

Preliminary investigation of Allosauroidea facial integument and the evolution of theropod facial armor

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SUMMARY

In amniotes, the growth of specialized facial integument, or external skin tissues, has a close relationship with the texture and morphology of underlying cranial bones. Osteological correlates of facial skin structures have been used before to reconstruct the integument of several extinct dinosaurian lineages but not for theropods from the clade Allosauroidea, whose members exhibit exceptionally rugose and heavily ornamented skulls. This study aims to investigate, in a preliminary sense, the facial integument of Allosauroidea by examining osteological correlates from high-resolution photographs of fossil material. We compared the inferred integument of allosauroids to analogous structures in modern animals in order to discuss potential biological and behavioral implications, with soft-tissue adaptations suggesting headbutting or sparring in some taxa. Allosauroids display an evolutionary trend for increasing cranial cornification throughout their history, and their most derived members exhibit greater development of facial armor than other tetanurans. We developed three hypotheses to explain the selective pressures that may have driven the independent evolution of this dermal armor in several unrelated theropod clades, namely abelisaurids, carcharodontosaurids, and tyrannosaurids. Empirical tests of paleoecological data did not support any of the three hypotheses of intraspecific conflict, competition from other carnivores, or dangerous prey items as the main pressure that drove the evolution of theropod facial armor. We suggest that more sampling of armor-faced theropods and their associated ecosystems, especially those from the Southern Hemisphere, is needed to reveal the reasons behind the convergent evolution of this integument.

INTRODUCTION

Theropods, the bipedal dinosaurian group that includes all birds and all carnivorous dinosaurs, have long been subject to a great amount of research interest on their biology, ecology, and evolution (1). An important area of theropod research is the anatomy of the soft tissues they bore in life, which is vital to understanding how these animals may have lived and interacted with their environment (1). However, soft tissues in non-bird theropods are extremely rare in the fossil record and

have only been preserved in a few remarkable specimens, leaving most theropod species known only from bones (1). A long-standing enigma for both scientists and paleoartists is the question of how to make accurate inferences about the living anatomy of theropods when the information on their soft tissues is so limited.

The biology of one group of theropods, the Allosauroidea, is particularly important to understanding many dinosaurian ecosystems because of their ubiquity and high position on the trophic chain (1–3). Allosauroidea was a diverse superfamily of typically massive and large-skulled carnivores with a widespread distribution in both time and space. At least 180 to 90 million years ago, from the Middle Jurassic to Late Cretaceous periods, allosauroids were found on every continent except Antarctica (1–3). Allosauroids are well known for their elaborate bony cranial ornamentation, but the integument, or external skin tissues, that these structures bore in life is currently unknown (4–9). Knowledge of allosauroid facial integument could provide vital information about their life appearance, paleobiology, evolution, and even behavior (5, 10–13).

It has been established that distinct patterns of bone texture are strongly correlated with different types of soft tissue in living animals, and cranial rugosities can be used as osteological correlates to infer unpreserved integument in extinct taxa (10–12, 14). This method has been used before to reconstruct the facial integument of other families of non-allosauroid theropods, such as the two-fingered Tyrannosauridae and the short-faced, short-armed Abelisauridae (5, 11–12, 14–15). Their skulls bear osteological correlates that point to the presence of two forms of specialized integuments that may have served as armor: (a) thickened dermis, similar to the stiff armor pads of rhinoceroses; (b) extensive cornified (keratin) sheaths, similar to the covering of bird beaks (5, 11–12, 14–15).

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York City, NY, USA
MCCM-LH	Museo de las Ciencias de Castilla-La Mancha, Cuenca, Spain
MOR	Museum of the Rockies, Bozeman, MT, USA
MUCPv	Museo de la Universidad Nacional del Comahue, Neuquén, Argentina
UCRC PV	University of Chicago Research Collection, Chicago, IL, USA
USNM	United States National Museum, Washington D.C., USA

Despite some species, especially members of the Cretaceous family Carcharodontosauridae, bearing heavily rugose skulls that could yield a considerable amount of information on their soft-tissue anatomy, allosauroids have been largely understudied in regards to their facial integument (3, 5–7, 9). This study sought to investigate, in a preliminary manner, the facial integument of allosauroids and other related theropods by using osteological correlates to infer unpreserved dermal structures following previously performed methods (10). This study also aimed to determine which factors drove the independent evolution of facial armor in three different groups of theropods by empirically testing paleoenvironmental data.

We developed three hypotheses to explain the selective pressures that may have driven the evolution of facial armor in abelisaurid, carcharodontosaurid, and tyrannosaurid theropods. Hypothesis 1 states that facial armor evolution was driven by high rates of interspecific conflict in environments with numerous Sympatric Large Carnivores (SLCs), which we define in this study as any large terrestrial or semi-terrestrial carnivores that coexisted with armor-faced theropods (Figure 1A). We define a “large” carnivore as weighing over 500kg based on the theropod mass classes of other studies (16-17). Because most armor-faced theropods were at least this mass, much smaller carnivores would have posed very little threat to them. Therefore, antagonistic encounters with carnivores of similar or greater mass would have a much greater potential to act as a selective pressure for the evolution of facial armor

(17). Thus, the mass threshold of 500kg was used to exclude smaller carnivore taxa and prevent them from skewing the count of sympatric carnivores (16-17).

Hypothesis 2 states that facial armor evolution was driven by feeding injuries in environments with many Sympatric Dangerous Herbivores (SDHs), which we define in this study as any herbivore coexisting with armor-faced theropods that had a high capacity to inflict injury on an attacking predator (Figure 1B). Herbivorous dinosaurs were classified as SDHs if they either exhibited obvious defensive weaponry such as horns, spikes, osteoderms, etc., or if they weighed over 1,000kg, because even unarmed megaherbivores in modern ecosystems can be very dangerous to potential predators due to their large size and strength (18). The weight cutoff for SDHs only applies to herbivores that did not bear obvious defensive weaponry, such as large duck-billed hadrosaurs and the long-necked sauropods (17). Conspicuously armed herbivores were counted regardless of their mass.

Hypothesis 3 states that facial armor evolution was driven by high rates of intraspecific conflict over limited resources in dry climates. This hypothesis was inspired by an explanation offered by other authors for the development of facial armor in the abelisaurid species *Majungasaurus crenatissimus*, which lived in an arid or semiarid habitat and exhibited evidence for violent antagonistic behavior between individuals (11). Since several other species of armor-faced theropods have been found in rock formations with dry paleoclimates, we believe this hypothesis may apply to armor-faced theropods

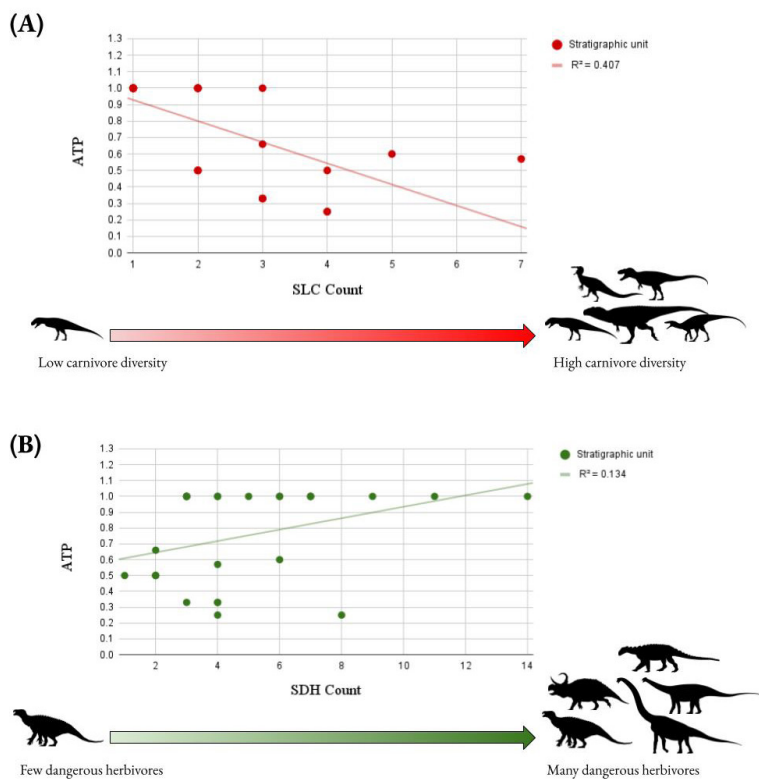


Figure 1: Linear regression tests for Hypothesis 1, between ATP and SLC count, and Hypothesis 2, between ATP and SDH count. Scatterplots and regression lines for (A) ATP vs. SLC count, and (B) ATP vs. SDH count. The individual data points represent stratigraphic units, not species. The r^2 values for both are very low (< 0.5), suggesting a very weak correlation. The relative abundance of armored taxa actually seems to decrease with increasing SLC abundance (A). Neither hypothesis 1 or 2 are supported. Silhouettes are by Jagged Fang Designs, Tasman Dixon, Michael Taylor, and Scott Hartman, accessed from Phylopic.org, public domain.

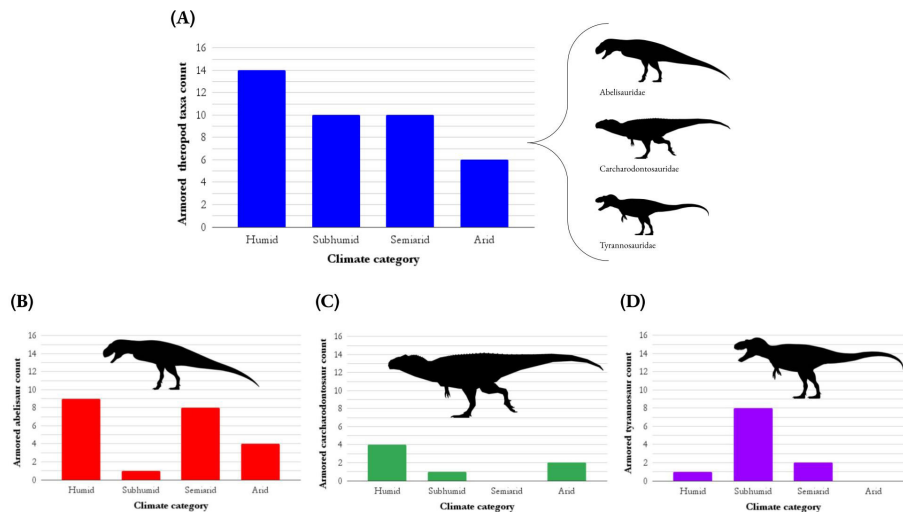


Figure 2: Distribution of armor-faced theropods among four paleoclimate categories. Bar graphs showing the number of armor-faced theropod species in each of the four paleoclimate categories of humid, subhumid, semiarid, and arid. The different bar graphs are for (A) all armor-faced taxa (blue), (B) armor-faced abelisaurids only (red), (C) armor-faced carcharodontosaurids only (green), and (D) armor-faced tyrannosaurids only (purple). The four climate categories are based on the classification system previously established by other authors (25). Note that most armor-faced theropods occur in humid or subhumid climates, contrary to the predictions of Hypothesis 3. The χ^2 tests did not find any significant climate preferences except that tyrannosaurids preferred subhumid zones. Hypothesis 3 is not supported. Silhouettes are by Jagged Fang Designs and Tasman Dixon, accessed from Phylopic.org, public domain.

in general (Figure 2) (12).

Our examination of osteological correlates suggests that allosauroid facial integument primarily consisted of scales alongside regions of heavily-keratinized skin, analogous to the cornified coverings of bovid horns or bird beaks (10). Of the three evolutionary hypotheses that we tested, none were empirically supported, although no conclusions about the cause of facial armor evolution can be drawn with certainty because of the small size of the dataset.

RESULTS

Integument of studied theropods

We examined photographs of the skulls of six tetanuran theropods, including five allosauroids (*Allosaurus fragilis*, *A. jimmadseni*, *Concavenator corcovatus*, *Carcharodontosaurus saharicus*, *Giganotosaurus carolinii*) and one tyrannosaurid (*Tyrannosaurus rex*), for rugose bone surface textures (4, 19–23). We then used the rugosity profiles as osteological correlates to identify unpreserved skin structures that were present on the skulls in life based on strong associations between distinct bone textures and distinct skin types in living animals (10).

The distribution of rugosity profiles on the skull of *Allosaurus fragilis* (Allosauridae) suggests that this allosauroid may have had a mosaic of scales on the sides of the snout with cornified sheaths covering the postorbital bone (behind the orbit), the lacrimal horns (in front of the orbit), and the nasal ridges (along the top of the snout) (Figure 3). A subsequent

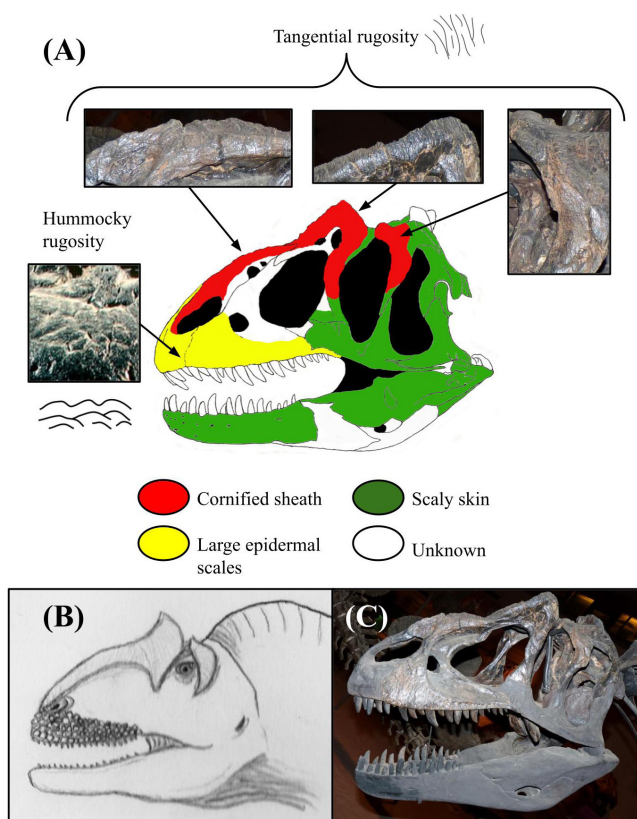


Figure 3: Osteological correlates and inferred integumentary anatomy of *Allosaurus fragilis*. Schematic diagram displaying the distribution of osteological correlates and inferred facial integument of *Allosaurus fragilis* including (A) color-coded skull drawing with localized photo insets of the specimen USNM 4734, (B) life illustration, and (C) specimen photo in lateral view, courtesy of the Smithsonian Institution. Image (A) has been traced from the skull reconstruction of Gilmore and colorized to schematically show the arrangement of different osteological correlates and skin tissues (49). The integument of the other species, *Allosaurus jimmadseni*, does not differ significantly from that of *A. fragilis*. Note the presence of large scales on the side of the snout and cornified sheaths on the lacrimal/nasal crests and postorbital. The illustrated integument of the facial region is based on osteological correlates, but all skin features of the throat and neck are speculative.

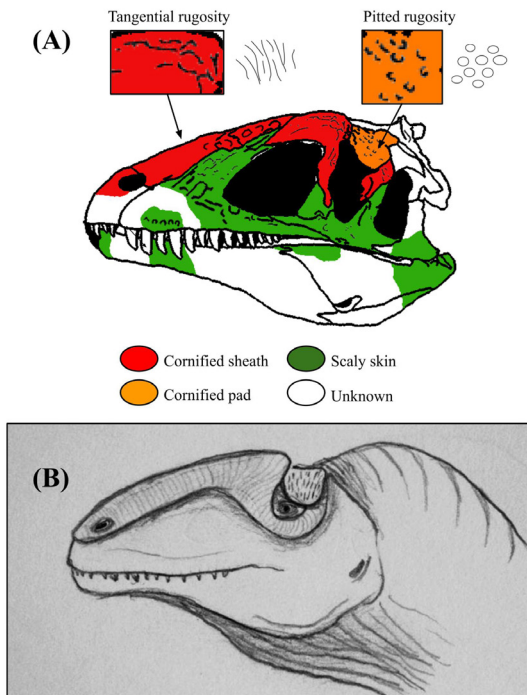


Figure 4: Osteological correlates and inferred integumentary anatomy of *Concavenator corcovatus*. Schematic diagram displaying the distribution of osteological correlates and inferred facial integument of *Concavenator corcovatus*, including (A) color-coded skull drawing based on specimen MCCM-LH 6666, and (B) life illustration. Image (A) has been traced from the skull reconstruction of Cuesta *et al.* and colorized to schematically show the arrangement of different osteological correlates and skin tissues (50). The specific photos of the bones that were used for examination could not be displayed due to copyright reasons. Note the presence of cornified sheaths similar to *Allosaurus*, but also a thick cornified pad on the lateral wall of the robust postorbital brow. The illustrated integument of the facial region is based on osteological correlates, but all skin features of the throat and neck are speculative.

examination of the skull of *A. jimadseni*, the sister species to *A. fragilis*, has revealed that its integument did not differ significantly from that of the latter (4).

The carcharodontosaurid allosauroid *Concavenator corcovatus* may have had a thick, cornified pad on the postorbital brow with cornified sheaths on the lacrimal, nasal, and the premaxilla (at the tip of the snout) (Figure 4) (20). On the other hand, *Carcharodontosaurus saharicus* (Carcharodontosauridae; Carcharodontosaurinae) may have borne cornified sheaths on the lacrimals and postorbitals, pointed scales on the nasals, and an extensive cornified sheath on the maxilla (main lateral region of the snout) (Figure 5) (21-22, 24). Similarly, *Giganotosaurus carolinii* (Carcharodontosaurinae; Giganotosaurini) may have had cornified sheaths on the lacrimals and maxilla, but also on the dentary (tip of the jaw), as well as very dense, pointed scales on the nasals (Figure 6) (23–24). In contrast, the tyrannosaurid coelurosaur *Tyrannosaurus rex* may have had leaf-shaped scales on maxilla, pointed scales on the nasals, cornified sheaths surrounding the orbits, and a pair of horns projecting from above the orbits, differing significantly from the integument of allosauroids (Figure 7) (14, 19).

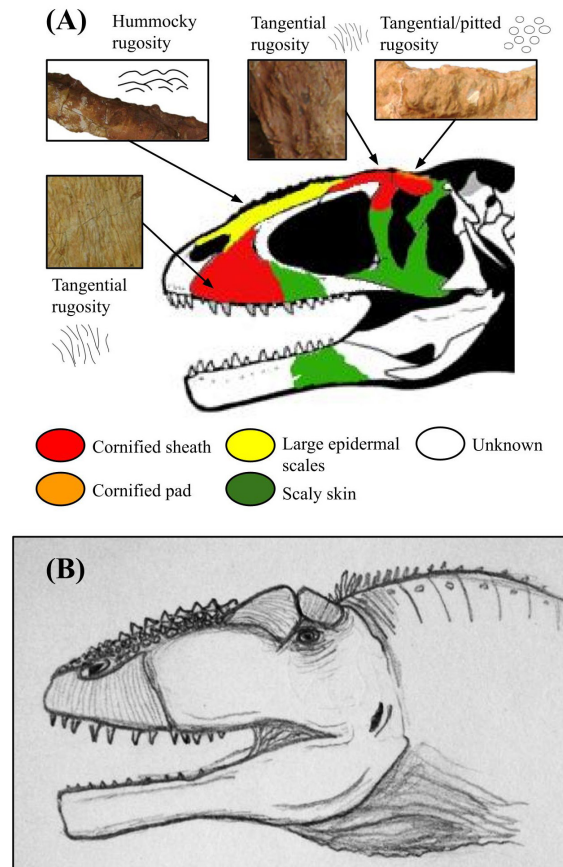


Figure 5: Osteological correlates and inferred integumentary anatomy of *Carcharodontosaurus saharicus*. Schematic diagram displaying the distribution of osteological correlates and inferred facial integument of *Carcharodontosaurus saharicus*, including (A) color-coded skull drawing with photo insets of specimen UCRC PV 12, and (B) life illustration. The skull reconstruction and bone photos were taken from Ibrahim *et al.*, but the former was colorized to schematically show the arrangement of different osteological correlates and skin tissues (22). Note the presence of a large, armor-like cornified sheath on the snout, and large epidermal scales on the nasals. The illustrated integument of the facial region is based on osteological correlates, but all skin features of the throat and neck are speculative.

Evolutionary tests

We used a dataset consisting of armor-faced theropod occurrences and other information on the climate and faunal composition of their respective paleoenvironments to test our three hypotheses (Table 1). In order to represent the relative number of armor-faced taxa in each environment in a way that accounted for variation in the number of total carnivore species per environment, we used a statistic which we dubbed the Armored Theropod Proportion (ATP), which is the number of armor-faced theropod taxa divided by the total number of large carnivore taxa in each environment (Table 1). To test Hypotheses 1 and 2, we ran two separate linear regressions between ATP and SLC count and between ATP and SDH count, respectively (Figure 1). The rationale behind this approach was that if facial armor in large theropods truly evolved because of either pressure from other carnivores or hazardous prey items, then there should

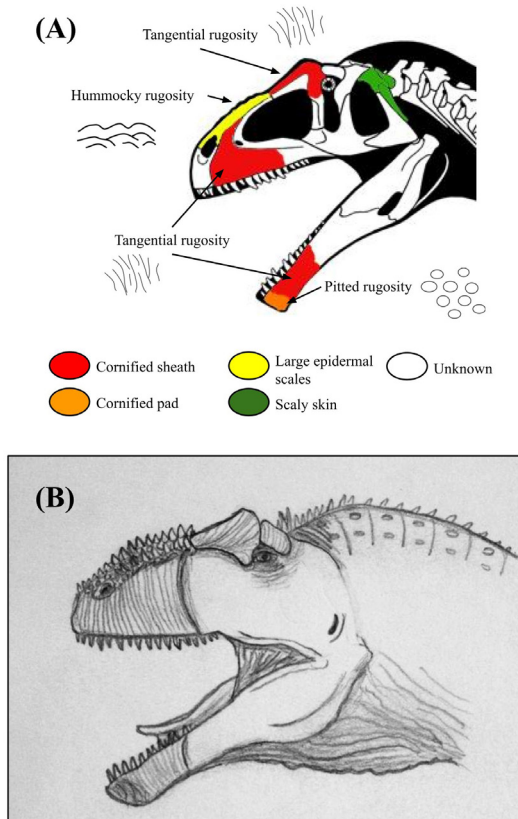


Figure 6: Osteological correlates and inferred integumentary anatomy of *Giganotosaurus carolinii*. Schematic diagram displaying the distribution of osteological correlates and inferred facial integument of *Giganotosaurus carolinii*, including (A) color-coded skull drawing based mainly on specimen MUCPv-Ch1, and (B) life illustration. Image (A) has been modified from a skull reconstruction copyright Scott Hartman, used with permission, and colorized to show the arrangement of different osteological correlates and skin tissues. The specific photos of the bones that were used for examination could not be displayed due to copyright reasons. Note the greater expansion of cornified sheaths relative to *C. saharicus*, and the taller, denser nasal scales reflecting a more prominent rugosity. The illustrated integument of the facial region is based on osteological correlates, but all skin features of the throat and neck are speculative.

be a significant positive correlation between the relative abundance of armored taxa and either SLC or SDH count. To test Hypothesis 3, we used a χ^2 analysis for preference of climate, where the data points were individual taxa rather than whole ecosystems. The rationale behind this approach was that if theropod armor truly evolved in response to increased competition with conspecifics over limited resources in dry climates, then armor-faced taxa should be relatively more abundant in dry (arid or semiarid) paleoclimate zones than wet (humid or subhumid) zones (11, 25).

Linear regression did not support Hypotheses 1 and 2 because the r^2 values for both were very low and therefore weak ($r^2 < 0.5$) (Figure 1). There is no significant correlation between ATP and either SLC count or SDH count. The χ^2 analysis failed to reject the null hypothesis in favor of Hypothesis 3, meaning there is no statistically significant preference for either dry or wet climates among armor-faced taxa in general (Figure 2). Individual χ^2 tests for the three

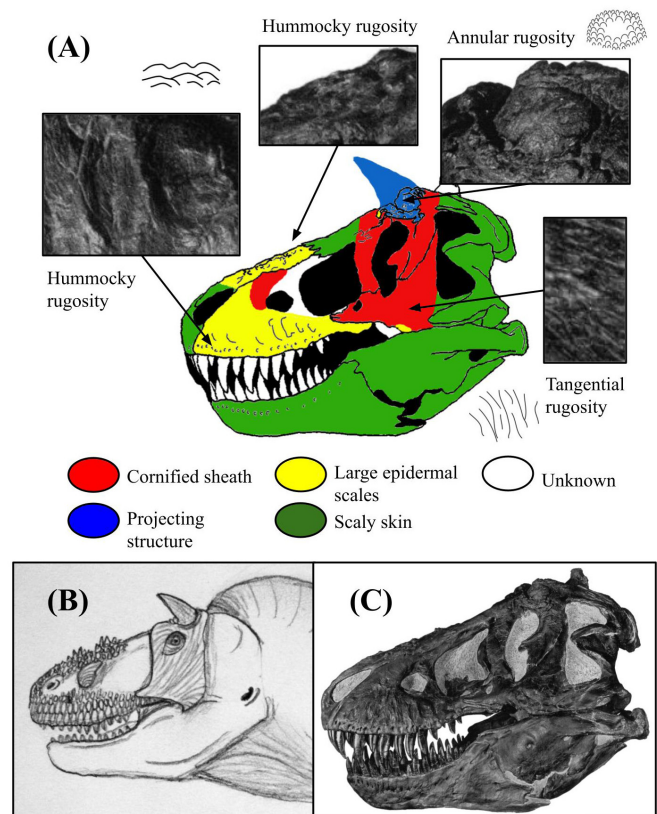


Figure 7: Osteological correlates and inferred integumentary anatomy of *Tyrannosaurus rex*. Schematic diagram displaying the distribution of osteological correlates and inferred facial integument of *Tyrannosaurus rex*, including (A) color-coded skull drawing with photo insets of specimen AMNH 5027, (B) life illustration, and (C) specimen photo. The skull reconstruction and photo were taken from Osborn, and the skull diagram has been traced from the original and colorized to show the arrangement of different osteological correlates and skin tissues (19). Note how unlike the carcharodontosaurines, *T. rex* had a mosaic of scales on the snout and a large cornified sheath around the orbital region. Also note the unpreserved integumentary horns indicated by the distinct annular rugosity, similar to the attachment for a rhinoceros horn. The size and shape of the horns are speculative. The illustrated integument of the facial region is based on osteological correlates, but all skin features of the throat and neck are speculative.

armor-faced theropod clades yielded no significant climate preferences among abelisaurids and carcharodontosaurids, but tyrannosaurids significantly preferred subhumid climates (Figure 2). Overall, none of the three hypotheses were supported by empirical tests, but this must be considered within the small size of the dataset, and a much larger sample may yield different results (Table 1).

DISCUSSION

The examination of osteological correlates on the skulls of allosauroid theropods has allowed for their facial integument to be reconstructed for the first time. Allosauroids generally exhibit an integument arrangement intermediate between modern birds and reptiles, having cornified sheaths covering the crests and upper regions of the skull, with epidermal scales covering the rest. Only the most derived allosauroids

Stratigraphic unit	ATP	SLC count	SDH count
Arid			
Echkar Fm.	0.66	3	2
Elrhaz Fm.	0.33	3	4
Kem Kem Grp.	0.5	4	2
Quiricó Fm.	0.5	2	2
Semiarid			
Adamantina Fm.	0.25	4	4
Anacleto Fm.	0.6	5	6
Argiles Rutilantes Fm.	1	1	4
Bajo de la Carpa Fm.	0.33	3	4
Judith River Fm.	1	2	9
Maevarano Fm.	1	1	3
Presidente Prudente Fm.	0.5	2	2
Subhumid			
Candeleros Fm.	1	2	6
Dinosaur Park Fm. (MAZ 1)	1	2	14
Dinosaur Park Fm. (MAZ 2)	1	2	7
Kaiparowits Fm. (middle)	1	1	7
Kirtland Fm. (Hunter Wash Mbr.)	1	1	5
Nemegt Fm.	1	1	7
Oldman Fm.	1	1	6
Wahweap Fm. (middle)	1	1	4
Humid			
Bahariya Fm.	0.33	3	3
Bajo Barreal Fm.	0.25	4	8
Cerro Barcino Fm. (Cerro Castaño Mbr.)	0.5	2	1
Horseshoe Canyon Fm.	1	1	11
Huincul Fm.	0.57	7	4
La Colonia Fm.	1	2	3
Lameta Fm.	1	3	3
Mulichinco Fm.	1	1	3

Table 1: List of known paleoenvironments bearing armor-faced theropods, showing their calculated ATP, associated SLC counts, SDH counts, and paleoclimates. Table showing stratigraphic units in which demonstrably armor-faced theropods have been found (1st column), the calculated ATP value (2nd column), the SLC count in number of taxa (3rd column), and the SDH count in number of taxa (4th column). The stratigraphic units have been grouped by their paleoclimate categories (25). Stratigraphic abbreviations: Fm, formation; Grp, group, Mbr, member; MAZ, megaherbivore assemblage according to other authors (48).

exhibit a remarkable expansion of large, armor-like cornified sheaths onto the snout and jaw.

Statistical testing did not find any significant associations between ATP and carnivore diversity, dangerous herbivore abundance, or climate type. There is not enough statistical support for a correlation between ATP and either SLC or SDH count, nor is there enough support for a significant preference for dry climates among armor-faced theropods (Figures 1-2). Therefore, the hypotheses that theropods acquired facial

armor in response to (a) competition from other predators, (b) an abundance of hazardous prey items, or (c) intraspecific conflict over limited resources in dry climates, are all so far unfounded by the data.

Although none of the three hypotheses are supported by the current data, no conclusions can be drawn with certainty about the exact reason behind the evolution of theropod facial armor because of the small size of the dataset (40 taxa, 27 environments). There are only a limited number of stratigraphic units in which demonstrably armor-faced theropods have been found (Table 1). It is also possible that the dataset contains biases from its aggregate origin in eclectic scientific papers. There may be many undescribed fossils in collections around the world that would alter the current data on armor-faced theropods and their respective ecosystems. For example, the presence of only one described large herbivore in some environments is likely the result of incomplete study, based on other penecontemporaneous dinosaur faunas from similar areas (Table 1) (26-28).

Alternative hypotheses that may explain the independent evolution of facial armor in carcharodontosaurid, abelisaurid, and tyrannosaurid theropods include sexual selection or prey preference. Sexual selection may explain why only mature carcharodontosaurines bear the osteological correlate for a large cornified sheath and not juveniles, although this could equally be explained by an extended period of parental care (29). Another explanation may be that armor arose in response to specific types of prey items. Despite not being closely related, both abelisaurids and carcharodontosaurines developed similar large cornified sheaths and were often sympatric with one another in ecosystems dominated by giant titanosaur sauropods, which may have been relatively more dangerous as prey items due to adaptations such as osteoderms, robust limbs, and enhanced tail flexibility (5, 11-12, 22, 28, 30-32). On the other hand, tyrannosaurids, which lived mainly alongside horned ceratopsids and armored ankylosaurs, had scales on the snout and a different cornified sheath restricted to the orbital region (Figure 7) (17, 33). Future studies on the relationship between theropod facial armor and the defensive adaptations of their prey items may lend support to this hypothesis.

The distribution of certain integument features may shed light on evolutionary patterns of tetanuran theropods (3). The basal condition for Tetanurae (tyrannosaurids + allosauroids) seems to be a mosaic of scales on the snout, with cornified lacrimal horns being ancestral for Allosauroidea (see Figures 3-4, 7) (2-4, 14). Only in the carcharodontosaurid subfamily Carcharodontosaurinae was the mosaic of scales replaced by a cornified sheath (Figures 5-6) (7, 24). Overall, allosauroids show a trend for increasing cranial cornification throughout their history, with their most derived members exhibiting a greater development of facial armor than tyrannosaurids (Figures 5-7) (14, 24, 33).

Some osteological correlates may also have taxonomic implications. *G. carolinii* is unique among theropods in having an extraordinary nasal texture consisting of very tall, densely spaced nodes and bumps, more similar to the head ornamentation of some herbivorous armored dinosaurs (34-36). The origin of this texture as an osteological correlate of nasal scale growth may suggest that a more recent carcharodontosaurine, *Mapusaurus roseae*, could be synonymized with *G. carolinii* because slight differences in

the nasal texture are one of the only features distinguishing these taxa, and scale growth is quite variable between individuals in modern reptile species (3, 6, 11, 37-38). The potential synonymy of these two taxa is an important future research subject because it may suggest an unusual species longevity for the apex predator *G. carolinii*, potentially lasting over a total period of ten to twenty million years (23, 39-40).

Specialized dermal structures require energy to grow and maintain, so they would not likely evolve unless they provided a fitness benefit. The cornified lacrimal horns of most allosauroids were too delicate for combat and may have been used for display or communication, as suggested by other authors (Figures 3-6) (13). However, the cornified pads on the robust postorbital brows of carcharodontosaurids support previous suggestions that they engaged in high-energy headbutting, because such thick, cornified pads are found exclusively in extant animals that headbutt (Figures 4-5) (5, 10). Also, the nasal rugosities of *G. carolinii* somewhat resemble the skulls of modern lizards that headbutt with very dense, hornlike scales (Figure 6) (6-7, 41-42). Future biomechanical studies on the structural performance of carcharodontosaurid skulls and soft tissues may reveal whether or not these animals were actually capable of headbutting.

Although most of these theropod species exhibit little evidence of sexual dimorphism, sexual selection may explain the development of many of their head ornaments (13). Mutual sexual selection, where both males and females of a species bear ornamentation and select mates, is not uncommon in modern dinosaurs (13). It is possible that *T. rex* may have borne a sexually dimorphic pair of integumentary horns above the eyes, based on the annular rugosity on the postorbital of specimen AMNH 5027, which is not present in the only confirmed female specimen (Figure 7) (43-45).

However, the reconstructions of theropod facial integument in this study are only preliminary because they are based on observations from high-resolution photos, which can be altered by lighting and perspective. Weathering or attached sediment matrix could also alter the bone surface texture, such as the skull of the megalosaurid *Eustreptospondylus oxoniensis*, which had too much matrix to be used in this study. However, most of the observed theropod skull textures retained similarities with each other across species, indicating they were not the result of postmortem processes.

MATERIALS AND METHODS

Data collection

The data was compiled using a combination of the Paleobiology Database (PBDB), an open-access online database of fossil occurrences from around the world, as well as searching for published articles online using Google Scholar. The PBDB was used by searching for “Abelisauridae,” “Carcharodontosauridae,” and “Tyrannosauridae” separately in the query bar, then clicking on each fossil locality on the global map and taking note of the geological unit in each site that contained at least one of the three carnivore families.

Then, for each identified rock unit, a more extensive web search of published articles on Google Scholar was made to determine if the described theropod fossils included cranial remains with osteological correlates for thickened dermis, indicated by bony tubercles, or large cornified sheaths, indicated by dense vascular grooves on the snout or the jugal

(below the orbit) (10). The presence of these osteological correlates was determined by examining photographs of the specimens or reading published descriptions when photos were not available. Most of the information was cited from peer-reviewed articles, but in some cases the data had to be taken from published symposium abstracts because peer-reviewed articles were not available.

After rock formations bearing armor-faced theropods were identified, three more searches of Google Scholar articles were made to determine the number of SLC taxa, the number of SDH taxa, and the paleoclimate type, for each stratigraphic unit (Table 1). SDHs included ceratopsids, stegosaurs, ankylosaurs, large iguanodontians, and sauropods, as well as some rare herbivorous theropods that bore large claws (46-47). The ATP was then calculated for each environment by dividing the number of armor-faced taxa by the SLC count. The ATP was then used as the dependent variable in two separate linear regressions against SLC and SDH count, respectively (Figure 1).

The climate type of each paleoenvironment was sourced from paleoclimate estimates in published literature and were classified as either humid, subhumid, semiarid, or arid, based on the classification system of Thornthwaite (25). The paleoclimate data was then used in eight different χ^2 analyses on a TI-83 graphing calculator for preference of climate type among abelisaurids only, carcharodontosaurids only, tyrannosaurids only, and armored theropods in general (Figure 2). Half of the tests were for preference of dry (arid and semiarid) or wet (humid and subhumid) climate bins, and the rest were for preference of a single climate category (arid, semiarid, subhumid, or humid).

Identification of osteological correlates from photographs

High-resolution photographs of theropod skull bones were used as a substitute for in-person examination. The photos were either provided by researchers at museums or accessed from online articles or collections databases. Each photo was examined for rugose bone surface features that matched the rugosity profile classification scheme previously established by other authors (10). Once identified, the rugosity profiles were used as proxies for different types of facial integument based on the close relationship between skull texture and dermal anatomy in modern vertebrates (10). Osteological correlates identified in the six studied theropods include tangential (Figures 3-7), hummocky (Figures 3, 5-7), pitted (Figures 4-6), and annular (Figure 7) rugosities, which correspond to cornified sheaths, large scales, cornified pads, and projecting structures, respectively (10).

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