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15. Cranial Ornamentation of Ankylosaurs (Ornithischia: Thyreophora): Reappraisal of Developmental Hypotheses

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Abstract

The presence of cranial ornamentation on the dorsal and lateral surfaces of the skull has long been considered diagnostic for the Ankylosauria. Ornamentation and the highly fused nature of the ankylosaur head skeleton have constrained our understanding of cranial anatomy. Two alternative hypotheses have been proposed to explain the origin of cranial ornamentation. The most widely accepted hypothesis suggests that superficial osteoderms coossified with the external surface of the skull, whereas the alternative hypothesis proposes that ornamentation was derived from the elaboration of the dermatocranium. Evidence from the Late Cretaceous ankylosaurids *Euoplocephalus tutus* and *Pinacosaurus grangeri*, and comparative data from extant squamates demonstrating similar conditions support both hypotheses. The developmental model we propose suggests that the dermis of ankylosaurs demonstrated a propensity for the formation of

osteoderms under normal ontogenetic conditions. This propensity accounts for the postcranial “armor,” the buccal ossifications, and some of the cranial ornamentation. However, evidence from subadult *Euoplocephalus* and *Pinacosaurus* specimens suggests that a second mechanism, dermatocranial elaboration, also plays a role in the development of ornamentation. The demonstrable association between developmental processes and osteologic correlates illustrated here provides a means of inferring ontogenetic mechanisms in extinct taxa.

Introduction

The ankylosaur head skeleton is arguably the most enigmatic and poorly known area of osteology within the Dinosauria. In contrast to what is known about most other extinct vertebrates, the paucity of knowledge of ankylosaur skull anatomy appears to be more the result of peculiar morphology than a limited fossil record. In particular, members of the Ankylosauria demonstrate three major architectural novelties: secondary closure of the supratemporal and antorbital fenestrae, nearly complete obliteration of cranial sutures in adult-size specimens, and extensive development of ornamentation across the dermatocranium (Fig. 15.1; Sereno 1986). Whereas all three architectural modifications obscure the topography and morphology of individual dermatocranial elements (and otherwise impede research dealing with homology and phylogeny), the development of cranial ornamentation is the most conspicuous synapomorphy of the taxon. Despite its conspicuous nature and near ubiquitous presence within the clade Ankylosauria, the nature of this ornamentation has received scant attention. Through a reappraisal of the fossil evidence and an analysis of extant nondinosaurian vertebrates with comparable morphology, we attempt to elucidate the developmental mechanisms intrinsic to the formation of cranial ornamentation.

Ornamentation, defined as novel anatomic attributes or modifications (i.e., elaborations) of a preexisting structure not appearing to have a primary role in food acquisition or locomotion (Vickaryous and Rybczynski, in press), is prevalent throughout the Dinosauria, and as such, it is by no means unique or restricted to the Ankylosauria. Although such features are generally osseous in a paleontological context (e.g., horn cores, bony crests and frills, bosses, nodes, and foveae or pitting), modern avian dinosaurs demonstrate a suite of soft tissue derivatives (e.g., wattles, combs, feather crests, and colored loreal regions) that are unlikely to withstand the rigors of preservation. In ankylosaurs, the osteologic manifestation of cranial ornamentation has relatively little surface relief, with few elongate projections or protuberances. Elements of the dermatocranium (those parts of the skull derived from intramembranous ossification—e.g., the nasals, frontals, and parietals) appear to have become externally embossed with continuous, amorphous, or rugose bone, or some combination of these. Additionally, the skull may also exhibit a series of interconnected superficial furrows that subdivide the external surface into a mosaic of polygons and hornlike bosses, resulting in the manifestation of cranial sculptur-



Figure 15.1. *Euoplocephalus tutus* adult cranium (AMNH 5405), oblique rostradorsolateral view.

ing (Fig. 15.1; Coombs 1971). Variants of this phenomenon have often been cited as a means by which the Ankylosauria may be subdivided (e.g., nodosaurids versus ankylosaurids; see Carpenter 1990; Coombs 1971; Coombs and Maryańska 1990; Sereno 1986). Cranial sculpturing is most prominent across the antorbital region, with many taxa demonstrating a gradation of the mosaic pattern into a more random, amorphous texture posterior to the orbits.

Previous work has resulted in the erection of two competing hypotheses that attempt to explain the development of cranial ornamentation (including cranial sculpturing) in ankylosaurs: overlying bony plates (osteoderms) coossifying with the dermatocranium, or osteologic elaboration of the dermatocranial elements. Within the limited confines of the fossil record, problems of development are difficult to examine. Therefore, it is necessary to draw on ontogenetic processes that occur within extant taxa to further elucidate the applicability of these two competing, but not necessarily mutually exclusive, hypotheses. The issue of cranial ornamentation development in ankylosaurs was investigated by reappraising fossil evidence and reviewing extant taxa that demonstrate similar conditions of osseous ornamentation. In this instance, application of the extant phylogenetic bracket (Witmer 1995, 1997) results in a decisively negative assessment (i.e., a level 3 inference); neither modern birds nor modern crocodylians possess osteologic correlates of the cranial ornamentation of ankylosaurs. However, examination of more remote outgroups identifies a common pattern of development present within modern amniotes. This common

pattern of development is herein considered to represent a biological generalization (Bryant and Russell 1992), and as such, this study relies heavily on the ahistorical extrapolatory approach (Bryant and Russell 1992; also see Weishampel 1995; Witmer 1995). Our observations lead us to conclude that the cranial ornamentation of ankylosaurs developed as a result of two independent developmental processes: the ossification of overlying intramembranous bone to the skull and the elaboration of existing cranial elements. The primacy of each of these mechanisms is apparently quite region specific.

Because of the erratic and inconsistent nature of terminology used to describe cranial ornamentation, some clarification is required at the outset. The term “osteoderm” (“bone-skin”) refers to any superficial dermal ossification that supports overlying epidermal scales (e.g., Hildebrand 1988; Romer 1956; Zylberberg and Castanet 1985; cf. osteoscut: de Buffrénil 1982; Meszoely 1970; cf. dermal scute: Camp 1923). Although it is generally accepted that at least some members of most tetrapod clades possess or possessed osteoderms (e.g., mammals, squamates, and crown-group archosaurs; Fig. 15.2), the accuracy of the term has been disputed. Moss (1969) found that although the dermal skeletal tissue of the various tetrapod lineages is homologous, the histologic structure of the tissue is not homogeneous, ranging from dense calcified tendon to true bone. Often these tissues grade seamlessly into one another, preventing segregation of distinct types. Consequently, Moss (1969: 510) advocated use of the term “sclerification” to emphasize the inconsistent tissue histology. However, with the excep-

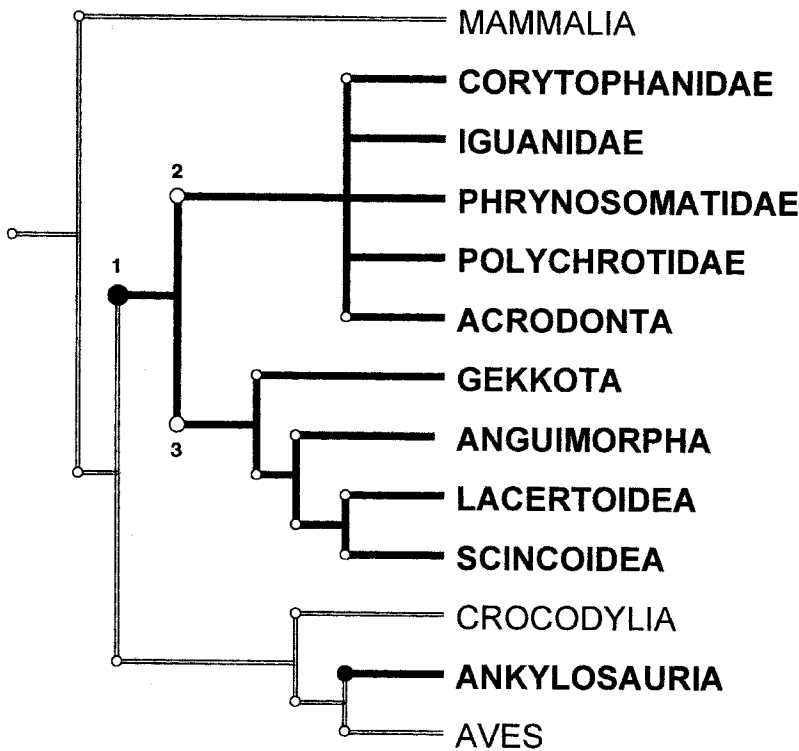


Figure 15.2. Modified phylogeny of the Amniota, providing a phylogenetic framework for the taxa discussed in this article (after Estes et al. 1988; Gauthier et al. 1988; Witmer 1997). Taxa in bold typeface are of primary importance to this study. Node 1 = Squamata; node 2 = Iguania; node 3 = Scleroglossa.

tion of teeth and perhaps eggshell, preservation of nonosseous tissues in the fossil record is rare, and the term "sclerification" (although technically more accurate) is not appropriate for the present study. The term "coossification" ("ossified with"; Trueb 1966) refers to the fusion of two or more structures through the deposition of bone, reorganization of bone, or both.

Materials

The development of cranial ornamentation is nearly ubiquitous within the Amniota, and thus, a comprehensive systematic examination is beyond the scope of this article. For reasons of practicality (relative size and abundance, or ease of transport), the comparative (homoplasious) portion of this study focuses on the development of cranial ornamentation in extant squamates. All amniote lineages appear to maintain the capacity to develop true osteoderms (both under normal ontogenetic conditions and pathologically) by similar processes (Moss 1972), although this is variably expressed within a given clade. The Squamata (see Fig. 15.2) is a monophyletic clade encompassing the majority of taxa commonly considered as structural grade "reptiles." Squamates may be subdivided into two major lineages: the Iguania and the Scleroglossa (Fig. 15.2). Members of both lineages exhibit a wide array of cranial ornamentation, including osseous and soft tissue structures. A survey of alcohol-preserved and skeletal specimens representing most of the major squamate clades (see Appendix 15.1), supplemented with data from the literature (see reviews by Camp 1923; Estes et al. 1988; and Gadow 1901), suggests that particular patterns of osteology are strongly correlated with phylogeny. The presence of both cephalic and postcranial osteoderms in squamates appears to be restricted to members of the Scleroglossa, in particular scincoids and anguimorphs (exclusive of the Ophidia), as well as some members of the Gekkota and Lacertoidea. In contrast, members of the Iguania (with the exception of *Amblyrhynchus cristatus*) rarely, if ever, develop osteoderms (Camp 1923; Gadow 1901). However, many iguanian taxa exhibit the development of osseous horn cores, bosses (e.g., phrynosomatids and some acrodonts), and exostoses (polychrotids).

Extant iguanians serve as the basis for modeling the dermatocranial elaboration hypothesis. Of primary concern for this study were several embryo and adult combinations of *Phrynosoma* (including *P. cornutum*, *P. hernandesi*, and *P. modestum*), embryonic *Chamaeleo pumilus*, neonate *C. calyptratus*, and adult *C. jacksonii*, *C. montium*, and *C. parsoni* (see Appendix 15.1). Extant scleroglossans were similarly used as models for testing the osteodermal coossification hypothesis. The principal specimens examined for this study were subadult and adult *Heloderma suspectum*, adult *Gerrhosaurus major*, and adult *Tarentola mauritanica* (see Appendix 15.1).

The developmental models were generated through observations made from a combination of cleared and double-stained, alcohol-preserved, fresh-frozen, and dried skeletal specimens. Alcohol-preserved and fresh-frozen specimens were subjected to radiographic imaging.

Despite demonstrating prominent cranial ornamentation and a relatively close phylogenetic relationship to dinosaurs, members of the Crocodylia were not considered for use as extant developmental models. The ornamentation of crocodylians, a collection of shallow pits and grooves, is morphologically divergent from that of known ankylosaurs. Although the developmental mechanism giving rise to this morphology (differential resorption of the periosteum; de Buffrénil 1982) is not precluded from occurring within the Ankylosauria, herein, we do not consider it to play a major role. Postcranial osteoderms of crocodylians are presumed to share a homologous developmental pathway with those of scleroglossans (*sensu* Moss 1972).

A superficial consideration of osseous cranial ornamentation in mammals suggests that the developmental pathways noted in squamates are representative of a more inclusive clade. Among extant mammals, only dasypodids (armadillos) commonly develop osteoderms (DeBlase and Martin 1974). Morphologically, the condition appears to parallel that of scleroglossans. The elaboration of the frontals in the Bovidae is likewise similar to the developmental process noted in iguanians.

A review of original ankylosaur material was based largely on two taxa; *Euoplocephalus tutus* (Fig. 15.1) and *Pinacosaurus grangeri* (Fig. 15.3). Both taxa were medium-size ankylosaurid ankylosaurs, from the Late Cretaceous of North America and Asia, respectively. We selected these taxa because both are relatively common and skull material is

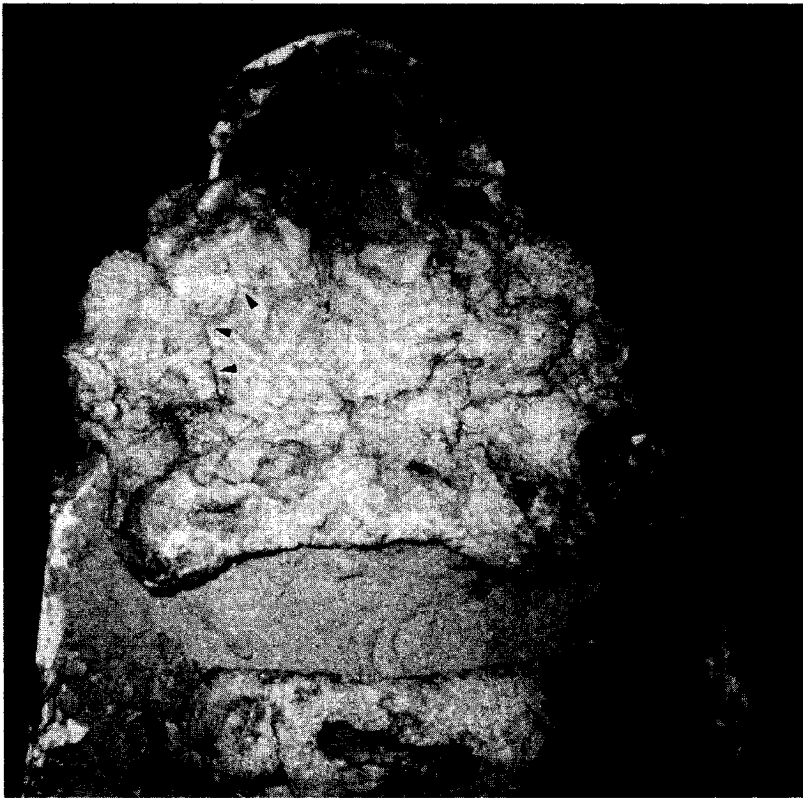


Figure 15.3. *Pinacosaurus grangeri* subadult cranium and first cervical half-ring (TMP 90.301.1), dorsal view. Small arrowheads indicate the lateral sutural border of the left frontal.

abundantly available. Although the majority of *Euoplocephalus* specimens appear to represent adult-size individuals, a number of undescribed elements referable to subadult individuals have recently been identified (Vickaryous, unpublished data). Nearly all the material referable to *Pinacosaurus* represents subadult individuals. Wherever possible, additional material assigned to other ankylosaur taxa was examined.

Institutional Abbreviations. AMNH: American Museum of Natural History, New York. APRC: Personal reference collection of A. P. Russell, University of Calgary, Calgary, Canada. LACM: Los Angeles County Museum, Los Angeles, California. NMC: Canadian Museum of Nature, Ottawa, Canada. PJBC: Personal reference collection of P. J. Bergmann, University of Calgary, Calgary, Canada. TMP: Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada. UCMZ: University of Calgary Museum of Zoology, Calgary, Canada.

Hypothesis 1: Coossification of Osteoderms

Historical Development

Overwhelmingly, the majority of dinosaur researchers have advocated (usually incidentally) the hypothesis of osteoderm coossification with the dermatocranium as the developmental mechanism responsible for ankylosaur cranial ornamentation (e.g., Brown 1908; Lambe 1902, 1919; Russell 1940; Sereno 1997; Sternberg 1929). Often this interpretation has been invoked circumstantially (and inappropriately) during discussion of morphology, but it has yet to be critically tested or substantiated.

Development of Cranial Ornamentation in Extant Scleroglossans

A review of the literature suggests that the development of osteoderms (both cranial and postcranial) in scleroglossans is a character that undergoes repetitive reversal within the clade (Arnold 1973; Camp 1923; Estes et al. 1988; Gadow 1901; Zylberberg and Castanet 1985). Morphologically, there is a high degree of variability among members demonstrating the condition, ranging from the imbricated “shingle” morphotype of *Gerrhosaurus* (Scincoidea) and *Anguis* (Anguimorpha) (the so-called primitive condition; Otto 1909), to the polygonal “pavement” morphotype of *Heloderma* (Anguimorpha; see Fig. 15.4) and *Tarentola* (Gekkota) (the so-called advanced condition; Otto 1909). Developmental mechanisms investigated to date have been largely restricted to the polygonal pavement morphotype, although all osteoderms are presumed to be homologous (Camp 1923; Moss 1969).

Moss (1969) investigated the ontogenetic development of osteoderms in the anguimorph *Heloderma horridum*. Presumptive osteoderms develop as domed regions of thick collagen within the dermis, first appearing over the ossified head skeleton, then spreading caudally (Fig. 15.4). Topographic distribution of these collagen “domes” over the cranium bears no direct relationship to the underlying, and well-



Figure 15.4. *Heloderma suspectum* subadult specimen (UCMZ [R] 2000.001; snout-vent length = 192 mm), radiographic image illustrating the pervasive development of osteoderms in the taxon. The osteoderms located in the head region are pronounced as compared with the more posterior areas of the body. Scale bar = 10 mm.

established, dermatocranial elements. As the individual matures, the collagen domes increase in size before finally becoming ossified. With later development, the osteoderms may fuse directly to the dermatocranium (e.g., *Heloderma*) or remain suspended within the overlying dermis (e.g., some gekkotans such as *Tarentola*). An ontogenetic study of the anguimorph *Anguis fragilis* by Zylberberg and Castanet (1985) indicates that the shingle morphotype undergoes a similar process.

Osteologic Correlates

Because of the nature of osteoderm development, a number of biological generalizations (*sensu* Bryant and Russell 1992) can be made with regard to the resulting osteology. Osteoderms develop within the dermis, superficial to the head and postcranial skeletons, and as such, they are not confined to the topographic limitations of individual elements. Thus, osteoderms may originate in positions that overlap several elements, sutural boundaries, or both. Additionally, osteoderms may form in regions where underlying skeletal elements are absent

(e.g., between adjacent ribs, superficial to the temporal fenestrae and orbits; Fig. 15.4). Consequently, the position and morphology of the cranial openings and the sutural arrangement of dermatocranial elements may become obscured in mature individuals. Before fusion with the cranium, however, it is possible to remove the osteoderms by removing the integument.

Although the gross morphology of postcranial osteoderms may be highly variable, those that develop over the skull generally form polygons (Fig. 15.4). These polygons appear to develop as the incipient osteoderms (centers of ossification within individual collagen domes) expand radially and begin to encroach on one another. Continued growth is constrained by adjacent (incipient) osteoderms, thereby giving rise to the polygonal morphology. Abutment of adjacent polygonal osteoderms may cover the cranial openings with extradermatocranial dermal bone (e.g., the supraorbital ossifications of the gekkotan *Tarentola*; Bauer and Russell 1989). The polygonal configuration of the cranial osteoderms closely resembles the morphologic condition noted in the carapace of placodonts (Westphal 1976) and some mammals (e.g., dasypodids). A brief analysis of dasypodid material suggests that the presence of osteoderms in mammals is derived from developmental processes similar to those of scleroglossans. Dried adult *Dasypus novemcinctus* skeletal material and alcohol-preserved adult *Chaetophractus* sp. demonstrates the presence of both the polygonal pavement morphotype and the imbricated shingle morphotype osteoderms, covering the entire dorsal surface of the head and body. However, no osteoderms were identified through the radiographic imaging of alcohol-preserved fetal *Chaetophractus vellerosus*. Because of the presence of the osteologic correlates identified in scleroglossans, dasypodids are presumed to undergo a similar developmental process.

Hypothesis

Despite their phylogenetically distant relationship to ankylosaurs, many scleroglossans appear to present a pattern of cranial ornamentation that is morphologically congruent with them. On the basis of this gross similarity, it may be hypothesized that ankylosaur cranial ornamentation developed in an analogous manner—that is, osteoderms overlying the dermatocranium fuse with the skull, resulting in a polygonal pattern of ornamentation that obscures sutural contacts and cranial openings. Before maturation (and subsequent fusion), the dermatocranium of ankylosaurs should not exhibit cranial ornamentation in any areas associated with this mode of formation.

Testing the Hypothesis

To test the coossification hypothesis, osteologic correlates within the Ankylosauria must be identified. Requirements for satisfying the hypothesis of osteoderm coossification include the following: (1) the complete absence of ornamentation in immature specimens, (2) the presence of ornamentation that obscures (overlaps) the sutural arrangement in mature specimens, and (3) the presence of osseous ornamentation in regions of the skull without underlying dermatocranial elements.

The ubiquitous presence of cranial ornamentation has been purported to obscure the sutural arrangement of the head skeleton of ankylosaurs (Coombs and Maryańska 1990). Evidence to support this assertion is derived from the examination of material referred to *Pinacosaurus grangeri*. Several specimens of *Pinacosaurus* (TMP 90.301.1; Fig. 15.3; Maryańska 1971, 1977) illustrate the morphology of individual dermatocranial elements. On the basis of, in part, the lack of cranial ornamentation and the relatively small and unfused nature of the skeletal elements, these specimens are considered to represent subadult or immature individuals. Examination of the holotype (AMNH 6523), a larger specimen with ornamentation, suggests that the state of development of cranial sculpturing is ontogenetically regulated. Assuming that skull morphology is conservative (although see Carpenter et al. 2001 for a new ankylosaur taxon with a divergent element morphology), comparison of subadult *Pinacosaurus* crania with those of other, related ankylosaurids suggests that there is no relationship between the individual dermatocranial elements and any overlying polygonal ornamentation. Subadult cranial material is not yet known for all taxa, thus thwarting a more comprehensive systematic review. (Cranial material referred to an undescribed species of *Minmi* also appears to demonstrate the sutural arrangement of the dermatocranium, although further study is required; Molnar 1996.)

The majority of ankylosaur taxa are known, at least in part, from cranial material considered to represent adult or mature individuals. In every case, the specimens demonstrate extensive development of cranial ornamentation (most often cranial sculpturing). With the exception of some specific topographic regions (e.g., the premaxillary beak), the sutural arrangement across the skull roof in these specimens is unknown and presumed to be obscured by the presence of cranial ornamentation.

In addition to the widespread development of postcranial osteoderms, a number of ankylosaur taxa have been found preserved with in situ osseous eyelids (*Euoplocephalus tutus*, AMNH 5238, AMNH 5404; Coombs 1972) and buccal ossifications (osseous cheek plates; *Edmontonia rugosidens*, AMNH 5381; *Panoplosaurus mirus*, NMC 2759). All these dermal elements develop in the apparent absence of underlying skeletal tissue.

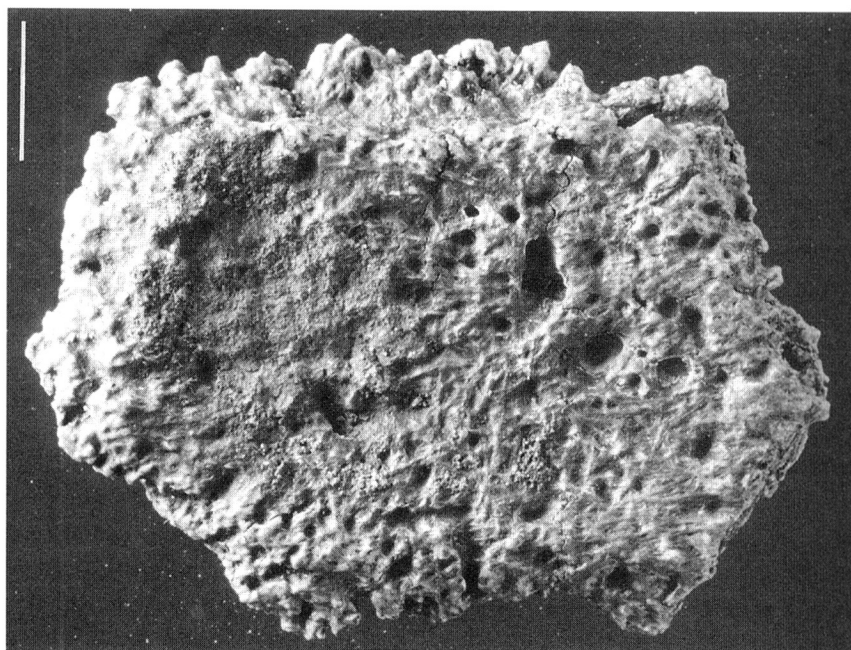
The hypothesis of osteodermal coossification giving rise to cranial ornamentation was originally dismissed by Coombs (1971) in his comprehensive review of the Ankylosauria. Coombs cited two major flaws with the argument, one based on gross morphology and the other on bone histology. Before Coombs's research, no subadult ankylosaur skull had been described, and thus all the cranial material he examined demonstrated extensive development of cranial ornamentation. He reasoned that if the cranial ornamentation of ankylosaurs was the result of osteoderms coossifying with the skull surface, then a specimen should exist where the dermatocranium proper was visible. Despite referring to an unseen subadult specimen of *Pinacosaurus* (via communication with Teresa Maryańska), he submitted that "no such specimen exists" (Coombs 1971: 157).

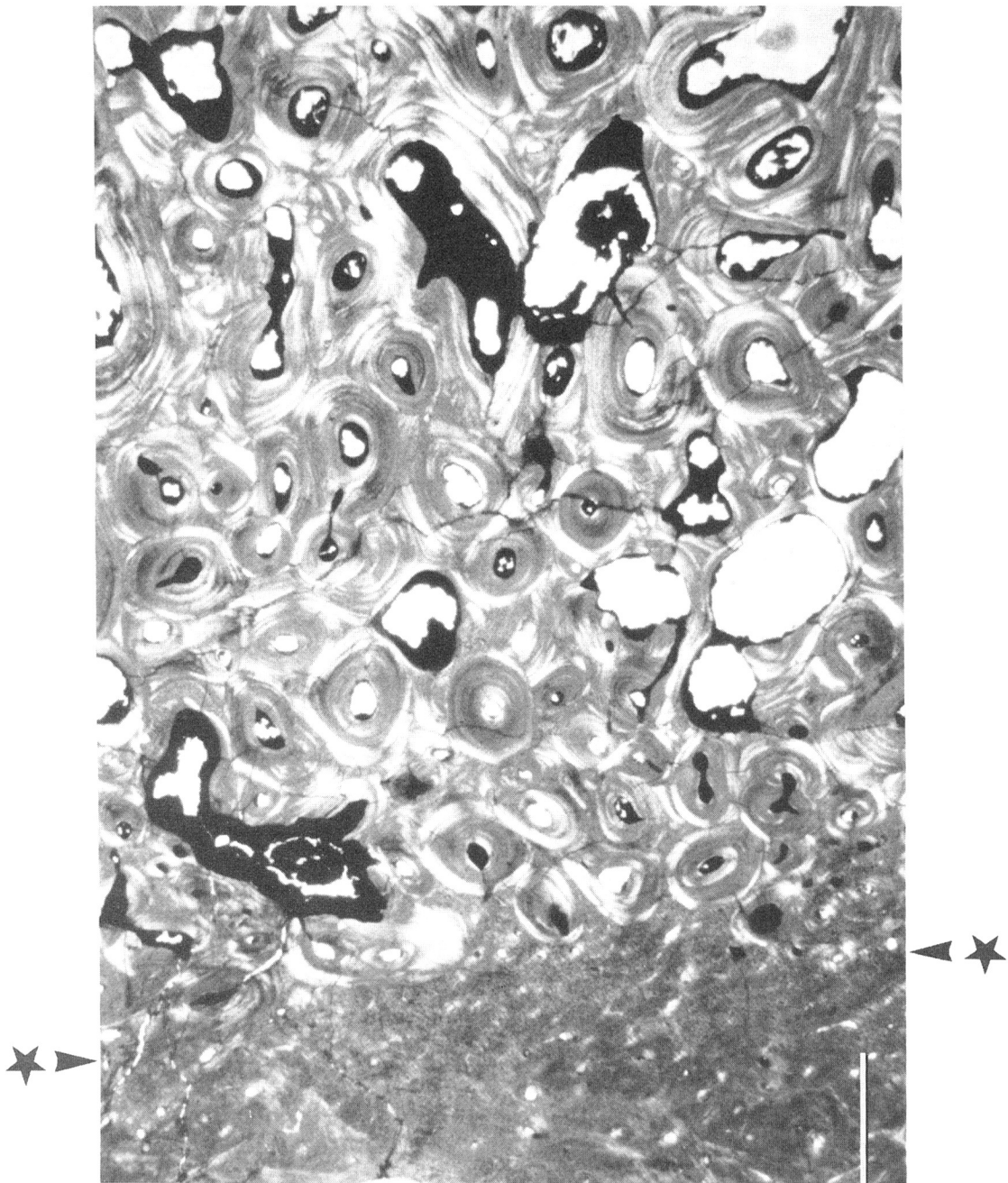
Coombs found further evidence to refute the coossification hypothesis by examining the bone histology of an ankylosaur skull. He suggested that if overlying osteoderms did contact and fuse with the dermatocranium, then an appreciable thickening of the skull roof should be noted when compared with that of other nonpachycephalosaurian ornithischians. A single cranium of *Euoplocephalus tutus* (AMNH 5403) was transversely sectioned across the antorbital region. Examination of the cross sections indicated that the thickness of the *Euoplocephalus* skull roof was “modest” (Coombs 1971: 156) and generally comparable to that of most other ornithischians. He also noted that there was no indication of a juncture between the dermatocranium and the ornamentation. This led Coombs to surmise that *Euoplocephalus*, as a representative of the Ankylosauria, did not have osteoderms fused to the skull roof proper.

A review of the present evidence, supplemented by new cranial thin sections, accounts for the misgivings of Coombs (1971). Detailed examination of subadult *Pinacosaurus* specimens confirms the absence of cranial ornamentation in immature ankylosaurs (see above). Additionally, an undescribed bony plate (TMP 89.36.183; Fig. 15.5) may represent unfused cranial ornament. The element has a rugose and pitted texture, similar to that of postcranial osteoderms (to which it was originally referred). However, the specimen is thin (<10 mm thick), flat with a slightly concave upper surface, and hexagonal in dorsal view. A comparison of this specimen with other known ankylosaur postcranial osteoderms suggests that the morphology is unique. It most closely resembles the polygons associated with the rostral cranial sculpturing of *Euoplocephalus* and is herein referred to as an unfused cranial osteoderm.

To review ankylosaur cranial bone histology, the original thin sec-

Figure 15.5. *cf.* *Euoplocephalus* unfused cranial osteoderm (TMP 89.36.183), dorsal view. Scale bar = 10 mm.





tions of Coombs (from AMNH 5403) have been augmented with new material (TMP 67.20.20 and TMP 98.115.2). Two main histologic layers may be differentiated (Fig. 15.6); a thin (<2.5 mm) layer of isolated, unorganized primary osteons superficial to deeper, extensively remodeled Haversian bone (Coombs 1971). Thorough examination of all thin sections failed to identify any sutural junctions, either between overlying osteoderms and the dermatocranium or between individual dermatocranial elements. The highly reorganized nature of the bone histology suggests that the cranium underwent continual remodeling throughout ontogeny and that any sutural contacts have long since been obliterated. The functional implications of remodeled bone in the ankylosaur cranium are not presently understood. However, a super-

Figure 15.6. cf. Euoplocephalus thin section (TMP 98.115.2) from an isolated fragment of skull representing the frontal-nasal region. Section was taken in the transverse plane, with the periosteum toward the top of the page. Position of star symbols indicates the junction between the two main histological layers: a superficial layer of woven bone and a deeper layer of highly remodeled Haversian bone. Scale bar = 1 mm.

ficial layer of bone lacking a strict organizational pattern (i.e., woven bone), coupled with the presence of ornamentation, has been suggested as a structural mechanism for stress diffusion (Coldiron 1974). Thus, in a teleologic sense, the peripheral layer of an ankylosaur skull may have arisen in response to dispersing and dissipating any stresses incurred.

Conclusions

All the fundamental requirements for advocating the hypothesis of osteoderm coossification are fulfilled by ankylosaur cranial osteology. The expression of cranial sculpturing in ankylosaurs is governed by ontogeny, and the entire clade demonstrates a propensity for the production of osseous, nonpathologic dermal tissue. We consider the superficial furrows that subdivide the cranium (giving rise to the cranial sculpturing) to represent the areas of coossification between adjacent cephalic osteoderms. The unusual distribution of cranial sculpturing (i.e., concentrated around the rostrum) may reflect the degree of interaction between the epidermis and the dermis. However, the role of the epidermis in mediating osteodermal growth is not presently understood. In the anuran *Hyla septentrionalis*, dense connective tissue of the dermis is effectively replaced by bone over areas of the cranium (Trueb 1966). This integumentary derivative then coossifies with the dermatocranium, creating a casque. The lack of epidermal scutes may partially explain the absence of polygonal organization in this secondary dermal bone.

Whether the production and subsequent coossification of dermal bone to the skull is responsible for all the cranial ornamentation noted in ankylosaurs has yet to be addressed. The subadult crania of *Pinacosaurus grangeri*, although devoid of cranial sculpturing, do demonstrate small hornlike bosses over the orbits and at the posterior corners of the skull. In addition, Jacobs et al. (1994: 338) noted the presence of what they termed "excrescences" on some disarticulated elements of a very small, subadult nodosaurid skull. The development of these structures cannot be accounted for by osteoderm coossification.

Hypothesis 2: Elaboration of the Dermatocranium

Historical Development

As noted above, Coombs (1971) rejected the notion of osteoderm coossification as the predominant developmental mechanism of cranial ornamentation because of a number of perceived morphologic and histologic inconsistencies. Alternatively, he proposed that the osseous ornamentation of the dermatocranium was the result of individual cranial elements becoming elaborated under the influence of epidermal structures. Coombs noted that elaborate modifications of the cranium were not without precedent among the Ornithischia (e.g., the premaxillary–nasal crests of lambeosaurines and the squamosal–parietal frills of neoceratopsians). Therefore, although the possibility of some extradermatocranial contributions to the ankylosaur skull was not entirely precluded, it was thought to play a minor role.

A more recent review of the Ankylosauria by Coombs and Mar-

yańska (1990) puts forward a less polarized view by stating that the cranial ornamentation might be the result of either elaboration of the dermatocranium or the coossification of osteoderms.

Development of Cranial Ornamentation in Extant Iguanians

Analysis of an ontogenetic sequence of cleared and double-stained *Phrynosoma* specimens provide the basis for our discussion of the development of cranial ornamentation in iguanians.

Members of the taxon *Phrynosoma* are characterized, in part, by the presence of laterally and posteriorly directed cranial horns (Montanucci 1987). These horns can initially be distinguished as protuberances on the squamosals and parietal of neonates (e.g., *Phrynosoma modestum*; Fig. 15.7). Throughout the process of ontogeny, the protuberances may increase in size and become modified in appearance to form a variety of horns and bosses that are always confined to individual dermatocranial elements. Cranial sutures are generally not obscured by the development of osseous ornamentation, although the degree of elaboration is taxonomically variable. Examination of cleared and double-stained, alcohol-preserved, and dried skeletal material of various specimens of *Chamaeleo* corroborates these findings. The role of epidermal structures in the development of dermatocranial protuberances is not presently understood, although the horns of phrynosomatids and *Chamaeleo jacksonii* are sheathed by a single, much enlarged conical scale in life.

Osteologic Correlates

Early ontogenetic development is characterized by osseous outgrowths from dermatocranial elements, resulting in the development of horns, bosses, and protuberances in iguanians. Cranial ornamentation derived from elaborations of the head skeleton proper cannot be removed at any time during ontogeny without causing physical injury to the skeletal elements of origin. In addition, the cranial ornamentation of iguanians is restricted to individual elements and thus does not generally transgress sutural boundaries except sometimes during the late growth stages (e.g., *Chamaeleo jacksonii*). This condition appears to be paralleled by bovids in the development of frontal horn cores.

Hypothesis

The morphology of the posterolaterally directed horns and superficial protuberances on iguanian crania appears to parallel the condition of cranial ornamentation demonstrated by ankylosaurs. On the basis of this osteologic resemblance, we hypothesize that the cranial ornamentation of ankylosaurs developed in an analogous manner—that is, by elaboration of individual dermatocranial elements.

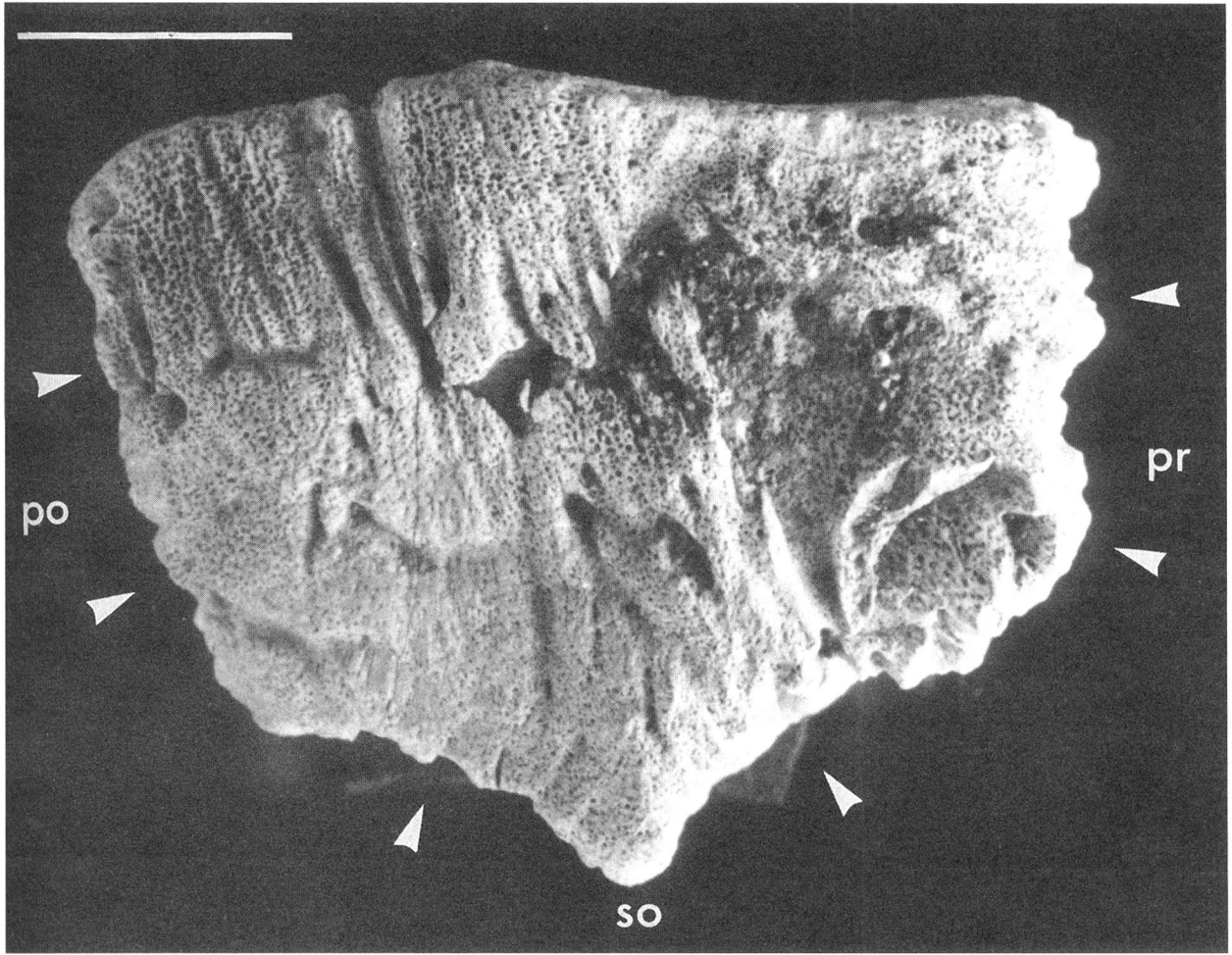
Testing the Hypothesis

Requirements for satisfying the hypothesis of dermatocranial elaboration include the presence of ornamentation in immature specimens and the restriction of ornamentation to individual elements.



Figure 15.7. *Phrynosoma modestum* neonate, cleared and double stained (LACM 123344; snout–vent length = 30 mm), dorsal view (right eye removed). Circle-star symbol indicates the position of an occipital (parietal) horncore. Scale bar = 1 mm.

The developmental nature of ankylosaur skulls is such that the majority of cranial sutures are rarely visible. Examination of material referred to subadult *Pinacosaurus grangeri* (TMP 90.301.1; Fig. 15.3; Maryńska 1971, 1977) suggests that this feature is related to ontogeny. Although the cranial sutures are readily apparent (the result of the specimens lacking the coossification of dermally derived cranial sculpturing), they are not without osseous ornamentation. The squamosals, quadratojugals, and supraorbitals all demonstrate the incipient development of triangular or pyramidal bosses. These bosses correspond to individual elements on a one-to-one basis and appear as direct outgrowths of the dermatocranium. Additional supporting evidence includes several undescribed subadult cranial elements. These unrelated elements (none are considered to represent the same individual) include a left supraorbital (TMP 88.106.5; Fig. 15.8), two left squamosals



(TMP 67.19.4 and TMP 93.36.79; Fig. 15.9), and a right and left quadratojugal (TMP 67.20.20 and TMP 79.14.164, respectively; Fig. 15.10). On the basis of morphology, all of these elements may be referred to the Ankylosauridae cf. *Euoplocephalus*. Of particular significance are the sutural boundaries on each element and the triangular to pyramidlike outgrowths or bosses.

Currently, little is known about the osteology of subadult nodosaurids. Several disarticulated cranial elements from the Albian of Texas suggest that at least some subadult nodosaurids developed rugose, encrusting elaborations (“excrescences”; Jacobs et al. 1994: 338). A number of nodosaurid taxa are also known to develop incipient bosses above the orbits and at the posterior corners of the cranium (e.g., *Pawpawsaurus campbelli*; Lee 1996).

Conclusions

Osteologic evidence suggests that the cranial ornamentation of ankylosaurs is partly the result of elaboration of outgrowths from dermatocranial elements. Such expression is consistent throughout known ontogenetic stages, at least among members of the Ankylosauridae. There is no evidence, however, to support the hypothesis that all of the cranial ornamentation of ankylosaurs is derived in this way.

Figure 15.8. cf. *Euoplocephalus* left supraorbital (TMP 88.106.5), dorsal view. Arrowheads mark the position of the sutural contacts. po = postorbital; pr = prefrontal; so = additional supraorbitals. Scale bar = 10 mm.

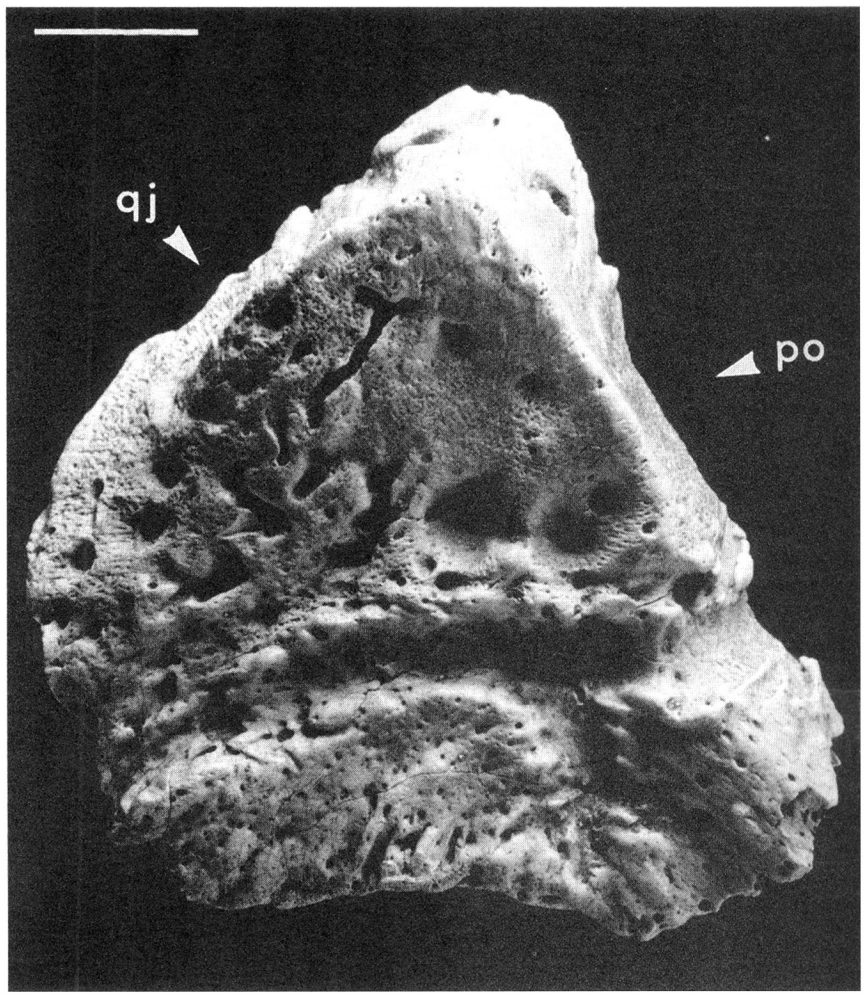
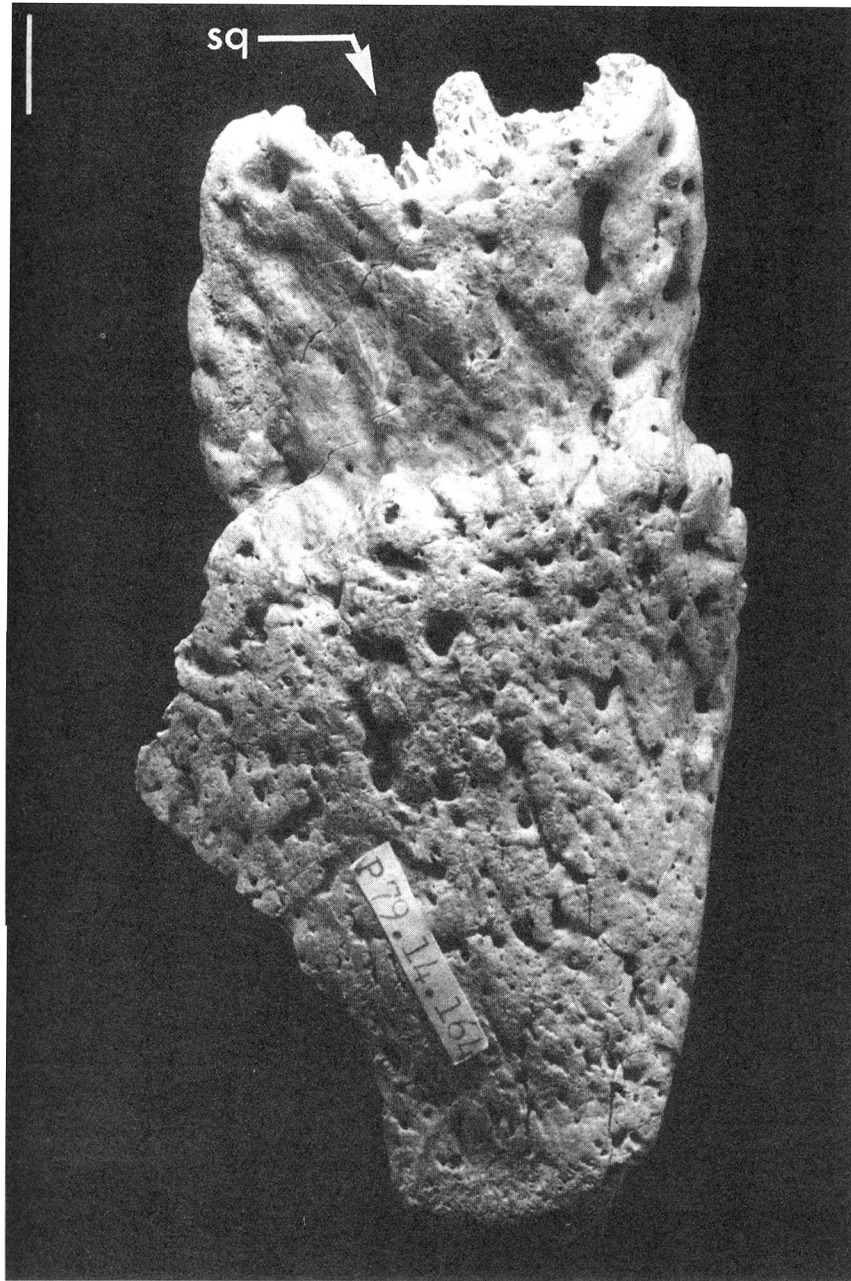


Figure 15.9. *cf.* *Euoplocephalus* left squamosal (TMP 93.36.79), occipital view. Arrowheads mark the position of the sutural contacts. *po* = postorbital; *qj* = quadratojugal. Scale bar = 10 mm.

A Synthetic Approach

A comparison of osteologic correlates associated with extant developmental processes with those demonstrated by fossils permits the reappraisal of ontogenetic mechanisms in extinct taxa. Previous work had suggested two alternative and competing hypotheses to explain the development of cranial ornamentation in ankylosaurs. A review of modern squamates demonstrates the independent occurrence of each process within selected taxa and presents the opportunity to determine the resulting osteologic expression of each mechanism. Comparisons of these skeletal correlates with ankylosaur cranial material suggest that ankylosaurs use both developmental processes. The degree of expression of each mechanism is highly variable among, and even within, taxa. Thus, the expressed pattern may be used to diagnose a taxon (e.g., ankylosaurids versus nodosaurids) or a particular ontogenetic stage. Carpenter (1990) noted the variability of cranial ornamentation expressed within the taxon *Edmontonia rugosidens*, and suggested that it may reflect a state of maturation. Contention over the taxonomic validity of the many synonyms of *Euoplocephalus* is based in part on subtle characters associated with cranial ornamentation morphology (Pen-



kalski 1998, 2001). Resolution of these issues is likely embedded within a greater overall understanding of developmental mechanics.

Summary

The developmental biology of dinosaurs has rarely received extensive consideration. Because of the inherent limitations of the fossil record, these investigations require alternative (e.g., extrapolatory) techniques to test the validity of interpretation. Despite being well established, the use of modern taxa as functional models for fossil organisms is often ineffectively applied. Efforts to minimize speculation rely upon the stringent analysis of available evidence and the identification of

Figure 15.10. *cf.* *Euoplocephalus* left quadratojugal (TMP 79.14.164), lateral view. Arrow marks the position of the sutural contact. sq = squamosal. Scale bar = 10 mm.

relevant osteologic correlates. Use of modern ontogenetic mechanisms as a research protocol for the induction of fossil structures has broad applications paleobiologically. A review of the ankylosaur head skeleton in this context suggests that the development of cranial ornamentation is the result of two independent and generally segregated processes involving the dermatocranium proper and extradermatocranial ossifications.

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APPENDIX 15.1.

Extant material examined and information on specimen type.

	Species; n; age	Specimen type	Collection
Iguania			
Corytophanidae	<i>Corytophanes cristatus</i> ; 1; ad	FF	PJBC*
Iguanidae	<i>Iguana iguana</i> ; 2; subad	C&S	APRC*
	<i>I. iguana</i> ; 1; ad	SD	UCMZ/R/1978-11
	<i>Dipsosaurus</i> sp.; 1; ad	PR	UCMZ/R/1975-67
Polychrotidae	<i>Anolis equestris</i> ; 1; ad	PR	UCMZ/R/1986-21
	<i>A. equestris</i> ; 1; ad	SD	PJBC*
Phrynosomatidae	<i>Phrynosoma cornutum</i> ; 1; neo	C&S	LACM 19897(12185)
	<i>P. cornutum</i> ; 1; subad	C&S	LACM 4307
	<i>P. cornutum</i> ; 2; ad	SD	UCMZ/R/1979-6,7
	<i>P. hernandesii</i> ; 3; neo	C&S	APRC*
	<i>P. hernandesii</i> ; 1; ad	FF	APRC*
	<i>P. modestum</i> ; 2; neo	C&S	LACM 19692(5536), 19694(5538)
	<i>P. modestum</i> ; 1; ad	SD	TMP 90.7.162
	<i>P. mcallii</i> ; 2; neo	C&S	LACM 123343, 123344
Acrodonta	<i>Chamaeleo calyptratus</i> ; 2; neo	C&S	APRC*
	<i>C. jacksonii</i> ; 1; ad	SD	TMP 90.7.350
	<i>C. montium</i> ; 1; ad	FF	PJBC*
	<i>C. parsoni</i> ; 2; ad	PR	APRC*
	<i>C. pumilus</i> ; 3; neo	C&S	APRC*
	<i>Draco volans</i> ; 1; ad	C&S	APRC*
	<i>Moloch horridus</i> ; 1; ad	PR	UCMZ/R/1975-106
	<i>Uromastix hardwickii</i> ; 1; ad	PR	UCMZ/R/1975-98
Scleroglossa			
Gekkota	<i>Gecko gekko</i> ; 1; ad	C&S	APRC*
	<i>Tarentola annularis</i> ; 1; ad	PR	APRC 10
	<i>T. mauritanica</i> ; 2; ad	C&S	APRC*
	<i>Lialis burtonis</i> ; 1; ad	C&S	APRC*
Lacertoidea	<i>Xantusia vigilis</i> ; 1; ad	PR	UCMZ/R/1975-136
	<i>Cnemidophorus soki</i> ; 2; ad	PR	UCMZ/R/1975-134, 135
Scincoidea	<i>Eumeces</i> sp.; 2; ad	PR	UCMZ/R/1975-115, 116
	<i>Tiliqua scincoides</i> ; 2; ad	PR	UCMZ/R/1975-119, 120
	<i>Gerrhosaurus major</i> ; 1; ad	SD	PJBC*
	<i>G. nigrolineatus</i> ; 1; ad	PR	PJBC*
Anguimorpha	<i>Gerrhonotus multicarinatus</i> ; 1; ad	PR	UCMZ/R/1975-137
	<i>Heloderma suspectum</i> ; 1; ad	SD	APRC*
	<i>H. suspectum</i> ; 1; subad	PR	UCMZ (R) 2000.001
	<i>Heloderma</i> sp.; 1; subad	SD	TMP 90.7.26
	<i>Varanus bengalensis</i> ; 1; subad	SD	UCMZ/R/1993-1
	<i>V. nebulosus</i> ; 1; ad	PR	UCMZ/R/1976-32

APPENDIX 15.1. (cont.)

	Species; n; age	Specimen type	Collection
Mammalia			
Dasypodidae			
	<i>Chaetophractus vellerosus</i> ; 1; neo	PR	UCMZ/M/1975-67
	<i>Chaetophractus</i> sp.; 1; ad	PR	UCMZ/M/1984-7
	<i>Dasypus novemcinctus</i> ; 2; ad	SD	UCMZ/M/1975-65, 1977-119

NOTE. C&S = cleared and double stained for bone and cartilage; SD = dried skeletal material; FF = fresh frozen; PR = alcohol-preserved whole specimen. All specimens were assigned to one of three different ontogenetic stages, as follows: neo = neonate/embryo; subad = subadult; ad = adult. An asterisk denotes an unnumbered specimen.