THE FUNCTIONAL MORPHOLOGY OF DERMAL BONE ORNAMENTATION IN TEMNOSPONDYL AMPHIBIANS

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Abstract—The dermal bones of the skulls, jaws, and shoulder girdles of temnospondyl amphibians are ornamented with patterns of raised, reticulate, polygonal texture often referred to as "honeycomb-like" and/or ridge-and-groove patterns. The function of this texture has been the subject of inquiry in several previous studies. The most prominent of the competing hypotheses propose that the texture: (1) increases the surface area of the skin to support cutaneous respiration and/or thermal regulation, (2) strengthens the bone against stresses incurred during feeding, (3) protects blood vessels supplying the skin, (4) results from the growth of nutrient channels through the bone and/or (5) provides a large surface for tightly anchoring the overlying skin. These interesting hypotheses have been largely qualitative in nature. Instead, we take a quantitative approach, particularly towards testing the skin-breathing, thermal regulation, and structural strength hypotheses. To do so, we studied dermal bones of the Middle Triassic cyclostosaurid Eocyclotosaurus, and the Late Triassic metoposaurid Koskinonodon. Allometric analysis of the surface area increase due to ornamentation shows very strong negative allometry. The rate of surface area increase is more than an order of magnitude too low to maintain support of skin breathing or thermal regulation throughout growth. Thus, while some skin breathing is possible in these animals, particularly the smaller forms, the surface area increase due to dermal bone texture cannot be a significant contributing factor. In contrast, our calculations show that the dermal bone texture provides a substantial increase in strength and stiffness accompanied by a relatively small increase in mass. The ridge-and-groove texture requires a smaller investment to construct and is lighter weight than the reticulate texture, but its strength is unidirectional, whereas the reticulate texture provides omnidirectional strength. Thus, our quantitative results reinforce the argument for structural significance of the dermal bone texture, and weaken the support for the idea of its contributing to skin breathing and/or thermal regulation.

INTRODUCTION

Temnospondyl amphibians were a long-lived and diverse group of tetrapods. Their fossil remains have been found on every continent. They first appeared in the Carboniferous and reached their ecological zenith during the early Mesozoic (Triassic) when they were represented by a wide variety of animals, from < 250 mm-long trematosaurus to the five-meter-long Mastodonsaurus. Most became extinct at the end of the Triassic, but a few persisted until the Early Cretaceous (Schoch and Milner, 2000).

Temnospondyls were quadrupedal aquatic to semi-aquatic predators that typically had relatively large, dorsoventrally flattened skulls with numerous sharply pointed teeth, relatively small limbs, and long mediolaterally compressed tails. Their four-fingered hands and five-toed feet, together with their palatal vacuities, short straight ribs, bilateral occipital condyles, and numerous other anatomical features place them in the Amphibia.

One of the most characteristic features of temnospondyl amphibians is the heavily textured, or "ornamented" dermal bone that covered their skulls, lower jaws, and shoulder girdles (Fig. 1). Schoch and Milner (2000) show many very high quality illustrations of temnospondyl skulls, lower jaws, and shoulder girdles that clearly define the dermal bone ornamentation of numerous taxa. Clearly, the animals invested considerable energy to grow and to carry around this ornamentation, which we will show increases the mass of dermal bones by 10% to as much as 50%. Both the energy investment required to produce the ornament and its unusual appearance beg the question, what was its function?

Excellent, detailed summaries of the various hypotheses and previous work regarding the purpose of dermal bone ornamentation in temnospondyls have been provided by Coldiron (1974) and more comprehensively by Witzmann et al. (2010). These various studies propose that the dermal bone ornament (1) increases the surface area of the skin to support cutaneous respiration and/or thermal regulation, (2) strengthens the bone against stresses incurred during feeding, (3) protects blood vessels supplying the skin, (4) results from the growth of nutrient channels through the bone and/or (5) provides a large surface for tightly anchoring the overlying skin.

Different hypotheses have been largely qualitative in nature. Instead, we take a quantitative approach, particularly towards testing the skin-breathing, thermal regulation, and structural strength hypotheses. To do so, we studied dermal bones of the Middle Triassic cyclostosaurid Eocyclotosaurus, and the Late Triassic metoposaurid Koskinonodon. Allometric analysis of the surface area increase due to ornamentation shows very strong negative allometry. The rate of surface area increase is more than an order of magnitude too low to maintain support of skin breathing or thermal regulation throughout growth. Thus, while some skin breathing is possible in these animals, particularly the smaller forms, the surface area increase due to dermal bone texture cannot be a significant contributing factor. In contrast, our calculations show that the dermal bone texture provides a substantial increase in strength and stiffness accompanied by a relatively small increase in mass. The ridge-and-groove texture requires a smaller investment to construct and is lighter weight than the reticulate texture, but its strength is unidirectional, whereas the reticulate texture provides omnidirectional strength. Thus, our quantitative results reinforce the argument for structural significance of the dermal bone texture, and weaken the support for the idea of its contributing to skin breathing and/or thermal regulation.

PREVIOUS WORK

Bystrow (1935) described the polygonal reticulate and ridge-and-groove structure of temnospondyl dermal bone ornamentation and believed that the ridges and grooves form as a result of, and show the direction and extent of growth from a center of ossification (e.g., Bystrow, 1944). Later, he proposed that the ornamentation supported cutaneous respiration by increasing surface area (Bystrow, 1947).

Romer (1947) hypothesized that the texture of "labyrinthodont" amphibian dermal bone served for tightly anchoring the skin, but Coldiron (1974) pointed out that in extant crocodylians the skin is just as tightly
Sharpey fibers around the scales and the morphology of the ornamentation supported by dermal bones and scales. They concluded that the presence of *Australerpeton* ornamentation supported the cutaneous respiration argument. However, in agreement with Bystrow (1947), found that highly vascularized dermal cracks would no longer propagate. Plausibly because the ornament diffuses the stress to the point where it showed that they terminate at the ornamented areas on these skulls, map the trajectory of microscopic stress cracks in crocodylian skulls and showed that they terminate at the ornamented areas on these skulls, mapping the trajectory of microscopic stress cracks in crocodylian skulls and showing the dermal bone ornamentation of the skull, lateral jaw surface, and pectoral girdle in *A*. dorsal, and *B*. ventral view. Abbreviations: *Cl*. clavicle; *F*. femur; *T*. tibia; *c. tr*. sacral rib; *P. isch.*, pubo-ischium. From Dutuit (1976, pl. 31). Total length = 1.14 m.

bound to smooth bone as it is to textured bone. Additionally, Romer (1972) disagreed with Bystrow (1947) on the issue of skin-breathing, believing that the temnospondyl amphibians relied on lungs and that skin-breathing was a "degenerate condition" present in some extant amphibians.

Coldiron (1974), concluding that the previous explanations were "inadequate or incomplete," applied a histological technique to fossil dermal bones to show that cutaneous respiration was "impossible" and brought forward the idea that ornamentation strengthened dermal bones by reinforcement and diffusion of stresses. He employed a "split line" technique (chemical preparation followed by dying with India ink) to map the trajectory of microscopic stress cracks in crocodylian skulls and showed that they terminate at the ornamented areas on these skulls, plausibly because the ornament diffuses the stress to the point where cracks would no longer propagate.

Soon after Coldiron's (1974) work, Cosgriff and Zawiskie (1979), in agreement with Bystrow (1947), found that highly vascularized dermal bone surfaces in combination with increased surface area due to ornamentation supported the cutaneous respiration argument. However, Dias and Richter (2002), in their study of the Permian temnospondyl *Australerpeton*, argued against dermal respiration, at least in areas covered by dermal bones and scales. They concluded that the presence of Sharpey fibers around the scales and the morphology of the ornamentation indicated a skin-anchoring function and probable dermal bone strengthening.

Schoch (2001) pointed out that the dermal bone ornamentation could act to mechanically protect the blood vessels and nerves that reside just under the overlying skin. Witzmann et al. (2010) argued against cutaneous respiration, strengthening, and thermal regulation as being the purpose of the ornamentation. Instead, they reasoned that the morphology and arrangement of the dermal bone texture and the vascularization of the overlying tissues were inseparable; that the course of the blood vessels through the bone to the surface, whether it was normal to the surface or oblique, determined whether the surface texture would be reticulate or ridge-and-groove, respectively. They stated that the texture could have assisted in cutaneous respiration in smaller animals and, possibly, thermal regulation in more terrestrial forms, and also argued that it was phylogenetically significant, and reflected to some degree the aquatic versus terrestrial modes of life.

Janis et al. (2012) proposed that the dermal bone ornamentation developed in primitive tetrapods for the purpose of buffering acidosis and lactic acid build-up in their tissues due to anaerobic activity. This would allow them to spend longer times on land and thus better exploit the terrestrial environment. In agreement with Witzmann et al. (2010), they state that the terrestrial forms show more pronounced sculpture than aquatic forms.

All of the above arguments were based on careful reasoning. Frequently, they used comparisons to extant animals that possess textured dermal bones to imply the purpose of textured bones in extinct animals. This kind of analogy has been sound practice since the time of James Hutton and Charles Lyell (e.g., Lyell, 1830), but the vast majority of the argumentation is qualitative and general disagreement as to what might have been the primary, secondary, or multiple functions of the ornamentation remains.

**INSTITUTIONAL ABBREVIATIONS**

MNHN, Muséum National D'Histoire Naturelle, Paris; MOU, Missouri University Vertebrate Paleontology Collection, Columbia, MO; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, NM; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart; UCMP, University of California Museum of Paleontology, Berkeley, CA.

**METHODOLOGY**

Here, we quantitatively assess the possible contributions of dermal bone ornamentation to strength, cutaneous respiration, and thermal regulation. The possible contribution of ornamentation to skin-breathing and thermal regulation is assessed by measuring the surface area increase provided by the ornamentation and allometrically comparing this increase to the volume of the animal that it would be required to support. The strength of the dermal bone, with and without ornamentation, is assessed using simple beam mechanics.

**DERMAL BONE TEXTURE TYPES AND LOCATIONS**

Two types of dermal bone texture are prevalent in temnospondyl amphibians. A network of raised, reticulate ridges that enclose approximately flat-bottomed, interlocking, polygonal cells is the most common type and is referred to in this study as "reticulate" (Fig. 2A). The vast majority of these cells are four-, five-, or six-sided, creating a honeycomb- or waffle iron-like texture. In some temnospondyls, this is essentially the only texture present.

The second texture type comprises raised, parallel to sub-parallel ridges separated by round-bottomed grooves (Fig. 2B). This texture pattern is referred to as "ridge-and-groove" in this study. On the skull the ridges generally form an anastomosing pattern. On shoulder girdle elements, the anastomosing pattern is seldom seen; the sub-parallel ridges gently fan out into a more radial pattern.

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**FIGURE 1.** A typical temnospondyl amphibian skeleton, *Dutitosaurus ouazzoui*, MNHN AZA270, from the Upper Triassic of Argana, Morocco, showing the dermal bone ornamentation of the skull, lateral jaw surface, and pectoral girdle in *A*. dorsal, and *B*. ventral view. Abbreviations: *Cl*. clavicle; *F*. femur; *T*. tibia; *c. tr*. sacral rib; *P. isch.*, pubo-ischium. From Dutuit (1976, pl. 31). Total length = 1.14 m.
estimate of cutaneous respiratory capacity because of differences in skin thickness and capillary density (Feder and Burggren, 1985; Wells, 2007). However, for species where the other variables are essentially the same, comparison of surface area with and without ornamentation should give a direct comparison of skin-breathing capability.

Living amphibians and most other ectotherms bask in the sun to absorb energy as part of thermal regulation. During basking, the energy input to the animal equals the power density of the incident solar flux multiplied by exposure time (recognizing that not all frequency components of the incident flux can be converted to heat at the skin surface). Power density equals power per unit area (Watts/m²), so the energy acquired is directly proportional to the irradiated surface area.

Heating or cooling the animal through heat transfer at the skin surface, either in water or in air, is a complex problem involving conduction, convection, and radiation, and these elements are rarely encountered alone (Tsederberg, 1965). All three of these factors are directly proportional to the surface area involved (Besançon, 1974) as shown by the following expressions for heat transfer power, P (= energy/unit time = Joules/sec = Watts) by:

\[
P_{\text{conduction}} = \frac{A \times K_s \times (T_s - T_f)}{d} \\
P_{\text{convection}} = \frac{A \times K_w \times (T_s - T_f)}{d} \\
P_{\text{radiation}} = \frac{A \times K_s \times T_s^4}{d^2}
\]

where A equals the area over which the transfer occurs, \(K_s\) equals the coefficient of heat transfer, d equals the distance across which the heat is transferred, \(K_s\) is the Stefan-Boltzmann constant (a proportionality constant associated with blackbody radiation), \(T_s\) equals the temperature of the surface and the medium, and \(T_f\) equals the absolute temperature. Thus, all other factors being equal, surface area alone determines the amount of energy transferred per unit time, and a comparison between the surface area of ornamented and smooth bone describes the contribution of the ornament to thermal regulation.

Having shown that the capacity for both thermal regulation and cutaneous respiration depends directly on surface area, we now investigate whether surface area increase throughout the growth of a temnospondyl maintains an isometric relationship with the volume of the animal that it must support. If isometry, or near-isometry, is found, it would indicate that the surface area increase due to texture could effectively function to support skin breathing and/or thermal regulation.

Measuring Surface Area Increase Due to Texture

Three essentially complete skulls of the Middle Triassic temnospondyl *Eocyclosaurus* with good texture preservation were selected as a partial growth series for study. Midline lengths of these specimens are: 230 mm (NMMNH P-63328), 300 mm (NMMNH P-64360), and 389 mm (NMMNH P-64166). Latex rubber was painted on the preorbital and postorbital areas and then peeled off to "record" the surface texture (Fig. 4A-B). Numerous thin coats were applied, and cheesecloth was imbedded in the last few coats to provide mechanical support. The resulting peels were cut longitudinally and transversely to reveal the texture in cross section. The cross sections were photographed with a scale, enlarged, and printed (Fig. 4C). From these photographic prints, both the transverse and longitudinal lengths of the straight-line traces and texture traces, shown in Figure 4C as the long-dashed and short-dashed lines, respectively, were measured using a map wheel calibrated in mm. Several measurements were made on each skull, including both texture types. The products of these trace lengths were then calculated to yield the surface areas of equivalent portions of flat, smooth surface and textured surface. The reticulate texture provided a slightly greater area increase than the ridge-and-groove. In each case, the texture provided an area increase of ~1.1 to ~1.2 over the smooth surface area, being slightly greater in the larger skulls.

The increases in length of the surface traces due to texture as illustrated in Figure 4C (surface trace length/straight line length) were

![FIGURE 2. Examples of dermal bone texture types. A. Reticulate texture on the intercleavage of Koskinonodon (NMMNH P-18111) showing interlocking rectangular, pentagonal, and hexagonal cells (illumination is from the top of the page) and B. anastomosing ridge-and-groove texture on the central snout region of Eocyclosaurus (NMMNH P-64166) involving portions of the nasals, lacrimals, prefrontals, and frontals. Scale bars equal 1 cm.](image-url)
FIGURE 3. Examples of dermal bone texture in temnospondyl skull, jaw, and pectoral girdle elements. A, Holotype skull of the metoposaurid *Koskinonodon perfectum* almost entirely covered by reticulate ornamentation (right posterior portion reconstructed) (MOU 537). B, Skull of the metoposaurid *Dutuitosaurus ouazzoui* showing approximately equal portions of reticulate and anastomosing ridge-and-groove texture (MNHN AZA355). C, Skull of the mastodonsaurid *Mastodonsaurus giganteus* showing mostly ridge-and-groove texture (SMNS 80704). D, Left mandible of *Mastodonsaurus giganteus* showing heavy reticulate texture pattern on the angular, the point of attachment of the large jaw-closing muscles (SMNS 54677). E, Articulated clavicles and interclavicle of *Mastodonsaurus giganteus* showing small areas of reticulate texture with large areas of fan-like, radiating, non-anastomosing ridge-and-groove texture (SNMS 81293). Scale bars = 10 cm.
FIGURE 4. Large and small skulls of *Eocyclotosaurus*. A, NMMNH P-64166, a 389 mm midline length skull and B, NMMNH P-63328, a 230 mm midline length skull with latex patches applied to the preorbital and postorbital areas to record the dermal bone texture. C, Cross section of a latex peel “negative” of the dermal bone surface texture used to determine surface area increase due to the texture. The large dashes show the straight line distance (mm scale) and the small dashes show the surface trace. This particular peel is of the preorbital “ridge-and-groove” texture. Millimeter scale.
averaged, natural log transformed, and plotted against the natural logarithms of the skull lengths to generate an allometric evaluation of the increase in surface area versus skull length (a measure of overall size) (Fig. 5). In Figure 5, the slope of the curve fit, ~0.095, is the allometric constant representing the rate of increase in surface trace length versus the rate of increase in the linear dimensions of the skull. This allometric constant is very low, indicating strong negative allometry (Gould, 1966). McGowan (1999) has shown that a positive allometric constant of 1.5 is required in the linear dimensions to demonstrate isometry between area and volume. This results from the fact that area = length^2 and volume = length^3. So, length must increase as v1 = l^2 = l^3 to show an isometric relationship between area and volume. Thus, the slope of a line on the allometry plot (Fig. 5) would need to be 1.5 to show that the surface area increase was isometric with the volume increase.

We plot a line with a slope of 1.5 (the arrow) in Figure 5 for comparison to the data. The slope of the data line (0.095) is more than an order of magnitude too low to show that surface area increases isometrically with volume. Thus, throughout the growth range of our sample, surface area does not increase rapidly enough to supply additional area in support of cutaneous breathing or thermal regulation. This result does not show that skin breathing was not present to some degree in these animals, nor does it indicate that they did not bask or shade themselves to regulate their body temperature. However, it does show that the surface area increase due to dermal bone texture could not have been a significant factor in increasing cutaneous respiration or enhancing heat transfer for thermal regulation.

**STRUCTURAL SIGNIFICANCE OF THE DERMAL BONE TEXTURE**

Dermal bone ornamentation comprises raised ridges that form either closed cells in the reticulate texture pattern or long, approximately straight ridges in the ridge-and-groove pattern (Fig. 2). In either case, the strength of the structure may be assessed by simple beam mechanics (Fig. 6). The flat, smooth bone between these ridges may be thought of as a rectangular beam with width (W) greater than depth (D), and the ridges plus their underlying bone may be modeled as a rectangular beam with depth greater than width (Fig. 6A). The entire structure of flat underlying bone and ridges may thus be reduced to a complex of simple beam components. The strength of each of these component beams may then be calculated (Marks, 1951):

\[
\text{Strength} = W \times D^2
\]

Then the strengths of all the components may be summed, resulting in the strength of the complete reintegrated structure (Fig. 6B). The quality of the fit of this beam model to the actual surface is shown by schematically overlaying the beams on a latex peel of the surface (Fig. 6C).

Dermal bone contains a layer of cancellous (trabecular) bone sandwiched between two layers of cortical (compact) bone. The proportions of the cortical and cancellous components varies somewhat between the study bones, especially the central portion of the interclavicle of Koskinonodon, which contains a relatively thick layer of cancellous bone. Cortical bone is significantly stronger and stiffer than cancellous bone (Rho et al., 1993), so this raises a question about how to calculate the relative strength of bones that include varying proportions of both cancellous and cortical bone. However, Ruff’s (1983) work with long bones showed that for quantities of cancellous bone between 10% and 40% of the total cross sectional area the effect of the cancellous bone on overall strength is essentially negligible. This is because the cancellous layer is located in the center of the bone. When a load is applied to the bone, the outer cortical layers are placed in tension or compression, depending on the direction of the load, but the central cancellous portion is in a rela-

**FIGURE 5.** Allometry plot showing the relative rates of linear distance increase due to texture and skull length for a growth series. Natural log transforms of distance increase (surface trace/straight line trace) and skull length increase are plotted. Very high negative allometry is indicated by the low slope of the curve fit line, showing that surface area increases at a much lower rate than volume. Positive allometry with a slope of 1.5 (arrow) is required to show that surface area increases isometrically with volume.

**FIGURE 6.** Calculation of strength of the surface texture and underlying bone using beam mechanics. A, Simple strength calculations for two similar rectangular cantilevered beams with horizontal and vertical orientations can be used to model the flat underlying dermal bone and the underlying bone plus a ridge of ornamentation. B, The strength of several such beams is then integrated to yield the overall strength of underlying bone plus ornamentation over a finite area. C, Fit of the horizontally- and vertically-oriented rectangular beams to a latex peel of the actual bone surface.
relatively stress-free zone. Thus, the strong cortical layers are positioned to provide the bulk of the resistance to bending or fracture. All of our study samples fall well within the 10% to 40% cancellous bone range with the possible exception of the Koskinodon interclavicle, so we ignore the presence of the cancellous bone in our calculations and assume the strength of the bone to be homogenous throughout the cross sections.

Fifteen relative strength calculations were made based on 12 specimens of Eocyclostusaurus and Koskinodon, including approximately equal numbers of reticulate and ridge-and-groove patterns on skulls, jaws, and shoulder girdle elements (Table 1). In each case the strength of the ornamented bone and an equivalent area of smooth, flat bone were compared to show the percent increase in strength of the ornamented bone over the smooth bone. Then we calculated the percent increase in mass of the ornamented bone over the smooth bone. The results show that across a variety of dermal bones, on average, strength was increased by 39% and mass was increased by 20% due to the presence of the texture. Of course, simply adding another 20% of bone mass to the flat, smooth bone would provide increased strength as well, but this increase would amount to less than 30%, so the texture adds more strength than an equal amount of smooth bone. Thus, for both texture types a substantial increase in strength was purchased by a relatively small increase in mass.

Finally, we plot the percent mass increase as a function of percent strength increase for the reticulate and ridge-and-groove textures (Fig. 7). The curve fits to the data show that the increase in mass per unit increase in strength is 0.47 for the reticulate texture and 0.37 for the ridge-and-groove texture. As shown by the data in Figure 7, the reticulate texture is heavier than the ridge-and-groove texture for a given increase in strength, but its strength increase is omnidirectional because of its rotational symmetry, whereas the strength increase due to ridge-and-groove texture is unidirectional, aligned with the direction of the strengthening ridges.

**DISCUSSION**

**Amount of Ornamented Surface**

With respect to increased surface area, thus far we have considered the possible contributions of dermal bone texture over the skull, jaw, and shoulder girdle. It must be remembered, however, that these parts make up only a fraction of the entire surface area of the animal. There-fore, even if the ornament developed so that its surface area increased isometrically with volume, it still only covers perhaps 20 to 25% of the animal’s surface. This fact further decreases the likelihood that dermal bone texture could have contributed significantly to skin-breathing or to thermal regulation.

**Jaw Muscle Origins and Insertions**

The position and type of ornamentation around the jaw muscle origins and insertions seems relevant to the question of structural significance. Bramble (1978) showed that in vertebrates during biting the lower jaw is probably best modeled as a beam with two fulcra, one at the jaw joint and one at the location of the food item, having an applied load at the site of the jaw muscle insertion. Consider a schematic representation of a temnospondyl skull and jaw showing the supports (fulcra) and load on the jaw during biting (Fig. 8A). The arrow, of magnitude W, represents the applied load due to the jaw muscles. The beam and fulcra (triangles) model the jaw according to Bramble (1978) (Fig. 8B). A bending moment diagram for the jaw model (Fig. 8C) shows that the moment (M) peaks at the point of muscle insertion in the adductor fossa (Laurson and Cox, 1938; Marks, 1951). In the temnospondyl jaw, this point is on the angular, the most extensively ornamented bone of the jaw (Fig. 8D, and see Fig. 3D). The implication is certainly that the ornamentation has developed to strengthen the jaw at the point where the bending moment is maximized.

The skull and jaw model (Fig. 8A) may be flipped upside down to show that the same fulcra, load, and bending moment apply equally as well to the skull as they do to the jaw. The maximum bending moment then, would be located at the jaw muscle origin on the roof of the skull’s adductor fossae, principally on the squamosals. The squamosals are generally ornamented with heavy ridge-and-groove texture radiating anteriorly and anterolaterally from the area above the jaw joints out over the adductor fossae (Fig. 3A-C). This also suggests that the heaviest texture on the skull is focused at the point of maximum stress due to feeding.

**Honeycomb Structural Materials**

The similarity between the appearance of the reticulate dermal bone texture pattern and honeycomb structural materials cannot be ignored in the assessment of strength. Strong, stiff, lightweight, honeycomb panels are used in applications ranging from aircraft wings to furniture. These panels comprise a layer of honeycomb-like material.

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**TABLE 1. Percent strength and mass increase of ornamented bone over smooth bone for the study specimens. Abbreviations: Ret, reticulate texture; R&G, ridge-and-groove texture.**

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<th>Texture Type</th>
<th>Specimen Number</th>
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<th>Mass Increase (%)</th>
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sandwiched between two thin flat layers. The honeycomb layer takes on
the attributes of the web of an I-beam, strengthening the structure by
adding substantial depth while increasing mass only slightly. The dif-
ference is that the added strength of the honeycomb material is omnidirec-
tional rather than unidirectional, as it is in an I-beam. It is the rotational
symmetry about the axis of the cells that is responsible for the omni-
directional strength increase.

Using manufacturers’ data sheets and bulletins for aluminum, fi-
berglass, and paper composite panels (Hexcell Composite Materials,
1999; Tricel Honeycomb Corporation, 2012), we generated a regression
describing relative strength increase for a given thickness of the honey-
comb material (Fig. 9). Here, the thickness is the total thickness of the
sandwich, and the units are the combined thickness of the flat sandwich
layers enclosing the honeycomb layer. So, from Figure 9, for example, if
the flat layers total one cm of thickness, the addition of only 1/3 cm of
honeycomb (total thickness = 1 1/3 cm), increases the strength by a
factor of approximately 1.9 over the flat layers alone. A similar result is
obtained if a 1/3 cm-thick ridge is added to 1 cm of flat bone. In this case,
strength is increased by a factor of 1.8. Thus, the reticulate ornamenta-
ment pattern is somewhat similar to the honeycomb structural material –
not only in appearance, but also in its omnidirectional strength and
roughly in the amount of strength increase it provides.

CONCLUSIONS

Our calculations show that in textured dermal bone, the surface
area increases in very strong negative allometry with respect to volume
(Fig. 5). This indicates that the rate of surface area increase cannot sup-
port cutaneous respiration or thermal regulation, both of which are area-
dependent, throughout growth. It certainly is possible that the texture
provided a minimal benefit to small animals where the surface area-to-
volume ratio is more advantageous, but it could not have been a signifi-
cant factor throughout ontogeny, especially for large animals.

Over a wide variety of skull, jaw, and shoulder girdle bones, the
ornamentation provides a significant increase in strength, averaging 39%,
but as high as 95% locally. The strength increase is accompanied by a
relatively small mass increase averaging 20%, but as high as 50% locally.
In every case, on all of the study bones, the percent strength increase
exceeded the percent mass increase (Table 1, Fig. 7). Simply increasing
the thickness of the smooth, flat bone mass by the amount of mass added
by the texture does not result in an equivalent strength increase. How-

FIGURE 8. Diagrammatic explanation of bending moment on lower jaw
during biting. A, Schematic of skull and jaw with food item and applied force
of the jaw musculature. B, Jaw modeled as a beam supported by two fulcra
(triangles), one at the jaw joint and one at the food item, with applied load
(W) exerted by jaw musculature. C, Bending moment diagram and equation
showing that bending stress (M) maximizes at the point of muscle attachment
(after Marks, 1951). D, Posterior portion of the jaw of *Eocyclotosaurus*
showing the typical heavy reticulate and ridge-and-groove ornamenta-
tion of the angular. Short vertical bars define the limits of the adductor fossa,
which opens dorsally. The arrow shows the location and direction of the
load as in the diagrams above. Note that the load is centered on the heavily
ornamented angular. Horizontal scale bar = 5 cm.

FIGURE 9. Relative strength of structural honeycomb panels as a function
of panel thickness. Units of thickness are the combined thickness of the flat
"sandwich" layers enclosing the honeycomb layer. Graph based on
manufacturers’ data for aluminum, fiberglass, and paper composite panels.
ever, the ridges of the dermal bone ornamentation act as the web of an I-beam does, strengthening the structure substantially with a relatively small mass increase. They do this because of their perpendicular orientation to the flat underlying bone, which effectively increases the depth of the structure and takes advantage of the depth-squared term in the strength equation (above, and Fig. 6).

The reticulate texture is more energy expensive for the animal to construct and to carry than the ridge-and-groove texture for a given strength increase. Its advantage is that its strength is omnidirectional, whereas the lighter ridge-and-groove texture’s strength is unidirectional. Thus, the lighter weight ridge-and-groove ornament is employed where stress is unidirectional, and the reticulate pattern is used as needed where stress direction is variable and omnidirectional strength is required. We have shown that the location and degree of development of the dermal bone texture is dependent, at least to some extent, on the location of muscle attachments where bending stress is maximized on the skull and jaws. The association of ornamentation patterns with applied stress due to muscle attachments opens interesting possibilities for evaluation of the musculature of the pectoral girdle.

As to the ultimate question regarding the function of dermal bone ornamentation, the quantitative results of this study significantly weaken the skin-breathing and thermal regulation hypotheses and strengthen the structural strength hypothesis.

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