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The Osteoderms and Palpebral in *Lanthanotus borneensis* (Squamata: Anguimorpha)

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Lanthanotus borneensis is an enigmatic species of anguimorph lizard known only from the Malaysian state of Sarawak on the island of Borneo, southeast Asia. It is the sole living representative of Lanthanotidae, a clade that may also include *Cherminotus longifrons* from the Cretaceous of Mongolia (Borsuk-Bialynicka, 1984; Gao and Norell, 1998). The great majority of anguimorph species are extinct and thus known only from skeletons (Norell and Gao, 1997; Gao and Norell, 1998, 2000). Although the phylogenetic position of *Lanthanotus* among extant anguimorphs has remained relatively stable since the publication of McDowell and Bogert's (1954) monograph, knowledge of the character states it possesses remains important for the determination of character state distributions within Anguimorpha.

Lanthanotus is rarely collected, probably because it is nocturnal, fossorial, and semiaquatic (Harrisson, 1962; Manthey and Grossman, 1997). Few specimens exist in collections worldwide, and skeletons are extremely rare. As a result of limited access to specimens, many phylogenetic analyses that include this species relied upon the same specimen (REE 1445, collection of Richard Etheridge, San Diego State University) to score osteological characters (e.g., Pregill et al., 1986; Estes et al., 1988; Norell and Gao, 1997; Gao and Norell, 1998).

This problem is not unique to *Lanthanotus*. Although skeletal anatomy has long been an important source of evidence for phylogenetic analyses of squamates (e.g., Cope, 1864; Camp, 1923; Estes et al., 1988), there is a dearth of skeletal material available for most species. The primary impediment to increasing this resource has been that it requires destructive sampling, with the coincident potential loss of useful anatomical data. These data include not only the external morphology upon which species identification rests but also skeletal elements that may be isolated in soft tissues, such as osteoderms.

High-resolution X-ray computed tomography (HRCT) provides a solution to this problem. HRCT uses the differential attenuation of X-rays as they pass through an object to detect density variation within that object, producing a series of slices of finite thickness that represent a continuous three-dimensional

digital map of the object's internal and external structure (Rowe, 1996; Denison et al., 1997). Because HRCT can resolve features on the scale of tens of microns (Denison et al., 1997), it is superior to conventional X-radiography, which previously was used to evaluate skeletal morphology in alcoholic squamate specimens (e.g., Haines, 1969; Renous-Lécuru, 1973), including *Lanthanotus* (Boulenger, 1899; McDowell and Bogert, 1954). An HRCT scan of the head of an intact *Lanthanotus* immediately revealed two features that previously were unknown in this species: the full extent of osteoderms surrounding the skull; and the presence of a palpebral bone.

The Yale Peabody Museum specimen of *Lanthanotus* (YPM 6057) was scanned at the High-Resolution X-ray CT Facility at The University of Texas at Austin. The alcoholic specimen was scanned obliquely on the ultra high resolution subsystem for a total of 204 slices. Slice thickness and interslice spacing of the scan equaled 0.09 mm, yielding an image resolution of 0.07 mm/pixel. The resulting HRCT data were volumetrically rendered in three dimensions and obliquely resliced along the coronal axis, for a total of 364 slices with an interslice spacing of 0.07 mm, using VoxBlast® 1.3 (VayTek Inc., Fairfield, IA). VoxBlast® was also used to render the flesh transparent by partitioning the HRCT data according to density. All resulting images were optimized and/or colorized in Photoshop® 5.0 (Adobe Systems Inc., San Jose, CA).

Osteoderms.—Osteoderms in *Lanthanotus* were first reported based on an X-radiograph (McDowell and Bogert, 1954: plate 4) that suggested they were confined to three rows on the temporal region of the head and a few rows on the neck, all corresponding to the enlarged tubercular scales. However, the HRCT scan reveals that the distribution of osteoderms is far more extensive (Figs. 1–2). The veil of osteoderms surrounding the skull reaches anteriorly to the external nares, dorsolaterally into the loreal region, and anteroventrally to the midpoint of the dentary. Each non-compound osteoderm, or cluster of osteoderms, corresponds to a granular or tubercular scale, but not every scale contains an osteoderm (Figs. 1A, C, 2A). Because the cephalic scales of *Lanthanotus* are not differentiated into loreals, labials, etc., the distribution of osteoderms around the skull will be described relative to gross head morphology and the underlying cranial bones.

On the dorsal aspect of the head (Fig. 1A–B), osteoderms are concentrated in three areas: anterior to the frontoparietal suture and in each of the temporal regions. The array anterior to the frontoparietal suture approximates a triangle, with the anterior apex extending almost to the midpoint of the ascending process of the premaxilla, and the posterior apices extending almost to the lateral corners of the postorbitofrontals. The arrangement of osteoderms within this triangle appears ordered, with the smallest osteoderms at the periphery following the margins of the orbits and external nares. The three largest osteoderms within this triangle are transversely aligned, one overlying the midline contact of the frontals and one overlying each of the prefrontals. Small patches of minute osteoderms, disjunct from the triangle, are pre-

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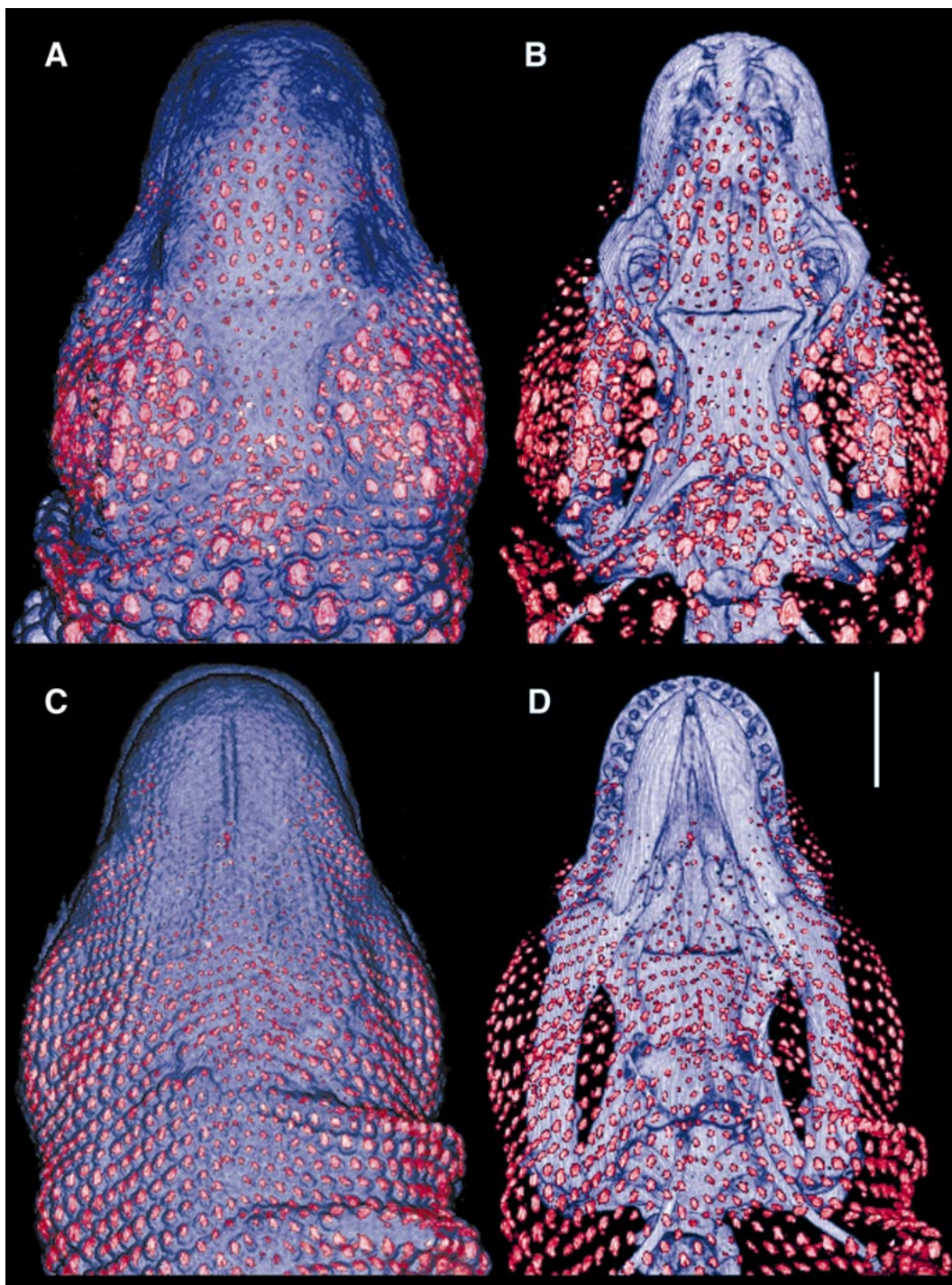


FIG. 1. Three-dimensional volumetric reconstructions of *Lanthanotus* from HRCT data. (A) Dorsal and (C) ventral views, rendered with flesh, showing position of osteoderms in skin; (B) dorsal and (D) ventral views, with flesh rendered transparent, showing relationship of osteoderms to skull. Bar = 5 mm.

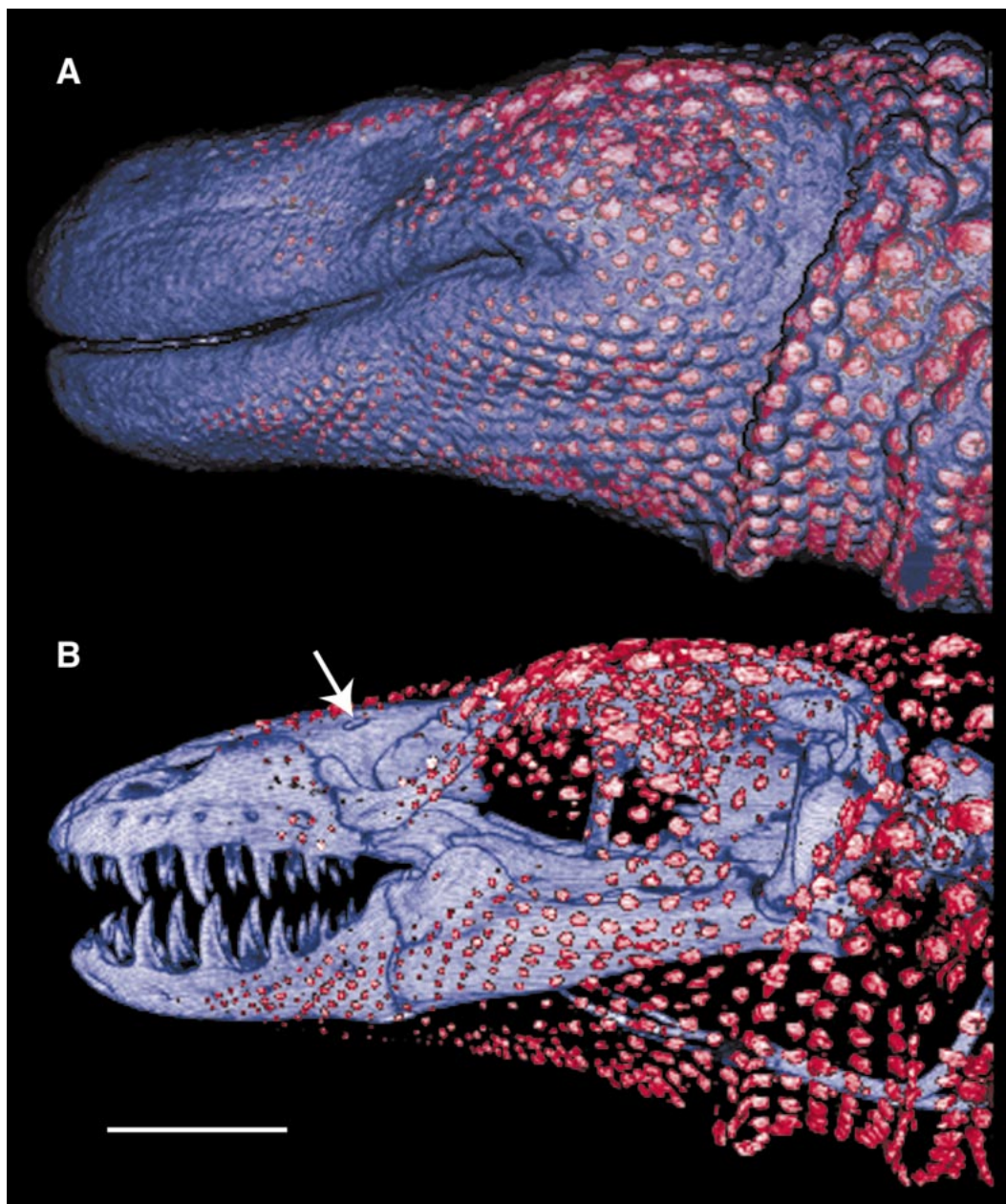


FIG. 2. Three-dimensional volumetric reconstructions of *Lanthanotus* from HRCT data. (A) Lateral view, rendered with flesh, showing position of osteoderms in skin; (B) lateral view, with flesh rendered transparent, showing relationship of osteoderms to skull, and the palpebral bone (indicated by arrow). Bar = 5 mm.

sent on the dorsolateral aspect of the head, overlying the posterior half of the facial process of the maxilla.

Osteoderms are more highly concentrated in the temporal regions, arrayed roughly concentric to the bulges of the temporal musculature (Figs. 1A–B, 2). They extend anteroventrally around the orbit to the lateralmost corner of the jugal, are diminished in size posteriorly where the temporal bulge meets the neck,

and are continuous with the ventral osteoderms along a path between the coronoid process and the quadrate. The largest osteoderms in each temporal bulge are those observed by McDowell and Bogert (1954), in three rows corresponding to the enlarged tubercular scales. The most dorsal row (Fig. 1B), consisting of seven to eight osteoderms, arcs lateral to the fused parietals, extending anteriorly to the jugal and pos-

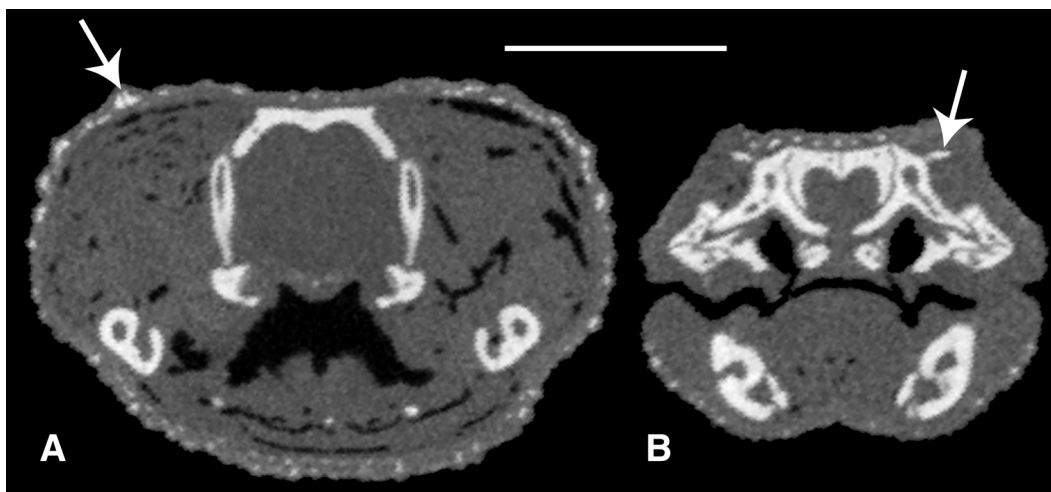


FIG. 3. Coronal slices from oblique reslicing of original HRCT data of *Lanthanotus*. (A) Slice #232 through temporal region, showing canal in osteoderm (indicated by arrow); (B) slice #132 through orbital region, showing position of palpebral (indicated by arrow) deep to osteoderms. Bar = 5 mm.

teriorly past the anterior end of the supratemporal. The next row, consisting of four osteoderms, includes the largest osteoderms on the head. They are arrayed anteroposteriorly along the midline of the temporal bulge in dorsal view (Fig. 1A), extending from just anterior to the position of the epipterygoid posteriorly to the anterior point of the supratemporal (Fig. 2B). The third row of osteoderms in the temporal region is actually doubled, with each parallel line consisting of approximately three osteoderms: in dorsal view, they lie at the lateralmost edge of the temporal bulge (Fig. 1A); in lateral view, they extend from just anterior to the level of the epipterygoid posteriorly to the wall of the braincase (Fig. 2B). The skin between the rows of enlarged osteoderms on the temporal bulges is partly filled with smaller osteoderms.

Other than in these three concentrated areas, osteoderms are largely absent from the dorsal aspect of the head, especially above the frontoparietal suture and the anterior end of the fused parietals (Fig. 1B). They become more concentrated posteriorly between the temporal bulges, near the posterior margin of the parietal table. This field of osteoderms sweeps posteriorly into the nuchal region, spreading laterally around the posterior margin of the temporal bulges. These smaller osteoderms give way in the neck to larger osteoderms that, as in the temporal region, correspond to the enlarged tubercular scales (Fig. 1A).

In ventral view (Fig. 1C–D), minute osteoderms extend anteriorly along the midline just past the anterior limit of the interpterygoid vacuity. The osteoderms become more substantial at the level of the anterior-most extent of the pterygoids. From there posteriorly as well as laterally, they become progressively larger. They are evenly spaced, in laterally arrayed rows, posteriorly into the nuchal region.

In lateral view (Fig. 2A–B), osteoderms are absent from the anterior end of the snout, the labial margins posteriorly past the coronoid process, and the auricular region. The osteoderms on the lateral aspect of the lower

jaw are relatively evenly distributed, extending anteriorly just past the midpoint of the dentary, and showing a gradual increase in size posteriorly, with the largest osteoderms on the lateral aspect of the neck.

The osteoderms in *Lanthanotus* range from about 0.07 to 1.20 mm in maximum dimension. They are fragmented and thickened (not thin and platelike, contra Pregill et al., 1986; Norell and Gao, 1997; Gao and Norell, 1998), reaching a maximum thickness of about 0.50 mm. Penetrating canals are discernible within the largest osteoderms (Fig. 3A); however, the data are not of high enough magnification to permit the description of these canals.

Palpebral.—The palpebral, a neomorph bone situated above the upper eyelid at the anterodorsal corner of the orbit (Peters, 1964), occurs in lacertids, scincoids, and anguimorphs (Estes et al., 1988). The HRCT scan reveals the presence of this bone in *Lanthanotus* (Fig. 2B) although it was previously thought to be absent (McDowell and Bogert, 1954; Pregill et al., 1986; Estes et al., 1988; Norell and Gao, 1997; Gao and Norell, 1998; Lee, 1998). The palpebral is reduced in size, roughly ovate in shape, and lies isolated in the dermis overlying the upper lid. Its position deep to the osteoderms is most apparent when the head is viewed in cross-section (Fig. 3B).

Discussion.—Even when the skeletonization of specimens is permitted, the skin and flesh are removed in the process. Thus, ossified structures isolated in soft tissues are rarely recovered. This, combined with the relatively poor resolving power of conventional X-radiography, probably accounts for why the palpebral and the full extent of cranial osteoderms in *Lanthanotus* previously were overlooked.

As in anguimorphs ancestrally (Gauthier, 1982), the osteoderms in *Lanthanotus* are present beneath virtually every scale and are more prominent dorsally than ventrally, on the head. *Lanthanotus* is noteworthy in that osteoderms are absent over much of the snout, along the margins of the mouth, and in the auricular

region. Osteoderms are reduced or absent in the skin superficial to kinetic regions of the skull, including the frontoparietal suture, the intramandibular joint, and the streptostylic quadrate. This suggests that osteoderms might impede cranial kinesis and auditory reception if better developed in these areas. The spatially complex pattern of cephalic osteoderms in *Lanthanotus* implies a potential for more phylogenetic insight to be gained from osteoderm character states than the limited presence/absence and thin/thick character states employed in most analyses (e.g., Pregill et al., 1986; Estes et al., 1988; Norell and Gao, 1997; Gao and Norell, 1998).

The canals penetrating the osteoderms of *Lanthanotus* are similar to those in the "free portion" (Strahm and Schwartz, 1977) of the osteoderms of anguids and gerrhosaurids; in these taxa, the canals contain nerves and vessels as well as pigment cells (Schmidt, 1912; Strahm and Schwartz, 1977; Richter, 1994). The distribution and function of osteoderm canals in other squamate clades requires further investigation.

The discovery of a palpebral in *Lanthanotus* suggests that this anguimorph synapomorphy (Estes et al., 1988; Gao and Norell, 1998) was lost only in *Heloderma*. However, its purported absence in *Heloderma* may be an artifact of preparation practices and rarity of specimens, as was the case with *Lanthanotus*. Consequently, applying HRCT to an intact *Heloderma* may reveal the presence of a reduced, free-floating palpebral.

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