

THE OSTEODERMS OF THE AMERICAN ALLIGATOR AND THEIR FUNCTIONAL SIGNIFICANCE

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ABSTRACT: The segmental arterial supply to the osteoderms of *Alligator mississippiensis* is described. Each transverse row of osteoderms is served by a single median artery that bifurcates in the midline. Typical osteoderm morphology is also described. A role in regulation of body temperature is proposed as one function for the osteoderms of *A. mississippiensis*.

Key words: Reptilia; Crocodylia; Alligatoridae; *Alligator*; Osteoderms; Temperature regulation; Arteries

CROCODYLIAN osteoderms are abundant in the fossil record and they are found in all living Crocodylia. This dermal armor is highly developed in dorsal longitudinal rows with the cervical rows being distinctly separated from those of the back region. The dorsal series is continuous over the sacrum into the dorsum of the tail and ends at a variable distance anterior to the end of the tail. The caudal termination of dorsal armor occurs at the end of the caudal epaxial musculature. Palpebrals are also a part of the dorsal armor with 1-2 ossifications in the upper eyelid being a common pattern. The vertical earflaps do not contain ossifications.

Of the living genera, *Caiman*, *Melanosuchus*, and *Paleosuchus* have ventral armor. A complete caudal sheath of dermal bone is present in *Caiman* and *Paleosuchus*. Several extinct taxa possessed ventral and appendicular armor. The highly developed armor in early Crocodylia such as *Protosuchus* and its presence in other archosaurs suggest that this is a primitive characteristic for Crocodylia (Colbert and Mook, 1951). It is found in Mesosuchian forms such as *Goniopholus*. Eusuchian dermal armor is probably derived from mesosuchian ancestors. Non-crocodylian archosaurian reptiles possessed dermal armor with the exception of most saurischian dinosaurs and pterosaurs. Spectacular examples of dermal armor are presented by stegosaurs and ankylosaurs. The occurrence of osteoderms in other reptilian groups is summarized by Romer (1956). The armor in liv-

ing squamate reptiles and *Sphenodon* seems to be a secondarily derived condition.

This report is concerned with observations on the dermal armor of *Alligator mississippiensis* that were made during research on the epaxial musculature.

MATERIALS AND METHODS

Two specimens of *A. mississippiensis* were dissected at Queens College, Flushing, New York. They were both obtained from Rockefeller Refuge, Grand Chenier, Louisiana. One specimen (an adult male) was 2.05 m in length. The second specimen (a juvenile of undetermined sex) was 41 cm in length (snout to occipital condyle = 6.5 cm). Skeletal material from the same locality was also examined.

Both specimens were dissected when fresh. The larger one was frozen and thawed several times between observations. The juvenile was preserved in 70% alcohol after initial skinning and dissection. The adult was grossly dissected and the juvenile was dissected with a magnification of 7 \times .

For purposes of muscle dissection and to preserve the relationships of various axial fascia compartments, the skin flanking the thoracic and abdominal regions was carefully reflected dorsally beginning with the lateral extent of the ventral scales.

RESULTS

The dorsal horny scales correspond to deeper osteoderms that cover the epaxial

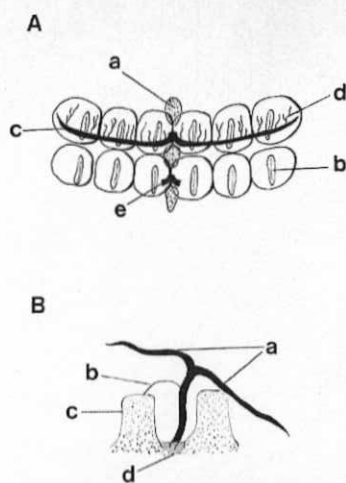


FIG. 1.—(A) Diagrammatic dorsal view of two transverse rows of osteoderms and three neural spines. The osteoderms are drawn transparent to show the arterial supply to their ventral surface. a = dorsal surface of the anterior neural spine of the three shown; b = longitudinal dorsal keel of an osteoderm; c = left lateral branch of the dorsal median artery; d = nutrient branch to an osteoderm; e = dorsal median artery with both lateral branches cut. Note the diagonal course taken by the lateral branches as they bifurcate beneath the medial pair of osteoderms. (B) A dorsal median artery is shown emerging between two adjacent neural spines and giving off its branches. a = left and right lateral branches; b = small branch to neural spine that is anterior to dorsal median artery; c = neural spine (stippled); d = interneural ligament. Anterior is to the left; the osteoderms are not shown.

musculature. The osteoderms of the back and tail are firmly attached to deep fascia in contrast to the skin over the neck and belly where the attachment is loose. The complex intermuscular myosepta have tendinous attachments to the undersurface and edges of each dermal plate.

After the skin was reflected from the sides, it was carefully separated from the body

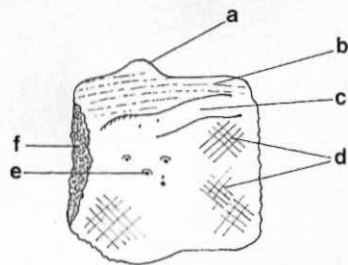


FIG. 2.—Ventral surface of an osteoderm. Anterior is toward the bottom of the page, medial is to the left. a = posterior end of dorsal keel projecting beyond edge; b = thin transverse ridges; c = groove for lateral branch of dorsal median artery; d = surface markings of tendinous deep fascia; e = nutrient foramen; f = rugose surface of medial side.

wall up to the dorsal midline where the arterial distribution to the transverse rows of osteoderms could be observed. A series of unpaired midsagittal arteries was found between the tips of successive neural spines. These arteries are bordered laterally by the transversospinalis system of muscles. The name, dorsal median artery, is applied to each member of this series. Due to the dense tough condensations of connective tissue binding the osteoderms to the deep fascia, these arteries are easily torn off and overlooked when the skin is removed.

At the level of the neural spine tips, a branch of the dorsal median artery serves the neural spine anterior to itself and enters the expanded dorsal neural spine surface. The dorsal median artery then bifurcates left and right, to supply one entire transverse row of osteoderms. The left and right lateral branches follow the posterior ventral surface of the scale row occupying a groove in the posterior edge of each osteoderm (Figs. 1, 2). Each osteoderm transverse row lies in line with the posterior half of one neural spine and the anterior half of the next caudal spine.

Each dorsal median artery emerges

through the deep fascia between successive neural spines in a position that corresponds to the middle of the anterior-posterior length of an osteoderm row. As each transverse row of osteoderms is associated with a single segmental artery and each artery also supplies the vertebra anterior to itself, then each transverse osteoderm row must be associated with the anterior vertebra of the pair overlapped by the row.

The lateral branches of the dorsal median artery give rise to smaller nutrient branches that extend anteriorly in the individual osteoderms of their row. Bifurcation of the artery occurs before the artery reaches the posterior edge of the scale row resulting in a diagonal groove on the deep surface of the two medial osteoderms.

The series of dorsal median arteries is interrupted at the level of the shoulder region where there is a tough condensation of connective tissue associated with the attachments of the trapezius and cervical musculature. This is the region where the dorsal armor and cervical armor are distinctly separated. In the neck the dorsal median arteries travel through the median intermuscular septum and supply the cervical osteoderms up to the occiput. The two major longitudinal rows of cervical osteoderms rest on the entire length of the transversospinalis capitis muscle.

Tracing the dorsal median arteries to locate their connection to the main arterial system was not successful. The arteries were followed as far as the base of the neural spines where they were lost between the ossified interneural ligaments.

Osteoderms of an adult alligator are more or less flat with a pitted sculptured dorsal surface. The pitting gives the dorsal surface a trabecular appearance. There is usually a well developed longitudinal keel near the center of the osteoderm. Lateral osteoderms have the longitudinal keel displaced medially. The pits and grooves radiate away from the keel. The lateral and medial edges of the osteoderms are roughened having an almost splintered appearance. This

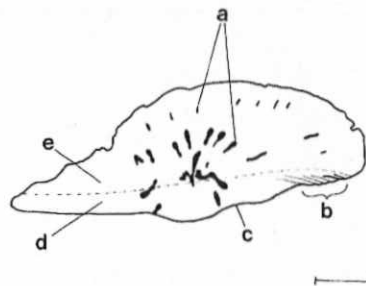


FIG. 3.—Longitudinal section of an osteoderm. The top of the page is dorsal, anterior is to the left. a = canals for arterioles; b = ridges on posterior ventral surface, continued inside bony matrix as dense lamellae below the dashed line; c = groove for lateral branch of dorsal median artery; d = dense compact layer of bone ventral to dotted line; e = loosely laminated vascularized bone, dorsal to dotted line. Scale = 1 cm.

is a result of fibrous attachments between osteoderms in a transverse row. The terminal members of a transverse row have smoothed, rounded lateral edges, but roughened medial edges.

The ventral surface of each osteoderm is divided unequally into anterior and posterior areas by the transverse groove of the lateral branch of the dorsal median artery. The two-thirds of the surface anterior to the artery is smooth and pierced by 4-5 nutrient foramina in its center. Occasionally criss-cross markings can be seen in the bone on this surface. These markings represent the former attachment sites of deep fascia. Posterior to the arterial groove the surface slopes dorsally and is crossed by thin weakly developed transverse ridges (Fig. 2).

A longitudinal section of an osteoderm (Fig. 3) reveals a flat ventral plate of dense laminae covered dorsally by more vascularized bone with a weaker layering. The laminae correspond to the posterior transverse surface ridges. The osteoderm is riddled throughout with a tangled mesh of canals presumably housing a rich vascular supply in the living animal.

with the reduction of the necessity for rapid thermal adjustments? They lived in a relatively stable environment where temperature fluctuations were mild and regulation of heat flow and body temperature was not a great problem.

It is possible that in large semiaquatic reptiles, basking is related to the presence of dermal armor. Examination of any living crocodilian reveals that the typical sculptured armor is present only on surfaces which would be available for absorption of solar radiation (not ambient heat). These surfaces are exposed to sunlight during basking on land and also while the animal is partly submerged.

Coldiron (1974) pointed out that sculpturing is a structural solution to stress and strain on bone. With this in mind it is interesting to observe that bones which sank below the skin surface during phylogeny of the Crocodylia (i.e., postorbital bar, quadrate, posterior half of quadratojugal) lost the pitted sculpturing, although these same bones retain about the same structural function. In addition, the extremely broad and flat palate of *A. mississippiensis* is not strengthened by bony sculpturing as are the corresponding bony parts on the external surfaces overlying the snout. There is actually no apparent structural need for the sculpturing of the osteoderms themselves as the very dense bone they are made of is at least as thick as the bones of the skull. The only forces the osteoderms could be experiencing stem from the ventral tendinous attachments. The osteoderms do not experience the same stresses which apply to the sculptured bones of the skull that are specialized for feeding, yet they are similarly sculptured.

If dermal armor is used for heat transfer and thermoregulation, how could this be carried out? As noted earlier, the dense bone of the osteoderm is riddled with small holes which are presumably filled in life with arterioles. Any heat absorbed by the surface of the osteoderm will be rapidly transmitted throughout the entire osteo-

derm via its compact mineral composition. The arterioles in the osteoderms could readily pick up the absorbed heat and carry it to other parts of the body. To control heat absorption, simple vasoconstriction could reduce osteoderm blood flow and thereby reduce heat transfer rate.

An additional advantage conferred by retaining arterioles in osteoderms is that many layers of blood vessels could be brought to the animal's upper surface without being in the least danger of destruction. In other words, dense bone affords protection to the arterioles which could not otherwise exist there.

The process of heat transfer could also work in a reverse way as a radiating device or as insulation against heat loss. If ambient temperature creates a heat drain, then slowing of peripheral blood flow would allow the osteoderm (and skin) to act as an insulator. I demonstrated that blood does flow from the osteoderms to at least the ventrum by injecting an osteoderm with methylene blue dye. A short time after injection (using a fresh unpreserved specimen) the dye traveled into the arterioles in the flanking skin eventually reaching the ventral scales.

Farlow et al. (1976) have discussed a similar hypothesis involving the peculiar structure of stegosaurian dermal plates. They suggested that osteoderm plates were heat radiators that were responsive to fluctuations in ambient heat and structured to stabilize the animal's body temperature. Although stegosaurian dermal plates might not be strictly homologous to crocodilian osteoderms, there may be analogy of function. It is also possible that the plates of the stegosaurs could have served as heat absorbers. In addition to vasoconstrictive control, the stegosaur plates could have been movably controlled by simple modification of the epaxial musculature. Because the epaxial myoseptal tendons insert on the osteoderms in Crocodylia, it is reasonable to assume that the same condition might have occurred in stegosaurians.

In conclusion, osteoderms are probably a mechanism for controlling absorption of radiant heat in addition to being capable of heat radiation and insulation. It is now becoming apparent that crocodylians regulate their body temperature within well defined limits even to the point of maintaining gradients between body and head (Johnson, 1974). In addition to behavioral heat regulation, a mechanism using osteoderms as a heat transfer device is proposed. Heat flow via osteoderms can be activated and physiologically controlled through hormones and the mediation of the autonomic nervous system.

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REFERRAL OF THE FOSSIL LIZARD *SCELOPORUS HOLMANI* (LATE PLEIOCENE OF NORTH-CENTRAL KANSAS) TO THE GENUS *PHRYNOSOMA*

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ABSTRACT: *Sceloporus holmani* from the late Pliocene of north-central Kansas, USA, is referred to the genus *Phrynosoma*. The fossil record of *Phrynosoma* is discussed.

Key words: Reptilia; Sauria; Iguanidae; *Phrynosoma holmani*; Pliocene; Kansas

SCELOPORUS holmani (Iguanidae) was first described from the Pliocene (late Blancan Land Mammal Age) White Rock Fauna of north-central Kansas by Eshelman (1975). Reexamination of the paratype (UMMP V61390; right dentary) indicates that this lizard is a horned lizard and should be placed in the genus *Phrynosoma*. The original description and illustration, locality

data, known distribution, and etymology are presented in Eshelman (1975). Measurements and a description of UMMP V61390 are also in Eshelman (1975). The fossil was compared with reference skeletons in the collection of T. R. Van Devender, including various *Sceloporus*, all United States species of *Phrynosoma*, and several Mexican species (*P. asio*, *P. ditmarsii*, *P. orbiculare*).

Phrynosoma holmani (Eshelman) comb. nov.

Amended diagnosis.—A species of *Phrynosoma* with the following unique combination of characters: (1) primitive tall teeth with transversely expanded tooth bases and reduced tricuspid crowns, (2) dentary very deep, especially anteriorly, (3) ventral surface of dentary flattened, (4) ventrolateral surface of dentary strongly angled, (5) well developed depressions of muscle scars on anterior end of ventral surface and the dorsolateral surface of the posterior end of dentary, (6) Meckel's canal not fused, constricted in middle of dentary, and medially located on anterior end of dentary, and (7) area around dentary symphysis well developed above and below Meckel's canal.

Remarks.—The fossil has teeth that are relatively tall with transversely expanded tooth bases and tricuspid crowns, and a relatively deep dentary as in *Sceloporus* and primitive species of *Phrynosoma*. The secondary cusps are more reduced than in *Sceloporus* and resemble the relatively narrow crowns of the extant horned lizards *Phrynosoma douglassi* and *Phrynosoma orbiculare*. The teeth of *P. holmani* are taller than any extant species of *Phrynosoma*, indicating a varied insectivorous diet. More advanced extant species such as *Phrynosoma modestum* and *Phrynosoma solare* specialize in eating ants and have teeth that are reduced to simple conical pegs.

The dentary of *P. holmani* is relatively deeper, especially anteriorly, than in the extant species of *Phrynosoma*. The ventral surface of the dentary in *P. holmani* is relatively flat as in *Phrynosoma* rather than in *Sceloporus*. The ventrolateral surface of the dentary in *P. holmani* is strongly angled as in the extant species, *Phrynosoma cornutum*, *P. modestum*, and *Phrynosoma platyrhinos*. The dentaries of *Sceloporus*, *P. douglassi*, *P. orbiculare*, and the extinct early Pleistocene species *Phrynosoma adinognathus* from Kansas (Rickart, 1976) are rounded on this surface. Depressions of muscle scars on the anterior end of the ventral surface and dor-

solateral surface of the posterior end of the dentary are well developed in *P. holmani*. The anterior surface depression is well developed in *Phrynosoma* but not *Sceloporus*. The depression on the posterior dorsolateral surface is similar to the condition in large *Sceloporus* and *P. cornutum* but less well developed in *Phrynosoma ditmarsii*, *P. douglassi*, and *P. orbiculare*. In *P. holmani*, Meckel's canal is medial, open, and constricted in the middle of the dentary as in *Sceloporus*, *P. ditmarsii*, *P. douglassi*, and *P. orbiculare*. Meckel's canal is open with little constriction in the middle as in *P. cornutum*, *P. platyrhinos*, and *P. solare*. Meckel's canal is located medially on the anterior end of the lingual surface of the dentary in *P. holmani* as in *Phrynosoma* and not ventrally as in *Sceloporus*. The dentary symphysis is well developed above and below Meckel's canal in *P. holmani*. The dental gutter and labial parapet are well developed in *P. holmani* and similar to those of *P. douglassi*.

DISCUSSION

The earliest fossil *Phrynosoma* are primitive forms reported as *Phrynosoma pdouglassi* from the middle Miocene (Hemingfordian Land Mammal Age) Split Rock Formation, Wyoming (Robinson and Van Devender, 1973), and as *Phrynosoma* sp. from the middle Miocene (late Barstovian Land Mammal Age) lower Valentine Formation, Nebraska (Estes and Tihen, 1964). By the late Pliocene, *P. cornutum* had evolved and was found in the Rexroad (early Blancan Land Mammal Age; Oelrich, 1954) and Saw Rock (early Blancan; Etheridge, 1960) faunas, Kansas, the Beck Ranch fauna, Texas (early Blancan; Rogers, 1976), and the Sand Draw fauna, Nebraska (late Blancan; Holman, 1972). *Phrynosoma holmani* from the White Rock fauna (late Blancan), Kansas, is an extinct species that has a combination of primitive and derived characters. Apparently none of the living species is derived from *P. holmani*. *Phrynosoma adinognathus* from the early Pleistocene (early Irvingtonian Land Mammal Age) Borchers