (Tra 145-165). This groove contains the main branch of the palatine plexus of cranial nerve VII (Oelrich 1956). The medial portion of the pterygoid process forms the lateral border of the interpterygoid vacuity, a V-shaped space between the two palatines and the two pterygoids with the wide, open end of the V directed posteriorly. The anterior, pointed end of this V-shaped space continues forward between the medial margins of the paired vomers. This space is broad in *A. skoogi* (Estes *et al.* 1988:

C48 (1)). The lateral side of the process forms most of the medial rim of the wide suborbital fenestra.

The short maxillary process extends anterolaterally from the junction of the pterygoid and vomerine processes (Tra 115-143). Its lateral border contacts the palatine process of the maxilla ventrally, and the anteroventral palatine process of the prefrontal dorsally. The palatine does not meet the ectopterygoid posteriorly. Behind the contact of the maxillary process with the prefrontal, is the palatine foramen (Tra 128-136), which is more of a canal in *A. skoo-gi*. This canal emerges within the nasal cavity and carries the intermediate branch of nerve VII (Oelrich 1956).

The lateral border of the maxillary process contributes to the suborbital fenestra, which transmits the superior alveolar nerve and artery (Oelrich 1956). A ridge situated at the junction of the maxillary and vomerine processes (Tra 128-131) provides attachment for the orbitonasal membrane (Oelrich 1956). Anterior to this ridge is an indentation between the maxillary and vomerine processes. This indentation forms the posterior rim of the choana. The ventral surface of the palatine is relatively smooth.

Ectopterygoid.—The ectopterygoid (Tra 172-218, Fig. 9) is a short, triradiate bone with dorsomedial and ventromedial processes that clasp the dorsal and ventral surfaces of the pterygoid flange. I am calling these processes the dorsal pterygoid process and the ventral pterygoid process (medial process of Oelrich (1956)), respectively. These processes are approximately equal in length. A laterally-directed process, referred to here as the jugal process, extends horizontally and contacts the ventromedial surface of the jugal. The jugal process also meets the posteromedial margin of the maxilla, but does not contact the palatine. The anteriormost end of the jugal process forms a distinct point. The ectopterygoid is a slender bone in *A. skoo-*

gi, as in all Cordyliformes, and does not restrict the size of the suborbital fenestra (Estes *et al.* 1988: C46 (0)). Its posterior end is broader than its anterior end, but both ends of the bone are broader than the narrow middle isthmus of the bone. The bone is oriented at an anterolateral angle, connecting the palate with the external roofing elements (Oelrich 1956).

The ectopterygoid is an attachment site for many oral membranes (Oelrich 1956). The dorsal side forms part of the orbit floor and receives the orbital temporal membrane (Oelrich 1956). The anterior edge of the bone receives the inferior orbital membrane, which fills the suborbital fenestra. The ventromedial surface of the posterior end of the ectopterygoid is concave and bounds the coronoid recess with the anterior tip of the transverse process of the pterygoid. This recess receives the coronoid process of the mandible (Oelrich 1956).

Pterygoid.—The pterygoids, comprising the posterior portion of the palate, (Tra 177-303, Figs. 8, 9) are a pair of dorsally-concave bones that are broad anteriorly and narrow posteriorly. Anteriorly, the pterygoid meets the ectopterygoid and the palatine. More posteriorly, the pterygoid meets the epipterygoid on its dorsal surface, and the basispterygoid process of the sphenoid bone on its medial surface. At its posteriormost end, the pterygoid contacts the medial margin of the quadrate. The broad anterior portion of the pterygoid is somewhat triangular shaped, while the posterior portion is a laterally-inflected and laterally-flattened, narrow process.

The broad anterior end of the pterygoid has two processes; the palatine process and the pterygoid flange. The palatine process (Oelrich 1956) dorsally meets the posterior end of the palatine (Tra 170-195). This contact is quite ragged, resembling two V-shaped extensions on the pterygoid interlocking with the W-shaped end of the palatine. The ventrolateral

surface of the palatine process is convex and as in other gerrhosaurids, houses ventrally-extending pterygoid teeth in *A. skoogi* (Estes *et al.* 1988: C83 (0); Lang 1991: CC15 (1)) (Tra 206-220). Medial to this convex surface are three foramina (Tra 197-214), which transmit palatine branches of CN VII (Oelrich 1956).

An anterolateral process of the pterygoid, called the pterygoid flange (Evans, in press; 'transverse process' of Oelrich (1956)), contacts the ectopterygoid laterally (Tra 193-218), and forms the posterior bony limit of the oral cavity. This process is shorter and narrower than the palatine process and extends anterolaterally from the posterolateral portion of the palatine process of the pterygoid to meet the ectopterygoid.

The sole posterior projection of the pterygoid is the quadrate process. This process articulates posteriorly with the ventromedial surface of the quadrate (Tra 290-302); anterodorsally it contacts the anteroventral end of the epipterygoid (Tra 240-245). That contact occurs within the fossa columellae of the quadrate process of the pterygoid. This fossa is a short and narrow pit running lengthwise toward the anterior end of the quadrate process. The medial wall of this pit extends more dorsally than the lateral wall.

The quadrate process of the pterygoid articulates anteromedially with the anterior edge of the basipterygoid process of the sphenoid bone (Tra 250-260) at the pterygoid notch (Oelrich 1956). Located medial to the fossa columellae of the quadrate process is the V-shaped pterygoid notch, a synovial joint between the basipterygoid process of the sphenoid bone and the pterygoid (Oelrich 1956). Posterior to this notch, along the medial side of the quadrate process, is a medially concave groove running posteriorly toward the posterior tip of the process (Tra 287-300). This groove is the site for insertion of the protractor pterygoideus muscle (Oelrich 1956). The lateral side of the

quadrate process is smooth and convex laterally. A small facet at the ventrolateral end of the process contacts the medial side of the quadrate as the pterygoid extends posteriorly and curves slightly around the medial edge of the quadrate.

Epipterygoid.—The epipterygoid is present (Estes *et al.* 1988: C47 (0)) as a thin, columnar bone in *A. skoogi* (Tra 233-271). Its ventral surface sits in the fossa columellae, a concavity in the dorsal surface of the pterygoid (Tra 233-248). Its dorsal end meets the membranous braincase (Evans, in press), and the lateral margin of the parietal via ligaments of the pseudotemporalis superficialis muscle (Oelrich 1956). The slender epipterygoid bone is positioned in the skull at an angle, its ventral end more anterior than its dorsal end. The ventral portion of the epipterygoid is broader than the rest of the bone, and flattened mediolaterally. The dorsal end of the bone tapers slightly as it extends posterodorsally and approaches, but does not contact the alar process of the prootic and the ventral downgrowths of the parietal. The space lateral to the dorsal end of the epipterygoid is called the cavum epiptericum. This space contains the trigeminal nerve ganglion (Evans, in press). In coronal view, the epipterygoid is slightly curved, bending laterally toward its dorsal end.

Lacrimal.—The lacrimal (Tra 110-121) is a small, anteroposteriorly-flattened bone confined to the anterolateral margin of the orbit (Estes *et al.* 1988: C28 (0)). This element meets the lateral margin of the prefrontal, but is not fused to it (Estes *et al.* 1988: C29 (0)). It meets the maxilla anterolaterally and the anteriormost tip of the jugal posteriorly. The medial margin of the lacrimal comes very close to, but does not contact, the lateral margin of the maxillary process of the palatine, thus forming a small space between the two bones (Tra 128-130). A single lacrimal foramen (Tra 128) pierces the posteromedial surface of the lacrimal (Estes *et al.* 1988: C30 (0)). In *Ctenosaura*, this foramen

transmits a vein that drains the skin closely covering the lateral surface of the bone (Oelrich 1956). In *Gerrhosaurus* (Malan 1941) and *Cordylus* (van Pletzen 1946), the nasolacrimal duct lies in a groove between the lacrimal and the prefrontal. The lacrimal is obscured in lateral view by the posterior portion of the facial process of the maxilla (Lang 1991: CC2 (1)).

Jugal.—The jugal (Tra 120-248, Figs. 6, 7, 9) is an L-shaped bone in lateral view. It meets the maxilla anteriorly in a tongue-and-groove articulation, the ectopterygoid medially, the postorbital posteromedially, and the squamosal posterolaterally. This latter contact with the squamosal was not found in the cordyliforms scored by Estes *et al.* (1988: C18 (1)), but is clearly present in *A. skoogi*. The anterior portion of the jugal contributes to the posteroventral margin of the orbit in lateral view. In both dorsal and medial views, this contribution to the orbit extends farther anteriorly. The jugal is divided into two processes: the anterior maxillary process and the posterior temporal process (Oelrich 1956).

The maxillary process extends anteriorly along the medial wall of the maxilla. The dorsal surface of the maxillary process is slightly expanded mediolaterally, to help form the ventral wall of the orbit. In life the orbital fascia attaches to this process of the jugal (Oelrich 1956). The anterior portion of the lateral surface of the maxillary process is pierced by several small foramina (Tra 179, 193). These suborbital foramina transmit cutaneous branches of the maxillary nerves (CN V) (Oelrich 1956).

The temporal process of the jugal extends posterodorsally and contributes little to the temporal region in *A. skoogi*. However, the jugal does meet the postorbital to form a complete jugal-postorbital bar in *A. skoogi* (Estes *et al.* 1988: C32 (0)). Just anterior to where the temporal process of the jugal and the postorbital meet is

a tiny foramen piercing the medial side of the jugal (Tra 209-212). In *Ctenosaura*, a similarly-placed foramen transmits branches 1 and 2 of the maxillary nerve (CN V2) (Oelrich 1956). A portion of the temporal process also provides attachment for the infratemporal fascia (Oelrich 1956).

Prefrontal.—The prefrontal is a roughly pyramid-shaped bone forming most of the anterior orbital margin (Tra 99-145, Fig. 6). The anterolateral border of this bone meets the posterior margin of the nasal process of the maxilla. In dorsal view, the anteromedial border of the prefrontal contacts the lateral edge of the nasal, while the posteromedial border of the prefrontal meets the anterior edge of the anterolaterally projecting process of the frontal. The posterolateral border of the prefrontal contributes to the anterior margin of the orbit. The posterolateral surface of the prefrontal meets the tiny lacrimal bone. The ventromedial extension of the prefrontal, called the palatine process (Oelrich 1956), meets the dorsal edge of the maxillary process of the palatine. There is no contact between the prefrontal and any posterior orbital elements (e.g., the postfrontal or the postorbital) in *A. skoogi* (Estes *et al.* 1988: C5 (0)), as is the case in all Cordyliformes (Cordylidae + Gerrhosauridae from Lang (1991)). The prefrontal precludes contact of the facial processes of the maxilla and the anterolateral margins of the frontal in *A. skoogi*.

The palatine process of the prefrontal and the ventrally-descending process of the frontal form the orbitonasal fenestra (Tra 127-130), an opening between the orbital and nasal cavities (Oelrich 1956). The borders of this fenestra provide attachment for the orbitonasal membrane (Oelrich 1956). The posterolateral edge of the prefrontal is much like that of other cordyliforms and like that in *Gerrhosaurus* (Malan 1941). It is concave posteriorly, smooth, and curved to form the anterolateral

rim of the orbit. In *A. skoogi*, the posterolateral edge of this surface articulates with the flat lacrimal bone, but does not contribute to formation of the lacrimal foramen, unlike in *Gerrhosaurus* where the prefrontal contributes to both the foramen and the lacrimal canal (Malan 1941). The posterior rim of the prefrontal bone also provides attachment for the orbital fascia (Oelrich 1956). The lateral, medial, and dorsal surfaces of the prefrontal are relatively smooth.

Frontal.—The paired frontal bones (Tra 90-229, Fig. 7) meet along the midline. They are not inseparably fused in *A. skoogi*, much like other gerrhosaurids (Estes *et al.* 1988: C6 (0); Lang 1991: CC6 (0)). The frontal bone meets its opposite medially, with the contact between the pair forming a straight line running along the sagittal plane. The frontal bone also contacts the prefrontal anterolaterally, the nasal anteriorly, the parietal posteriorly, the postfrontal posterolaterally, and contributes to the dorsal margin of the orbit laterally. The frontal bone does not contribute to the bony external naris in *A. skoogi* (Estes *et al.* 1988: C2 (0)), and thus is similar to the case in other cordyliforms. The paired frontal is dorsoventrally flattened. The posterior margin is broad, while the central and anterior portions of the sutured pair are narrow. When paired, the lateral borders of the frontals are roughly parallel to one another (Estes *et al.* 1988: C7 (0)).

The anterior tip of the frontal lies ventral to the posterior end of the nasal (Tra 90-103), but no broad frontal shelf is present (Estes *et al.* 1988: C8 (0)). Posteriorly, the frontal meets the parietal, and overlies anterolateral parietal tabs, which were scored as both present and absent in cordyliforms (Estes *et al.* 1988: C22 (1)). These tabs are thin, triangular-shaped, anteriorly-projecting extensions of the parietal on either side of its anterior border. There are no tabs on the posterior rim of the frontal (Estes *et al.* 1988: C11 (0)).

The ventral surface of the frontal is smooth, and has a ventrally-extending ridge, called the supraorbital ridge (Oelrich 1956), running along its lateral edge for the length of the bone (Tra 135-215). This ridge is short for most of its length, except at the anterior-most edge of the bone, where the ridge extends ventrally toward the palatine (Estes *et al.* 1988: C9 (1)). This ventral extension is called the crista cranii (Tra 127-234). In other lizards, a thin part of the cartilaginous solium suprasedal attaches to the cristae cranii (Oelrich 1956; Evans, in press). In *A. skoogi*, the cristae cranii do not contact one another below the olfactory tracts (Estes *et al.* 1988: C10 (0)), nor are they pierced ventrally by a small foramen present in other gerrhosaurids. Medial to the supraorbital ridge is a shallow groove. This groove is the olfactory tract (olfactory canal of Oelrich (1956)) and holds the olfactory stalks and olfactory bulbs of the brain (Oelrich 1956). In other lizards, a pair of narrow excavations in the posterior half of the frontal, located just medial to the supraorbital ridges (Tra 195-215), provide attachment for the thick part of the cartilaginous solium suprasedal (Oelrich 1956). Just posterior to these excavations is the attachment site for the epioptic membrane (Oelrich 1956). The posterior portion of the frontal also covers part of the membranous braincase. There is no contribution to the parietal foramen by the frontal in *A. skoogi* (Estes *et al.* 1988: C25 (0)).

Palpebrals.—The palpebral ossifications in *A. skoogi* are located at the anterior-most corner of each orbit (Tra 108-133). They meet the posterolateral margin of each prefrontal anteriorly, and meet the ventral margin of the supraorbital osteoderms that cover the orbits dorsally. These ossifications within the eyelid are known in other cordyliforms and scincids (Estes *et al.* 1988: C36 (1)).

Postfrontal.—The postfrontal is a small bone confined to the posterior rim of the orbit (Tra 219-230, Fig. 6) (Estes *et al.* 1988: C15 (1)).

This bone was said to be “extensive” and “not confined to the orbital rim” in Cordyliformes (Cordylidae in Estes *et al.* 1988: p. 129). However, the postfrontal in *A. skoogi* is small and does not extend posteriorly beyond the margin of the orbit. The medial margin of the postfrontal meets the posterolateral tip of the frontal and the anterolateral tip of the parietal just anterior to where the frontal and parietal meet. There is no contact between the postfrontal and the posterior end of the jugal. The postfrontal is not forked where it contacts the frontal, and does not clasp the frontoparietal suture in *A. skoogi* (Estes *et al.* 1988: C13 (0); Lang 1991: CC7 (1)). This is a reversal of a scleroglossan synapomorphy (Estes *et al.* 1988). This state reversal was scored similarly for *A. skoogi* by Lang (1991); however, in the analysis by Estes *et al.* (1988), the state scored for all Cordyliformes was that in which the postfrontal clasps the frontoparietal suture.

Laterally, the postfrontal overlies the medial edge of the postorbital. Osteoderms over the orbit and upper temporal fenestra obscure this tiny bone in dorsal view, but cross-sectional images (Tra 220-230) show that it is not fused to the postorbital and, thus, is a separate element (Estes *et al.* 1988, C12 (0), C14 (0)). This small bone functions as a splint between the frontal, parietal, and postorbital, to reinforce the postorbital arch (Oelrich 1956). In *A. skoogi*, the postfrontal is not the primary element restricting the upper temporal fenestra (Estes *et al.* 1988: C20 (0)).

Postorbital.—The postorbital (Tra 218-243, Figs. 6, 7) is present in *A. skoogi* (Estes *et al.* 1988: C16 (0)) as a flat, boomerang-shaped bone contributing to the posterior rim of the orbit. Its lateral side meets the posteromedial border of the temporal process of the jugal, while its medial side meets the lateral margin of the postfrontal. The postorbital has a strong, anteroventrally-directed process that runs along the medial margin of the jugal, forming

approximately one-half of the posterior margin of the orbit (Lang 1991: CC5 (1)). This character state for the postorbital bone was scored differently for cordyliforms by Estes *et al.* (1988: C17 (1)), as being primarily a temporal bone forming less than one half of the posterior rim of the orbit when viewed either medially or laterally. Although the upper temporal fenestra is overlain by osteoderms in *A. skoogi*, it is clear from the transverse slices that the postorbital is the primary restricting element of the anterolateral rim of this fenestra (Estes *et al.* 1988: C19 (1)).

The anterior rim of the postorbital, which forms the posterior margin of the orbit, is concave anteriorly. This rim also provides attachment for the infratemporal fascia and the anterior portion of the origin of the levator angularis oris muscle (Oelrich 1956). The dorsal and lateral surfaces of the bone are smooth.

Parietal.—The parietals (Tra 213-366, Figs. 6, 8) fuse ontogenetically to form a single roofing element lying along the midline of the skull and covering the osseous and membranous components of the braincase (Evans, in press). Anteriorly, it meets the frontal, and its anterolateral tip just meets the posterolateral margin of the postfrontal. Laterally, the parietal forms the medial margin of the upper temporal fenestra. Its posterolateral extensions, the paired postparietal processes (supratemporal processes of Oelrich (1956)), contribute to the posterior rim of the upper temporal fenestra dorsally and the dorsal rim of the post-temporal fenestra ventrally. Their lateral margins articulate with the medial margins of the supratemporal bones distally. The posterior margin of the parietal forms a long, forked process, called the parietal fork (Oelrich 1956), which is directed posteriorly and braces the supraoccipital crest (Lang 1991: CC11 (1)) (Tra 300-366).

The parietal in *A. skoogi* is slightly concave ventrally and somewhat rectangular in shape.

The postparietal processes and the parietal fork border the prominent emargination of the parietal in *A. skoogi* (Estes *et al.* 1988; Lang 1991), causing the posterodorsal surface of the osseous braincase to be exposed in dorsal view (Estes *et al.* 1988: C24 (1); Lang 1991: CC18 (0)). Prominent emargination of the parietals was not present in all members of Cordyliformes examined by Estes *et al.* (1988). I found no emargination in *Cordylus*, *Pseudocordylus*, and *Platysaurus*. The anterior rim of the parietal has two triangular-shaped parietal tabs (Estes *et al.* 1988: C22 (1); Lang 1991: CC10 (1)). These are thin, anteriorly-directed extensions overlain by the posterior border of the frontal (Tra 213-225). Although Estes *et al.* (1988) noted that presence of parietal tabs is variable in Cordyliformes, Lang (1991) scored them as absent in *A. skoogi*. Laterally, a V-shaped extension of the parietal extends into the medial margin of the upper temporal fenestra, with the pointed tip of the V directed laterally (Fig. 10). For the most part, the dorsal parietal surface is smooth. In *Gerrhosaurus* and *Ctenosaura*, the dorsolateral surface provides attachment for the origin of the jaw muscles, the pseudotemporalis superficialis, and the adductor externus medius (Malan 1941; Oelrich 1956).

The dorsal surface of the parietal is penetrated by a distinct parietal foramen (Estes *et al.* 1988: CC26 (0)), in the very center of the bone (Estes *et al.* 1988: C25 (0)) (Tra 250-253). The parietal foramen is obscured from view when the osteoderms are present, but digital removal of osteoderms reveals the presence of this foramen (Fig. 10).

The ventral surface of the parietal is concave, causing the whole bone to be slightly round and convex dorsally, in lateral view (Lang 1991: C12 (0)). Along the midline of the ventral surface, just anterior to the base of the parietal fork, is an excavation called the parietal fossa (Oelrich 1956). This fossa (Tra 277-287),

receives the anterior end of the processus ascendens of the tectum synoticum, a cartilaginous process that projects from the supraoccipital (Malan 1941; Oelrich 1956; Evans, in press). The parietal fossa is partly floored ventrally by a plate of bone originating from the anterior margin of the fossa, and has a finger-like process projecting anteriorly along its ventral surface. Anteriorly, on either side of the parietal fossa, are shallow grooves extending to the anteroposterior midpoint of the bone. In other lizards, these grooves house the taenia marginalis cartilage (Malan 1941; Oelrich 1956). Extending anterolaterally from the parietal fossa, and continuing anteriorly, are ventrally-directed ridges on either side of the midline of the bone (Tra 225-285). These ridges run along the length of the parietal and meet the frontal/postfrontal contact. These ventral ridges provide attachment for the origin of the levator pterygoideus muscle (Malan 1941; Oelrich 1956). However, the anterior portions of these ridges do not extend far ventrally toward the dorsal end of each epipterygoid (Estes *et al.* 1988: C23 (1); Lang 1991: CC9 (1)). Lateral to these ridges, on either side of the bone, are slight excavations within its ventral surface. These are for insertion of the cartilaginous extension of the paired epipterygoid bone (Malan 1941; Oelrich 1956).

The posterior border of the parietal bone creates the dorsal rim of the post-temporal fenestra. This rim also provides attachment for several occipital muscles, including the depressor mandibularis, the spinalis capitis, and the episternocleidomastoideus (Oelrich 1956).

Squamosal.—The squamosal (Tra 243-321, Figs. 6, 8) is present in *A. skoogi* (Estes *et al.* 1988: C33 (0)) as a flat, paired bone best seen in lateral view. This bone contributes to the lateral margin of the upper temporal fenestra and the posteriodorsal margin of the lower temporal fenestra. Its anterior-most extension comes to a pointed tip and meets the posterior end of the

jugal. The posteroventral surface of the squamosal meets the dorsal surface of the quadrate, while the posteromedial edge contacts the medial margin of the postorbital and the anterior edge of the supratemporal bone.

This flat bone is tadpole-shaped in lateral view, with the round, sagittally-expanded end of the bone directed posteriorly and a pointed extension projecting anteriorly. This basic shape is present in all gerrhosaurids examined. However, all other gerrhosaurids examined here have a bifurcated anterior end, while *A. skoogi* has a single anterior extension. The anterior process of the squamosal meets the jugal anteriorly and contributes a small portion to the posterior rim of the lower temporal fenestra. The posterior portion of the squamosal is expanded dorsoventrally, but there is no superior process of the squamosal in *A. skoogi* (dorsal process of Estes *et al.* 1988: C34 (0)).

In other lizards, the squamosal is held in place by ligaments and, thus, is potentially kinetic (Oelrich 1956). The lateral surface is smooth, providing attachment for the levator angularis oris muscle and the adductor externus superficialis muscle, whereas its medial side provides attachment for the adductor externus medialis muscle (Oelrich 1956).

Supratemporal.—The supratemporal (Tra 302-327, Figs. 6-8) is present in *A. skoogi* (Estes *et al.* 1988: C35 (0)) as a paired element at the posterior end of the skull. It contributes a small portion to the lateral rim of the post-temporal fenestra and the posterior rim of the upper temporal fenestra. This bone contacts the lateral side of the postparietal process of the parietal. The posterior process of the supratemporal curves ventrally to meet the posteromedial tip of the cephalic condyle of the quadrate. This bone anteriorly meets the posterior edge of the squamosal, and ventromedially meets the lateral border of the paraoccipital process of the otooccipital.

The supratemporal is shaped somewhat like a slender tadpole in lateral view. Two regions were previously recognized (Oelrich 1956); the pointed anterior region (Tra 302-314), which meets the postparietal process of the parietal, and the posteriorly directed process (Tra 315-327), which sits on the dorsal surface of the quadrate. The latter process appears to be wedged between the otooccipital, quadrate, and squamosal in posterior view (Fig. 8). This process, directed ventrally in *A. skoogi*, is concave on both its medial and lateral margins where it meets the paraoccipital process of the otooccipital and the posterior end of the squamosal, respectively. In other lizards, the anterior portion of the supratemporal bone provides attachment for the origin of the adductor externus medius muscle laterally, and provides attachment for the origin of the adductor externus profundus muscle medially (Oelrich 1956). In *Ctenosaura*, the supratemporal bone supports the posterolateral portion of the parietal, and serves as the center of motion between the occipital and maxillary segments of the skull (Oelrich 1956).

Braincase.—The osseous braincase, or oticooccipital region, is comprised of five bones, the sphenoid and basioccipital, midline bones which form the floor of the braincase; the prootic and otooccipital, paired elements forming the walls of the cranial cavity; and the supraoccipital, the midline roofing bone of the braincase. This bony region of the braincase houses the posterior part of the brain and the inner ear. As in other lizards, there is a membranous component to the braincase in *A. skoogi*, called the orbitotemporal region. The only ossified element to this region is the orbitosphenoid. Due to the density contrast between fully ossified material and the remaining cartilaginous, membranous component, adequate detail of the orbitotemporal region is not visible in the scanned images and only the

orbitosphenoid is discussed.

Orbitosphenoid.—The orbitosphenoid is a paired, ossified element suspended in the membranous orbitotemporal region of the braincase (Tra 224-239). The bone is crescent-shaped in lateral view and concave posteriorly. In large, adult Iguanine lizards, the orbitosphenoid bears four processes; an anterodorsally-projecting process that connects to the planum suprasetale, a posteriorly-projecting process that joins the pila accessoria and the pila antotica, an inferior process that is confluent with the cartilaginous portion of the pila metoptica, and a ventrally-projecting process that contributes to the anterior portion of the pituitary region (Oelrich 1956; de Queiroz 1987). In the adult specimen of *A. skoogi*, the orbitosphenoid lacks all of these well-developed processes except the posteroventrally-directed inferior process. It is continuous with the hypochiasmatic cartilage of the pila metoptica. This overall shape more closely resembles that of juvenile, large-bodied iguanines and adult, small-bodied iguanines (de Queiroz 1987). The anterodorsal ends of the two orbitosphenoids may fuse to each other medially in large-bodied iguanines (de Queiroz 1987), but are not fused in *A. skoogi* (Fig. 12; the image was difficult to render due to low density of the element).

Sphenoid.—The sphenoid (Tra 181-309, Fig. 9) forms the anterior floor of the braincase. This element is comprised of an inseparably fused basisphenoid and dermal parasphenoid in adult lizards (Bellairs & Kamal 1981; Evans, in press). These two components are distinct in developing skulls. The sphenoid bone shares a straight articulation with the basioccipital posteriorly and a dorsolateral suture to the prootic. Both of these sutures lack overlap between the structures. It has three anteriorly-directed processes. The thin, dermal parasphenoid rostrum (parasphenoid process of Oelrich (1956)) is fused to the median ventral border of the sphenoid underneath the ossified portion of the

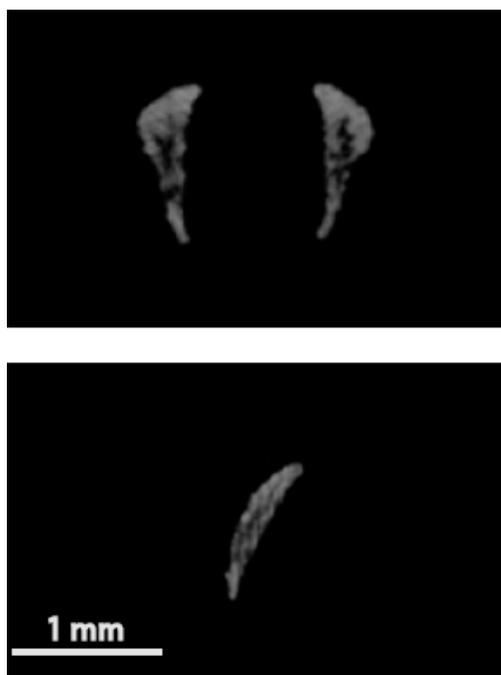


Figure 12. Three-dimensional HRXCT reconstruction of orbitosphenoid in *A. skoogi* (CAS 206978). Top: Paired orbitosphenoid in anterior view with dorsal margin toward the top of the figure. Bottom: Lateral view of left orbitosphenoid with anterior margin toward the left of the figure.

paired trabecular cartilages, called the cristae trabeculares (Tra 181-260). At the ventrolateral angles of the sphenoid, the paired basipterygoid processes (Tra 247-275) extend anteriorly; their broad, distal ends articulate with the medial edge of the quadrate processes of the pterygoids. In *A. skoogi*, the basipterygoid processes are short and broad, as is the case in all gerrhosaurids (Lang 1991: CC16 (0)). In between the paired basipterygoid processes, the narrow parasphenoid rostrum supports the ossified bases of the trabeculae cranii (Evans, in press). The sphenoid is broad anteriorly and tapers somewhat posteriorly.

On the dorsal surface of the sphenoid is the dorsum sella (Säve-Söderberg 1947), an anteriorly-concave, vertical plate of bone towards the

anterior end of the sphenoid (Tra 268-273). The top of the dorsum sellae forms a deep, dorsally-concave crest called the crista sellaris (Tra 265-270). More laterally, the dorsum sellae extends dorsally into the bases of the anterior inferior processes of the prootic. The abducens nerve (CN VI), the vidian branch of cranial nerve VII, the palatine artery, and the carotid artery pass through this wall via a series of canals. The anterior end of the vidian canal (Tra 265-293), through which the vidian nerve and the palatine artery pass (Oelrich 1956), is formed medially by the sphenoid bone and ventrally by the parasphenoid (Evans, in press). The anterior exit of this canal, located at the base of the basipterygoid process, is lateral to the anterior exit of the carotid canal (Tra 270-276), which is the passage for the internal carotid artery (Oelrich 1956). Posteriorly, these two canals merge inside the sphenoid bone, and exit posteriorly, ventrolateral to the anterior auditory foramen (Tra 290-296). The entire length of the vidian canal is bound medially and ventrally by the sphenoid (Estes *et al.* 1988: C53 (0)).

Dorsal to the vidian and carotid canals, the abducens canal pierces the dorsum sellae (Tra 269-272), and carries the abducens nerve (Oelrich 1956). This canal is located just under the crista sellaris in the retractor pit, a recess which gives rise to the bursalis muscle and the retractor bulbi muscle (Säve-Söderbergh 1946; Oelrich 1956). Posteriorly, this canal opens into the cranial cavity. The ventral surface of the sphenoid bone is smooth.

Prootic.—The paired prootic (Tra 267-325) forms the anterolateral wall of the braincase. The prootic contacts the sphenoid ventrally, the supraoccipital dorsally, and the otooccipital posteriorly. The prootic also forms the anterior margin of the fenestra ovalis, and contributes to the anterior portion of the vestibule, which contains the cochlear cavity, the anterior semicircular canal, and the horizontal semicircular canal (Evans, in press).

The prootic has three major processes, called the alar, the anterior inferior (Evans, in press), and a posteriorly-directed process which I call the otooccipital process. The most anterior of these paired processes are the short, broad alar processes (Tra 266-288), each extending anterodorsally in *A. skoogi* (Estes *et al.* 1988: C49 (1)). The anterior edge of each process is called the crista alaris (Evans, in press). Just posterior to the alar process, the prootic meets the supraoccipital and borders the acoustic recess anteriorly. The interior of the alar process is hollow, and opens posteriorly into the anterior and horizontal osseous semicircular canals.

The anterior inferior process of the prootic is located ventral to the alar process (Tra 267-280). The anteriorly-concave notch between these two processes is called the incisura prootica (trigeminal notch of Oelrich (1956)) (Tra 279-281). The median head vein and the trigeminal nerve (CN V) pass through this notch; the ganglion for CN V lies lateral to it in the cavum epiptericum (Evans, in press). In some squamates (e.g., iguanians), there is an anterodorsally-projecting process extending from the incisura prootica. However, this process, called the supratrigeminal process, is not present in *A. skoogi* (Estes *et al.* 1988: C50 (0)).

The otooccipital process extends posterolaterally to overlap and meet the anterolateral surface of the paraoccipital process of the otooccipital (Tra 295-305). This posterolaterally-projecting process provides a facet anterovertrally for the paraoccipital process and houses the horizontal osseous semicircular canal as it courses posteriorly through the prootic (Evans, in press).

The prootic contributes to the vestibule, which is formed anteriorly by the prootic and posteriorly by the otooccipital, and houses the organs of the inner ear (Wever 1978). Also housed

inside the vestibule is the large, dense, crystallized statolith mass (Tra 294-333). These structures are present in all vertebrates and aid in detecting movement and maintaining proper orientation (Wever 1978). Anteroventral to the vestibule is a laterally-concave recess within the medial wall of the prootic called the acoustic recess. This recess (Tra 290-304) houses the anterior auditory ganglion (Oelrich 1956). Ventrolateral and posterior to the acoustic recess and ventral to the vestibule is the lagenar recess (Tra 293-324). This recess houses the lagena, a major component of the cochlear duct in lizards (Wever 1978). Like the vestibule, the lagenar recess is formed anteriorly by the prootic and posteriorly by the otooccipital.

The prootic is pierced by several foramina. The anterior-most opening along the medial wall of the prootic is the facial foramen (Tra 292-295), through which passes the facial nerve (CN VII) (Oelrich 1956). This foramen is located anteroventral to the vestibule and anterior to the acoustic recess. Within the acoustic recess are two other foramina. The anteriormost of the two is the anterior auditory foramen (Tra 290-296). It transmits the anterior branch of the anterior ramus of the acoustic nerve (CN VIII) (Oelrich 1956), and opens into the otic capsule (Tra 281-336). Posterior to this foramen in the acoustic recess is the posterior auditory foramen (Tra 303-305), which opens into the lagenar recess. Dorsal and posterolateral to the lagenar recess is the fenestra ovalis (Tra 307-322), formed anteriorly by the prootic and posteriorly by the opisthotic portion of the otooccipital. The footplate of the stapes sits within this fenestra.

The lateral surface of the prootic is characterized by a prominent crest running posteriorly, called the crista prootica (Tra 276-295). In other lizards, this crest provides attachment for the protractor pterygoidei muscle, and helps form the roof and lateral wall of the tympanic

cavity (Evans, in press). In *A. skoogi*, the crista prootica is well-developed ventrally, creating a deep canal between its medial surface and the lateral surface of the prootic in ventral view. Just ventral to this crest is the lateral exit of the facial foramen, and a groove through which runs the principle head vein (Evans, in press).

Otooccipital.—The otooccipital (Tra 317-357, Fig. 8) is formed by fusion early in ontogeny of the exoccipital and the opisthotic bones (Bellairs & Kamal 1981; Evans, in press). These bones are inseparably fused in most adult squamates (Evans, in press), as is the case in *A. skoogi*. The anterior edge of the otooccipital meets the posterior edge of the prootic dorsally where they together enclose the fenestra ovalis, and ventrally where they form the lagenar recess. The posteromedial portion (the exoccipital contribution) forms the lateral rim of the foramen magnum (Tra 325-336), and articulates ventrally with the basioccipital. The laterally expanded posterior face of the otooccipital is called the crista tuberalis (Säve-Söderbergh 1947). In *A. skoogi*, the crista tuberalis does not extend far enough laterally to obstruct view of the anterior margin of the lateral aperture of the recessus scala tympani (LARST), when viewed posteriorly. The otooccipital forms the posterolateral and posterior wall of the braincase, and the posterior half of the vestibule. The exoccipital components form the ventrolateral portions of the occipital condyle in *A. skoogi*.

The otooccipital has one laterally-projecting process: the paraoccipital process (Tra 305-335). This process abuts the supratemporal bone dorsolaterally, and the dorsomedial aspect of the quadrate ventrolaterally. In coronal view, the paraoccipital process is slightly broader at its distal end than at its proximal end. Ventrally, this process bears a crest, called the interfenestral crest (crista interfenestralis of Säve-Söderbergh (1947)), which separates the fenestra ovalis from the secondary tympanic mem-

brane housed within the lateral opening of the recessus scala tympani (Evans, in press). Running through the proximal end of this process is the horizontal semicircular canal (Oelrich 1956) (Tra 299-336). This canal extends anterolaterally and courses around the auditory chamber.

There are a number of foramina piercing the otooccipital. The vagus foramen marks the boundary between the opisthotic and exoccipital components of the otooccipital, while the hypoglossal foramina pass entirely through the exoccipital component of the otooccipital (Kamal 1966b). Three hypoglossal foramina provide passage for CN XII (Sag 158-172, 228-237) and are visible on the posteromedial side of the otooccipital just dorsal to its suture with the basioccipital, and can be seen from the posterolateral side of the bone as well. The oval-shaped vagus foramen, which transmits cranial nerve X, is located dorsal to the hypoglossal foramina and posterior to the auditory capsule within the otooccipital (Sag 150-160, 236-243).

Posterior to the lagenar recess, the otooccipital contributes to the recessus scala tympani. This hollow cavity is floored by the basioccipital and houses the terminal end of the perilymphatic sac, which exits the vestibule via the perilymphatic duct through the perilymphatic foramen (Wever 1978). The round, medial opening of this recess, called the medial aperture of the recessus scala tympani (MARST) (Tra 315-322), is slightly anterior the LARST (Tra 317-326). While the MARST is formed entirely by the otooccipital, the LARST is formed dorsally by the otooccipital and ventrally by the basioccipital. In *A. skoogi*, the MARST is about half the size of the LARST. The recessus scala tympanum is connected with the vestibule by the perilymphatic foramen (Tra 315-324), which lies medial to the fenestra ovalis and on the ventral floor of the vestibule. This foramen is enclosed entirely within the otooccipital, and

carries the perilymphatic duct away from the braincase (Evans, in press).

The HRXCT images of *A. skoogi* show no indication of a separate foramen for the passage of the glossopharyngeal nerve (CN IX). Within squamates, there are three known courses CN IX takes as it exits the braincase (Kamal 1969). In a purely intracapsular course, the nerve passes through the internal glossopharyngeal foramen (Kamal 1969) in the medial wall of the vestibule, traverses it, exits the vestibule through the perilymphatic foramen, traverses the recessus scala tympani, and finally exits the braincase via the lateral opening of the recessus scala tympani. In a purely extracapsular course, CN IX exits the cranial cavity through the medial opening of the recessus scala tympani, traverses the recessus, and exits the braincase through the lateral opening of the recessus scala tympani (Kamal 1969). The third course is neither completely intra- nor extracapsular. Along this course, the glossopharyngeal nerve exits the cranial cavity through the glossopharyngeal foramen (Kamal 1969), located on the ventromedial edge of the vestibular wall. The nerve traverses the prootic, without entering the vestibule, to enter the recessus scala tympani, and then exits the recessus through the lateral opening of the recessus scala tympani. The course in *A. skoogi* appears to be purely extracapsular, with the nerve traversing the recessus scala tympani via its medial and lateral openings. Neither a separate foramen piercing the medial wall of the vestibule, nor a canal traversing the medial wall, are visible.

In *Gerrhosaurus major*, a separate foramen for CN IX was found in an articulated skull examined in this study (CAS 204767). This same specimen was scanned using HRXCT, and the resulting images also revealed a separate glossopharyngeal foramen. However, locating this foramen was difficult and required careful searching through all three anatomical slice planes to corroborate its position. Because the

foramen is so difficult to find in the HRXCT scan, and considering that the skull of that specimen of *G. major* is nearly twice the size of the scanned specimen of *A. skoogi*, it is conceivable that a separate glossopharyngeal foramen is present in *A. skoogi*, but the scan resolution is insufficient to reveal it.

Basioccipital.—The basioccipital is an unpaired element that forms the posterior floor of the cranial cavity (Tra 300-359, Figs. 8, 9). It is sutured anteriorly to the sphenoid, anterolaterally to the prootic, and posterolaterally to the otooccipital. Posteriorly, it forms the central component of the occipital condyle and the ventral rim of the foramen magnum.

In lateral view, the basioccipital is concave dorsally, with its posterior edge raised to form the medial portion of the occipital condyle. The ventral surface is, for the most part, convex; with a ventrally-directed ridge running along the midline of the bone (Tra 310-322). The ventral surface also bears two ventrally-projecting crests (Tra 301-315), called the basal tubera (Evans, in press) (sphenoccipital tubera of Oelrich (1956)). These crests provide attachment for hypaxial muscles (Evans, in press). In *A. skoogi*, posterior extensions of the sphenoid contribute to the anterior portions of the basal tubera (Lang 1991: CC17 (0)).

Supraoccipital.—The supraoccipital is an unpaired element that forms the posterior roof of the braincase (Tra 288-343, Fig. 8). It articulates anterolaterally with the prootic and posterolaterally with the otooccipital. It also contributes to the dorsal rim of the foramen magnum. The supraoccipital is comprised laterally and ventrally of the upper portions of the vestibules. The supraoccipital is convex dorsally and doubly concave ventrally where it roofs both vestibules. Medially, the supraoccipital covers the medulla and cerebellum.

The most prominent feature of the supraoccip-

ital is the large, posterodorsally-extending crest located on the dorsal surface of the bone (Tra 302-343). The lateral faces of this crest are smooth, and provide attachment for the ligamentum nuchae (Oelrich 1956). The dorsal-most tip of this crest is braced by the long parietal fork in *A. skoogi* (Tra 316-343).

The supraoccipital is intimately associated with the membranous labyrinth of the inner ear. The supraoccipital contributes a large portion of the anterior semicircular canal (Tra 272-310) continuing into the prootic, and the posterior semicircular canal (Tra 310-340) continuing into the otooccipital. Located toward the posterior portion of the vestibule is the osseus common crus, a vertically-directed canal forming the junction of the anterior and posterior semicircular canals (Tra 310-320). The osseus common crus opens inside the vestibule, just posterior to the endolymphatic foramen. This foramen pierces the medial wall of the supraoccipital, and is the medial opening for the endolymphatic canal (Tra 332-333). This canal transmits the endolymphatic duct from the cranial cavity to the vestibule (Wever 1978).

Stapes.—The stapes (Tra 307-319) is a slender rod derived from the hyoid arch (Bellairs & Kamal 1981; Evans, in press), expanded at its proximal and distal ends. The slender stapedial shaft lies within the middle ear, with the expanded medial footplate resting in the fenestra ovalis. The expanded lateral end contacts the tympanic membrane just medial to the quadrate.

Quadrate.—The quadrate (Tra 268-323, Figs. 6, 8) is a paired bone positioned at the rear of the skull. It facilitates motion between the cranium and the lower jaw (Oelrich 1956; Evans, in press). The quadrate meets the ventral margin of the squamosal and the ventral end of the posterior process of the supratemporal dorsally. Its medial surface contacts the ventrolateral tip of the paraoccipital process of the otooccipital

and, more ventrally, contacts the anterolaterally-inflated tip of the quadrate process of the pterygoid. Ventrally, the quadrate meets the condylar facet (Oelrich 1956) of the articular bone of the lower jaw. Unlike the condition found in most reptiles, this articulation in *A. skoogi* is more like a ball-and-socket joint, with the knob-like facet of the articular fitting into the cotyle of the quadrate. This condition previously was observed in other gerrhosaurids (Malan 1941). The quadrate is united with these other elements via a synovial joint (Malan 1941; Oelrich 1956), allowing for a great degree of mobility. This type of joint is characteristic of borrowing forms, like *A. skoogi* (Malan 1941). The entire anterior face of the quadrate contributes to the posterior margin of the lower temporal fenestra.

The quadrate resembles a T-shaped column forming a 90° angle with the horizontal axis of the skull, or parietal table, in lateral view. On its ventral surface is a concave, mandibular cotyle that meets the condylar facet of the articular bone (Tra 283-304). The mandibular cotyle of the quadrate is divided into a medial and lateral half by a median ridge. These two halves of the cotyle are of approximately equal size. When viewed posteriorly, the medial and lateral margins of the quadrate are nearly parallel to one another.

The dorsal surface of the quadrate also forms a somewhat convex cephalic condyle. Its lateral side lies slightly anterior to the medial side of the condyle (Tra 271-323). The lateral side also has a dorsally-projecting tubercle at its anterior end. The posterior end of the condyle slopes downward, creating a rounded appearance. The cephalic condyle of the quadrate contacts the paraoccipital process of the otooccipital medially, the supratemporal posteriorly, and the squamosal anterolaterally. Attachments to these bones are made by thick fibrocartilage, or 'intercalary cartilage' (Versluys 1912). In other lizards, the dorsal surface of the quadrate also

serves as attachment for the origin of the adductor mandibularis superficialis and the medius muscles (Oelrich 1956).

The medial side of the anterior face of the quadrate extends farther anteriorly than the lateral side. The anterior face is broader dorsally, tapering slightly toward the mandibular condyle. The dorsolateral portion of the anterior face has an anteriorly-projecting tubercle in *A. skoogi*. This condition is present in other gerrhosaurids examined (e.g., *Gerrhosaurus*, *Zonosaurus*). In the iguanid, *Ctenosaura pectinata*, there is a small foramen, the quadrate foramen, piercing the dorsolateral region of the anterior face of the quadrate (Oelrich 1956). However, no such foramen is visible in the scanned images of *A. skoogi*. Additionally, no such foramen is seen in the other examined specimens of gerrhosaurids and cordylids, and this foramen is not mentioned by Malan (1941) or van Pletzen (1946) in their studies of *Gerrhosaurus* and *Cordylus*.

A dorsoventral ridge called the curved central pillar (posterior crest of Oelrich (1956)), divides the posterior face of the quadrate into medial and lateral halves. The ridge is present for most of the length of the bone, flattening out just dorsal to the mandibular cotyle. The lateral half of the posterior face of the quadrate is concave posteriorly. Like the anterior face, it is broader dorsally and tapers ventrally just above the mandibular cotyle. Towards the ventral end of the medial half of the posterior face of the quadrate lies the contact between the quadrate and the quadrate process of the pterygoid. There is no pterygoid lappet of the quadrate (Estes *et al.* 1988: C37 (1)). The lateral side of the quadrate has a prominent crescent-shaped tympanic crest running dorsoventrally. This crest (Tra 284-296) provides attachment for portions of the tympanum, and the origin of the adductor mandibularis externus superficialis muscle, and for skin (Oelrich 1956).

Mandible.—The mandible (Fig. 11) consists of six paired elements: the dentary, splenial, coronoid, angular, surangular (supra-angular of Baur (1891); de Beer 1937; Oelrich 1956), and articular. These six bones surround a tubular canal that courses through them called the Meckelian fossa. This structure houses the remains of the embryonic Meckel's cartilage. The mandible articulates with the dorsal portion of the skull via the articulation between the articular and the quadrate.

Dentary.—The dentary is a paired bone comprising the majority of the anterior portion of the mandible (Tra 27-217, Fig. 11). The two dentary bones meet one another medially at their anterior ends. More posteriorly, along the length of its medial side, each dentary articulates with the thin splenial bone. There is extensive bone-to-bone contact between these two elements (Estes *et al.* 1988: C67 (0)). At its posterior end, the dentary meets the coronoid dorsally, the surangular laterally, and the angular ventrally. The dentary bone is hollow, with the Meckelian fossa coursing through its length. As in *Ctenosaura pectinata* (Oelrich 1956), the posterior elements of the jaw in *A. skoogi* form the continuation of this hollow tube because their anterior ends join the dentary (Estes *et al.* 1988: C64 (0)).

The dentary is a long bone, flattened mediolaterally toward its posterior end, and more rounded anteriorly. It is the only tooth-bearing bone of the lower jaw. Each dentary bears 15 pleurodont teeth (Estes *et al.* 1988: C84 (0)), filling each of the 15 tooth positions. The first five are unicuspid, while the remaining ten are polycuspid, with two to five cusps per tooth. A more detailed description is discussed below (see Dentition). These teeth are situated along the medial surface of the bone above the dental shelf, and along their lingual side are large resorption pits (Estes *et al.* 1988: C85 (0)). At the base of the teeth is a large, prominent ridge, called the subdental shelf (Estes *et al.* 1988:

C58 (1), C59 (0)).

The lateral surface of the dentary is relatively smooth and convex laterally. Anteriorly, six foramina in a row pierce the lateral surface, just ventral to the base of the teeth (Tra 36-128). These foramina transmit terminal branches of the mandibular nerve (Evans, in press) (inferior alveolar nerve of Oelrich (1956)) to the skin. These foramina continue medially through the dentary bone and open into the canal for the mandibular nerve, which passes through the dentary just lateral to the Meckelian fossa.

The medial surface of the dentary is convex where the splenial is attached along its length (Tra 108-245). The splenial forms the medial margin of the Meckelian fossa (Tra 50-275), but does not extend to the anterior end of the dentary. Near the anterior end of the dentary, the Meckelian fossa is incompletely closed medially (Tra 50-107). If the splenial were removed, the Meckelian fossa would be exposed medially for its entire length (Estes *et al.* 1988: C57 (0)). In *A. skoogi*, the dentary forms an open groove, not a closed, fused, or sutured tube around Meckel's cartilage (Estes *et al.* 1988: C55 (0)).

Inside the dentary bone, the Meckelian fossa is separated from the canal for the mandibular nerve by a thin plate of bone, which dorsoventrally traverses the sagittal plane, and is called the intramandibular septum (Tra 60-237). This septum is anterior to the most posterior tooth position in *A. skoogi* (Estes *et al.* 1988: C56 (0)). The Meckelian fossa runs along the medial portion of the dentary, while the canal for the mandibular nerve runs along the lateral portion. Only briefly do these two canals merge medially as the septum dividing them is reduced (Tra 140-157).

The dentary is bifurcated posteriorly in lateral view, forming dorsal and ventral posteriorly-pointed extensions. The large, dorsal extension

extends dorsally onto the dorsolateral surface of the coronoid in *A. skoogi* (Estes *et al.* 1988: C60 (1)). On the posterolateral surface of the dentary, there is no surangular or coronoid notch present in *A. skoogi* (Estes *et al.* 1988: C63 (0)).

Splénial.—The splénial is a thin, flat, paired element contributing to the medial margin of the Meckelian fossa (Tra 108-245). Most of the splénial has extensive bone-to-bone contact with the medial surface of the dentary bone (Estes *et al.* 1988: C67 (0)). It extends well anterior to the midpoint of the tooth row in *A. skoogi* (Estes *et al.* 1988: C65 (0)), and extends posterior to the apex of the coronoid (Estes *et al.* 1988: C66 (0); Lang 1991: CC21 (1)) to meet the angular and the surangular posteriorly along their medial margins. This posterior extension beyond the coronoid apex previously was observed in some cordyliforms (Estes *et al.* 1988), but not in *A. skoogi* (Lang 1991). Both the anterior and posterior ends of the splénial taper distally; however the anterior end is more severely tapered and becomes narrower than the posterior end. The middle portion of the splénial is expanded dorsoventrally.

The splénial is pierced by two foramina. The more anterior of the two is situated dorsally (Tra 134-152). This large foramen transmits the lingual branch of the mandibular nerve (Evans, in press). The more posterior of the two foramina is situated more ventrally along the splénial (Tra 162, 166). This foramen, called the anterior mylohyoid foramen (Oelrich 1956), transmits the anterior mylohyoid nerve (Malan 1941; Oelrich 1956).

Coronoid.—The coronoid is a paired bone lying towards the middle of the jaw on its dorsal surface (Tra 180-243, Fig. 11). The coronoid meets the dentary anteriorly, the surangular posteriorly, and the splénial ventrally. The coronoid bone is a dorsally-directed element on the jaw, with the base of the ascending portion

located just posterior to the last tooth position in the dentary and processes reaching anterior to the last tooth position. The posterolateral surface of the coronoid provides attachment for the adductor mandibularis externus and medius muscles, and the bodenaponeurosis (Oelrich 1956). The posterodorsal tip of the lateral side of the dentary overlies the lateral side of the coronoid (Tra 182-200) (Estes *et al.* 1988: C68 (0), C71 (1); Lang 1991: CC22 (1)). The coronoid has five processes, named by Evans (in press) as the dorsal, labial, anteromedial, posteromedial, and posterior process. However, here the dorsal process is referred to as the coronoid process, the anteromedial process as the dentary process, the posteromedial as the splénial process, and the posterior as the surangular process.

The coronoid process of the coronoid bone is broad at its base, concave laterally, and extends and tapers dorsally to a rounded end (Tra 200-230). The height of the coronoid process is equal to the height of the lateral face of the dentary bone at its anteroposterior midpoint in *A. skoogi* (Lang 1991: CC23 (0)). Both the labial (Tra 184-197) and the dentary (Tra 185-204) processes of the coronoid extend anteroventrally. These two processes clasp the posterior portion of the dentary (Estes *et al.* 1988: C70 (0)). This state of having two processes clasp the dentary differs from that discussed by Estes *et al.* (1988), because there is more coronoid overlap on the medial surface of the dentary than on the lateral surface of the dentary in *A. skoogi* (i.e., the two processes clasping either side of the dentary are not of equal length). The dentary process is slightly concave laterally and conforms to the medial margin of the dentary bone (Estes *et al.* 1988: C69 (0)).

The splénial process lies along the medial side of the jaw (Tra 218-235). This process contacts the splénial anteroventrally and the surangular posteriorly, and contributes to the rim of the adductor fossa (mandibular foramen of Oelrich

(1956)). This fossa (Tra 244-268) is of moderate size in *A. skoogi* (Estes *et al.* 1988: C81 (0); Lang 1991: CC26, (0)), meaning the fossa is not expanded to accommodate the extension of the adductor mandibulae muscle and does not cover the entire length between the coronoid and the anterior margin of the retroarticular process. The short surangular process extends posteriorly to meet the dorsal margin of the surangular (Tra 236-244).

Angular.—The angular is present in *A. skoogi* as a paired element located on the ventral surface of the mandible (Tra 210-250, Fig. 12) (Estes *et al.* 1988: C72 (0)). This bone inserts into the posteroventral end of the dentary, and meets the splenial anterodorsally, the surangular dorsally, and the articular posteriorly. The anterior end of the angular extends anteriorly past the apex of the coronoid process of the coronoid bone, but does not reach the last tooth in the dentary (Lang 1991: CC25 (1)). The angular is a dorsoventrally-flattened bone that contributes to the ventral curve of the jaw. It is visible on both the lateral and medial sides of the mandible in *A. skoogi* (Lang 1991: CC24 (0)).

Along the ventromedial side of the bone, at about the mid-point of the bone, is a small foramen (Tra 224-227). This foramen, called the posterior mylohyoid foramen, transmits the posterior mylohyoid nerve (Oelrich 1956). The ventral surface of the angular also provides attachment for fibers of the mandibulohyoid I muscle (Oelrich 1956).

Surangular.—The surangular is a paired element that lies near the posterior end of the lower jaw (Tra 200-306, Fig. 11). Its tapered anterior end (Estes *et al.* 1988: C61 (0)) inserts into the posterior end of the dentary, forming a tongue-and-groove articulation. It also contacts the coronoid anterodorsally, the angular ventrally, and the articular posteriorly. The surangular encloses most of the posterior portion of

Meckel's canal, although the canal is open dorsally as it traverses this bone (Tra 244-270). Both the dorsal and lateral surfaces of the surangular are smooth, and each provides attachment for various muscles in the jaw (Oelrich 1956).

The surangular is pierced by two foramina. The anteriormost of the two is located just ventral to the coronoid process of the coronoid bone, is directed anteriorly (Tra 206-233), and is referred to here as the anterior surangular foramen (anterior supra-angular foramen of Oelrich (1956)). The other foramen is located more posteriorly near the suture between the surangular and the articular (Tra 274-278), and is referred to here as the posterior surangular foramen (posterior supra-angular foramen of Oelrich (1956)). Both of these foramina transmit cutaneous branches of the inferior alveolar nerve (Malan 1941; van Pletzen 1946; Oelrich 1956).

Articular.—The articular is a paired bone forming the posterior end of the mandible (Tra 223-353, Fig. 11). The articular meets the splenial anteriorly, the angular ventromedially, and the surangular dorsally and laterally. The articular has a thin, anteriorly-projecting process, a posterior condyle, and a posteriorly-directed retroarticular process (Oelrich 1956). The anteriorly-projecting process, called the prearticular process here (anterior process of Evans, *in press*) develops from dermal prearticular, while the remainder of the bone develops from the endochondral articular (Evans, *in press*).

The prearticular process of the articular is narrow at its most anterior point, which extends anterior to the posterior end of the coronoid bone near the anterior-most point of the surangular (Estes *et al.* 1988: C62 (0)). There is no prearticular crest on the medial edge of this process in *A. skoogi* (Estes *et al.* 1988: C73 (0)). This process broadens posteriorly toward its base, which is just anterior to the condyle.

This process forms the lateral margin of Meckel's canal. Just anterior to the adductor fossa, along the medial wall of the prearticular process of the articular, is a small foramen (Tra 238-241). In other lizards, this foramen transmits the anterior part of the chorda tympani nerve, a branch of cranial nerve VII (van Pletzen 1946; Oelrich 1956).

The condyle of the articular inserts into the ventral cotyle of the quadrate. The contact between these two elements connects the lower jaw to the rest of the skull. The condyle is triangular-shaped in transversal view with the apex of the triangle directed dorsally (Tra 283-305). This triangular projection, called the condylar facet (Oelrich 1956), fits into the dorsal surface of the ventral cotyle of the quadrate. In most squamates, the nature of the contact between the articular and the quadrate is the opposite of what is described here, with the ventral end of the quadrate having a condyle that inserts into a cotyle in the articular (Malan 1941). However, the condition in *A. skoogi* described here is also present in *Gerrhosaurus* (Malan 1941). Just posterior to the condylar facet, the articular becomes concave dorsally. The lateral and medial margins broaden slightly mediolaterally as they continue posteriorly toward the end of the bone (Estes *et al.* 1988: C78 (1)). Ridges surrounding the condylar facet provide attachment for the ligaments of the articular capsule (Oelrich 1956).

Posterior to the condylar facet is the posterior-most extension of the articular, called the retroarticular process (Tra 305-353) (Oelrich 1956). This process is inflected medially in *A. skoogi* (Estes *et al.* 1988: C75 (1)). The depressor mandibulae and cervicomandibularis muscles attach to the medial edge of this process (Evans, in press). The dorsal surface of this process has a deep pit or sulcus (Estes *et al.* 1988: C74 (0); Lang 1991: CC27 (1)). Both presence and absence of this pit previously were observed in *Cordyliformes* (Estes *et al.*

1988). On the dorsomedial side of the retroarticular process is a tiny foramen (Tra 311-316). This foramen transmits the posterior part of the chorda tympani nerve and the posterior condylar artery (Oelrich 1956). There is also a small flange on the posteromedial margin of the retroarticular process (Estes *et al.* 1988: C76 (1)). There is no angular process extending from the condyle in *A. skoogi* (Estes *et al.* 1988: C80 (0)), and no offset forming a waist to the process (Estes *et al.* 1988: C77 (0)). There is posterior twisting of the process in *A. skoogi* (Estes *et al.* 1988: C79 (0); Lang 1991: CC28 (1)).

Dentition.—The functional teeth of *A. skoogi* are present in the premaxilla (Tra 15-31, Figs. 6, 9), the maxilla (Tra 35-177, Figs. 6, 9), and the dentary of the lower jaw (Tra 28-186, Fig. 11). The teeth are pleurodont (Estes *et al.* 1988: C84 (0)), meaning that the teeth are superficially attached to the medial surface of the tooth-bearing bone (Estes *et al.* 1988). This condition is present in all other gerrhosaurids and cordylids (Edmund 1969; Estes *et al.* 1988). The marginal tooth replacement type in *A. skoogi* is similar to the 'iguanid' type (Estes *et al.* 1988: C85 (0)). In this condition, the replacement tooth develops along the lingual side of the exposed tooth in a large resorption pit. This condition is also the same found in all other gerrhosaurids and cordylids (Edmund 1969; Estes *et al.* 1988). There is no basal infolding of these marginal teeth in *A. skoogi* (Estes *et al.* 1988: C86 (0)).

There are seven tooth positions in the premaxilla, each with a functional tooth in the adult specimen of *A. skoogi*. The same number of positions was observed in certain members of *Gerrhosaurus*, *Zonosaurus*, *Cordylus*, *Platysaurus*, and *Pseudocordylus* by Edmund (1969). In *A. skoogi*, one tooth lies in the midline of the bone, and both the right and left sides have three teeth. All teeth in the premaxilla are unicuspid.

In the maxilla of *A. skoogi*, there are 14 tooth positions, all of which house functional teeth in the adult specimen. The number of tooth positions present in cordyliforms examined by Edmund (1969) ranged from 16 in *Zonosaurus ornatus* and *Gerrhosaurus major grandis*, to 25 in *G. vallidus*. In tooth positions 5, 6, 8, 11, and 13 (with position 1 being the most mesial in the maxilla and position 14 being the most distal), replacement teeth are visible just medial to the base of the current functional tooth. The number of cusps on the teeth in the maxilla varies. Maxillary tooth 1 has one cusp, teeth 2 through 4 each have two cusps, tooth 5 has three cusps, teeth 6 and 7 each have four cusps, teeth 8 through 12 each have five cusps, tooth 13 has four cusps, and tooth 14 has three cusps (Tra 35-178).

In the dentary of *A. skoogi*, there are 15 tooth positions. This number ranges from 18 to 28 in gerrhosaurids and cordylids examined by Edmund (1969). In the adult *A. skoogi* specimen, twelve of these positions house functional teeth in the left dentary and 13 house functional teeth in the right dentary. Only replacement teeth are in tooth positions 5, 7, and 12 in the left dentary, although replacement teeth are visible just medial to the base of the functional teeth in positions 10, 13, and 15. In the right dentary, only replacement teeth are present in positions 5 and 7, while positions 10, 12, 13, and 15 have replacement teeth coming in medial to the base of the functional teeth. Like in the maxilla, the number of cusps on teeth in the dentary varies. In each dentary, teeth 1 through 5 each have one cusp, tooth 6 has two cusps, teeth 7 and 8 each have three cusps, teeth 9 and 10 each have four cusps, and teeth 11 through 15 each have five cusps.

ONTOGENETIC VARIATION IN *ANGOLOSAURUS SKOOGI*

Ontogenetic variation in the cranial osteology of squamates previously has been discussed in

the literature for only a few taxa (e. g., de Queiroz 1987; Barahona & Barbadillo 1998; Barahona *et al.* 1998, 2000; Evans, in press). Knowledge of such variation is relevant to any morphological or systematic study, particularly when dealing with fossils in which the age of the individual may be difficult to determine. A discussion of the ontogenetic variation within *A. skoogi* observed in this study is limited due to a sample size of only two specimens, including one adult and one juvenile. However, there are morphological differences between the two scanned specimens. These differences permit some preliminary comments on the ontogenetic variation in *A. skoogi*. Specific characters and features known to vary ontogenetically among iguanine and lacertid lizards (de Queiroz 1987; Barahona & Barbadillo 1998; Barahona *et al.* 1998) that also occur in *A. skoogi* are discussed here.

The overall skull shape differs between the adult and the juvenile specimens of *A. skoogi*. In the juvenile, the length of the skull from the tip of the snout to the posterior end of the skull is shorter, and the width of the skull is broader laterally (Fig. 13). The characteristic shovel-head shape of the adult *A. skoogi* is not as pronounced in the juvenile, and the snout is not as depressed dorsoventrally (Fig. 14).

All bones are present in both the adult and the juvenile; however, the degree of ossification in these elements and in the osteoderms is less in the juvenile. During ontogeny, there is a definite sequence of ossification within the skull. The bones of the snout region are the first to ossify, followed by the skull roof and posterior region of the frontal. Then, the anterior region of the parietal ossifies, followed by the simultaneous ossification of the remainder of the parietal and neurocranium (Barahona & Barbadillo 1998; Maisano 2001). As noted in the juvenile lacertids studied by Barahona & Barbadillo (1998), the anterior and central regions of the parietal, the posteromedial area

of the frontals, the facial process of the maxilla, the anterior portion of the nasal, the maxillary process of the palatine, and the rostrum of the parasphenoid are incompletely ossified in the juvenile *A. skoogi*. This incomplete ossification results in a large parietal fontanelle in the juvenile specimen of *A. skoogi*, and in other juvenile squamates (Maisano 2001).

The joints and contacts between many of the bones in the juvenile are separated by gaps. In lacertids, these gaps in juvenile skulls are filled with growing membranous connective tissue (Barahona & Barbadillo 1998). In the adult specimen of *A. skoogi*, the frontals meet medially throughout their entire length, while in the juvenile, the pair is separated by a gap posteriorly (Fig. 13). There is a gap between the premaxillary process of the maxilla and the premaxilla in the juvenile, whereas these two elements are in contact in the adult *A. skoogi*. There is more space between the cotyle of the articular and the condyle of the quadrate in the juvenile than in the adult specimen. In the mandible, the anterior end of the splenial is reduced in the juvenile, so a larger portion of the Meckelian fossa is open medially in the juvenile than in the adult *A. skoogi*.

In the braincase of the juvenile, the basicranial fenestra (an opening between the posterior margin of the sphenoid and the anterior margin of the basioccipital) is open, the bones surrounding the semicircular canals are incompletely ossified, and the distal end of the basiptyergoid process remains cartilaginous and does not contact the medial surface of the quadrate process of the pterygoid as closely as in the adult (Fig. 15). In large-bodied iguanine lizards, the paired orbitosphenoid bones are crescent-shaped in lateral view in early stages of ontogeny. During development, the orbitosphenoid extends processes anterodorsally, posterodorsally, and posteroventrally, becoming more triradiate in lateral view. In the adult stage, the anterodorsal process bifurcates,

resulting in a quadriradiate bone in lateral view (Oelrich 1956; de Queiroz 1987; Evans, in press). In both the adult and the juvenile specimens of *A. skoogi*, the orbitosphenoid is crescent-shaped and concave posteriorly in lateral view (Fig. 12), and lacks all but the posteroventral process found in adult, large-bodied iguanines. The stapedial shaft in the juvenile is broader throughout its length than in the adult, and the lateral end of the stapes is incompletely ossified in the juvenile *A. skoogi*.

The dentition of the premaxilla, maxilla, dentary, and pterygoid in the juvenile differs from that in the adult (Fig. 15). In the premaxilla, both adult and juvenile have seven tooth positions, but the medial functional tooth is absent in the juvenile.

In the maxilla, the adult has 14 tooth positions, whereas the juvenile has only twelve. Fewer teeth in the tooth row of a juvenile reptile compared to that of an adult is not uncommon; in one year, *Iguana* juveniles can add several tooth positions in the posterior end of the tooth row (Edmund 1969). In both the right and left maxillae of the juvenile, all positions are filled with nine functional teeth and three replacement teeth. The number of cusps per tooth in the juvenile differs from that in the adult, but is likely due to the reduced number of teeth in the juvenile, thus the tooth positions in the adult and the juvenile do not coincide. The cusps in the adult were discussed above. In the juvenile, tooth 1 has one cusp, teeth 2 and 3 each have two cusps, tooth 4 has three cusps, teeth 5 through 7 each have four cusps, teeth 8 through 11 each have five cusps, and tooth 12 has two cusps.

There are 14 tooth positions in the dentary of the juvenile, whereas the adult has 15 positions. In both the right and left dentaries of the juvenile, there are nine functional teeth and five replacement teeth filling these positions. As in the maxilla, the reduced number of tooth posi-



Figure 13. Dorsal view of the skull of juvenile *A. skoogi* (CAS 206977).



Figure 14. Lateral view of the skull of juvenile *A. skoogi* (CAS 206977).

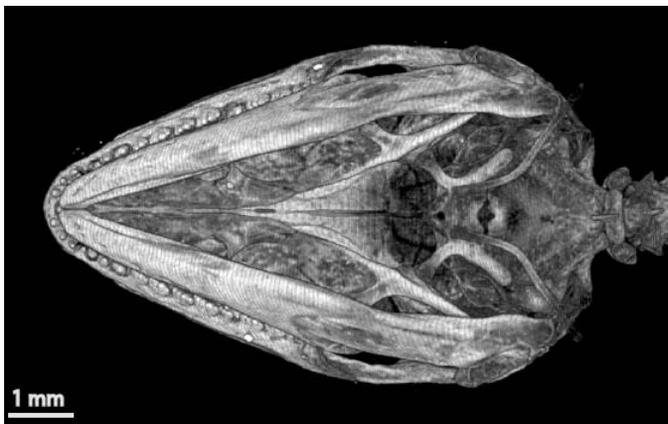


Figure 15. Ventral view of the skull of juvenile *A. skoogi* (CAS 206977) with jaw articulated.

tions in the juvenile is the likely cause for the difference in number of cusps per tooth. In the juvenile, teeth 1 through 5 each have one cusp, tooth 6 has two cusps, teeth 7 and 8 each have three cusps, teeth 9 and 10 each have four cusps, and teeth 11 through 14 each have five cusps.

On the ventral surface of the pterygoids in both the adult and juvenile, pterygoid teeth are present. In lacertids, there may be a single row of teeth in juveniles and multiple rows arranged laterally in adults (Barahona *et al.* 1998). However, both the adult and juvenile specimens of *A. skoogi* have only a single row of pterygoid teeth. In the adult, there is a single row of three teeth, running anterior to posterior, down each pterygoid. In the juvenile, there is a single row of two teeth on the ventral surface of each pterygoid.

DISCUSSION

With these new morphological data of *A. skoogi*, previously published characters (Estes *et al.* 1988, Lang 1991) were rescored and in some cases character states defined by these previous authors were changed. These changes, along with new characters found in *A. skoogi* and other disarticulated specimens of cordyliforms, were used to test current hypotheses regarding relationships both within Gerrhosauridae and among the closely related families Cordylidae and Scincidae (Nance 2003). This preliminary analysis supports *A. skoogi* as the most basal member of Gerrhosauridae (Fig. 16), not just of mainland African gerrhosaurids as in Lang (1991). These results also differ from a recent analysis based on mitochondrial DNA (Lamb *et al.* 2003), which suggests the genus *Angolosaurus* should cease to exist and *A. skoogi* should be renamed *Gerrhosaurus skoogi*. This analysis was based on mitochondrial DNA, which acts as a single gene in phylogenetic studies and therefore represents a small

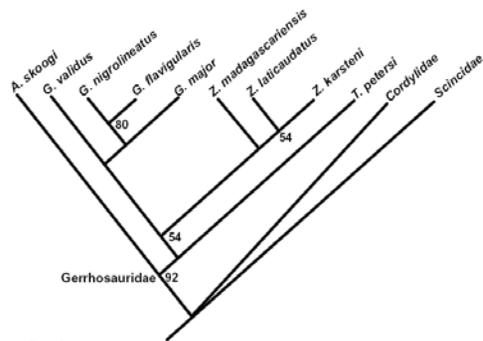


Figure 16. 50% majority rule consensus tree depicting all 48 equally-parsimonious trees (208 steps each), depicting hypothesized gerrhosaurid relationships based on cranial osteology data. Bootstrap support greater than 50% indicated at nodes.

portion of an organism's evolutionary history (Avice 2004). While the hypothesized relationships (Fig. 16) based on the cranial osteology described here have low bootstrap support, they nonetheless warrant the examination of more specimens, inclusion of more taxa, and more character data to further resolve relationships within these clades (Nance 2003).

Poor museum representation of rare or endemic taxa is a current problem in squamate systematic studies. For taxa such as *A. skoogi*, the few specimens that are available for study are largely preserved in alcohol. This is because much of squamate systematics is based on scale counts. In light of the current phylogenetic hypothesis for all of Squamata, which is largely based on the results of Estes *et al.* (1988), the discovery of new character data seems especially important now. Similar conclusions previously were made based on the examination of detailed cranial osteology of other taxa (e.g., Rieppel & Crumly 1997; Rieppel 1999). Although disarticulated cranial material is poorly represented in museum collections, this type of material is an excellent source of morphological data. Disarticulating the cranium and braincase of a specimen permits unob-

structed study of articulations and contacts between individual elements, foramina and processes associated with them, and detailed morphology of the individual elements that is otherwise hidden in articulated material. This detailed morphology provides phylogenetically informative data. This study using HRXCT to study the rare gerrhosaurid lizard, *A. skoogi*, demonstrates the wealth of detailed osteology that is attainable with this technology, as well as the utility of osteology in squamate systematics. Hopefully the new data provided by this study will help contribute to the ultimate goal of attaining a well-supported phylogeny of Cordyliformes, increase the use of detailed cranial osteology in phylogenetic systematics, and provide further insight into squamate morphology.

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