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POSSIBLE FUNCTIONS OF ORNAMENT  
IN LABYRINTHODONT AMPHIBIANS

By

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Potentially both endochondral and dermal bone can have sculptured surfaces. Such ornamentation (which for simplicity will be called ornament) occurs on the dermal skull roofing bones, dermal parts of the pectoral girdle, and neural arches. The rhachitome, *Cacops*, has ornamented dermal plates capping the neural arches. Ornament appears throughout the Labyrinthodontia. Within this group the dermal skull roofing bones invariably are sculptured. Ornament frequently covers the dermal girdle but only rarely the neural arch. In the more advanced cotylosaurian reptiles, ornament becomes less evident. Among modern vertebrates, dermal sculpturing is common in the crocodylians and some frogs. Some turtles and fishes possess ornamented dermal bone, but is rare.

Nearly all types of ornament can be put in two main categories—random, closely packed pits and interconnecting ridges, and longer ridges and furrows oriented radially or longitudinally to a center of ossification. Other forms occur but are rare: isolated pits sunk into a uniform surface; long, random ridges; rugose, horny projections. Within a single species nearly any combination is seen so that, for example, *Eugyrinus wildi* has individual pits and radial, asymmetric, and longitudinal ridges and furrows.

There are two opinions on the function of this ornament. Bystrow (1944, 1947) suggested that ornament is associated with vascular canals in the dermal skull roofing bones and hence aided in cutaneous respiration. Romer (1947) and others have proposed that orna-

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ment provided a cranial structure to which the skin may be tightly bound.

Romer's view very well may be true. However, the different types of ornament, its ubiquitous presence on the skull, and the fact that the skin is just as tightly bound to smooth bone as to the ornamented portions in modern crocodylians requires a further explanation. Bystrow explained the function of ornament on the basis of its internal structure. In the "hydrophilous" labyrinthodonts he divided the dermal bone into three layers—lower, middle, and upper. Each of these layers is penetrated by the normal Haversian canals, which anastomose with one another. Thus, the canals of the upper layer communicate with the larger Haversian canals in the middle layer and open as foramina to the bone surface at the bottom of each pit. He concludes that the Haversian system carried a small artery, larger vein, thin branches of nerves, and lymphatic vessels.

Bystrow termed this Haversian system a "Rete Vasculosum" which appears only in association with the sculpture. Therefore he correlated the sculpture with a vascular system supplying the skin and hence with cutaneous respiration.

However, the correlation between "round-celled" sculpture (random pits and ridges) and cutaneous respiration does not hold for what he called the "xerophilous" labyrinthodonts. In places these have ridges and furrows instead of the "round-celled" sculpture of the "hydrophilous" forms and no "Rete Vasculosum" (and thus no cutaneous respiration). There is no neat division of sculpture related to a given species. As mentioned earlier, an individual can have two or three different types of sculpture. Therefore, although a correlation exists in that wherever cutaneous respiration is implied by bone microstructure there also exists "round-celled" sculpture, the reverse does not hold. It does not hold because both the "round-celled" and ridge and furrow types of ornament exist on the same specimen and yet no "Rete Vasculosum" exists. Hence, the presence of sculpture, regardless of type, does not imply the existence of cutaneous respiration. In *Benthosuchus*, a "hydrophilous" form, Bystrow associated a respiratory function to the clavicle ornament, yet this ornament is the ridge and furrow type. In the "xerophilous" forms, however, the ridge and furrow sculpture has no "Rete Vasculosum" and thus has no association with cutaneous respiration. Clearly, the correlation between ornament and cutaneous respiration does not hold.

Other difficulties exist with his interpretation of the bone microstructure (canals). The irregularity and complexity of the canals within the bone seems to provide a circuitous and inefficient route to the ornamented surface and to the skin. Furthermore, the canals are arranged horizontally to the bone lamellae. If blood were

to be directed to the surface, a more adaptive route would be via a less complex canal pathway. It is unlikely that random anastomoses between canals is related to a systematic connection to the outside epidermis. Also, if the main function of the canals is to carry blood vessels, those of the lower bone layer feeding into the larger middle layer canals would cause a drastic decrease in blood pressure. This would be very inefficient for rapid blood flow and efficient oxygen exchange at the skin surface. Finally, the large Haversian canals of the middle layer are found in the ornamented dermal bone of the "xerophilous" forms which do not have an upper layer "Rete Vasculosum."

Romer (1972) leveled the most striking criticism of Bystrow's theory. Romer suggested that cutaneous respiration is a degenerative characteristic of modern amphibians. Within this group, blood is supplied from a pulmocutaneous artery (frogs) or from smaller arteries distributed more evenly over the body surface (salamanders). It is generally concluded that the cutaneous blood supply does not pass through bone. The ancient amphibians probably relied on lungs for respiration. The fossil record shows lungs in *Bothriolepis*, a placoderm. Thus, lungs were not a new and unimportant development at the labyrinthodont stage. Furthermore, the presence of a well-developed thoracic basket makes aspiration breathing probable in the labyrinthodonts. Finally, the labyrinthodonts most likely had a full covering of dermal scales. In various labyrinthodont groups, as better specimens become available, dermal armor is being discovered on the dorsal surface (Baird, 1964; Bystrow, 1944; Carrol, 1969; Colbert, 1955). The scalation in *Seymouria*, well-developed dorsally, suggests that scalation was not a specialization of isolated amphibian groups but more probably a primitive character which persisted well toward the reptilian level of evolution.

If ornament strengthens bone by resistance and diffusion of stress, then one can explain its presence wherever it occurs. Changes in ornament relative to different skull sizes, dimensions, and jaw musculature support ornament as a strengthening adaptation. Fox (1964) has proposed that ornament may strengthen bone by reinforcement. In studying the cheek region of *Captorhinus*, he noticed that ornament is aligned parallel to presumed directions of stress. Where less stress was assumed to exist, bone is thinner and the ornament is random. Fox's functional interpretation of the ornament is supported by its orientation not being merely a result of differential bone growth. Different ornament orientations are laid down in specific and predictable areas.

Random sculpturing (pits and ridges), by diffusing stress, serves an active rather than a passive role. The rest of this study will analyze and hopefully support a strengthening function for orna-

mented bone. Four experimental approaches are taken. The first is called a "split-line" technique in which the collagen fiber orientation in a modern crocodylian is exposed. This shows the distribution of stress throughout the skull. The second experimental approach is a histological study of bone and its surrounding tissues, again in a modern crocodylian. This study confirms criticism of Bystrow's hypotheses. The third is a series of thin sections of *Eryops* dermal skull roofing bones at various depths. This reveals the collagen fiber orientation and establishes an analog to the "split-line" technique of the modern crocodylians. The last is a review of 30 genera of labyrinthodont amphibians with respect to skull proportions and intensity of ornament.

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#### MATERIALS AND METHODS

The biological materials are as follows. An immature *Alligator mississippiensis* was used for the split-line technique. The length from snout to occipital condyle was 16 cm. For the histological study, a formalin-preserved head, 7.5 cm in length, of *Caimon sclerops* was used. Because different taxa are involved, positions of ornament differ. However, absolute position is important only in the mechanical studies, where ornament position affects skull trajectories brought out by the split-line technique. In the histological studies, ornament is considered only in terms of surrounding tissues. Dermal bone fragments from various parts of the skull of *Eryops* were used for thin sections.

The materials and methods involved in the split-line technique are discussed thoroughly by Benninghoff (1925). A more general discussion is found in Tappen (1953) and Seipel (1946). A brief summary follows: 1.—Fix specimen in 10% formalin for one week; 2.—decalcify in 5% nitric acid, the acid being stirred occasionally and changed once a day (usual time is three days followed by one or two days of washing); 3.—bleach in 3%  $H_2O_2$  for one day to facilitate later photography; 4.—dessicate in alcohol for three days (60%, 70%, and finally 80%) and preserve specimen in 80% alcohol



during time of preparation; 5.—puncture the surface of the bone with a sharpened teasing needle; 6.—inject with a hypodermic needle india ink into the fractures. The fractures occur parallel to the collagen fibers. Hence the split-line technique reveals the orientation of the bone microstructure. The result is the formation of trajectories along the bone surface when the small fracture lines are joined.

The method used in sectioning, staining, and embedding are systematically covered in Geyer (1936). The sections were cut to  $1 \text{ cm}^2 \times \frac{1}{8}$  inch thick, and the celloidin method of embedding was employed. A triple stain of hematoxylin, eosin, and azure was used to differentiate the tissues.

The *Eryops* bone thin sections were made as follows: 1.—Mount dermal bone fragments on a glass slide with Lakeside, a thermal plastic cement; 2.—grind specimen to the desired level with water and coarse to fine grit and powder (coarse, #400 grit silicon carbide; medium, aluminum oxide No. 9½; fine, aluminum oxide No. 3); 3.—reheat cement, turn specimen over, and repeat procedure (after each phase of grinding the slide should be washed thoroughly with fast running water to remove all grinding material); 4.—place cover slip over the finished specimen using Canada balsam as a fixative.

Data for the 30 genera of labyrinthodonts came from the literature (see Appendix) and from specimens at the American Museum of Natural History and Museum of Natural History, The University of Kansas (see Specimens Examined).

## RESULTS

The alligator dermal skull roofing bones exhibit three general collagen fiber orientations by the split-line technique. First, the

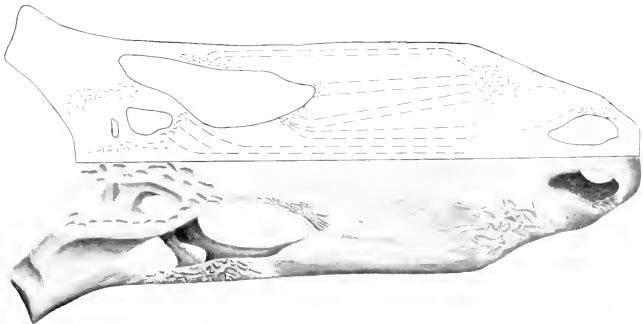


FIG. 1.—Composite view of skull of *Alligator mississippiensis*. Below, location of ornament; above, stress trajectories, where the dashes represent fractures in the bone brought out by the split-line technique.

fractures along unornamented sections of bone are linear and parallel, running antero-posteriorly along the skull. Second, the lines converge toward ornamented areas. Third, within ornamented areas, lines of stress (trajectories) do not appear. Instead, either the bone fractures non-linearly in random directions, or there is no fracture but only round puncture holes.

Specifically, there are five main ornamented areas around which trajectories converge (Fig. 1). The two main areas are (1) at the anterior end of the maxilla directly over the largest tooth and (2) on the squamosal. Two of the smaller, less ornamented areas occur at the prefrontal along the medial orbital boundary and on the jugal at the lateral orbital boundary. The least ornamented areas occur on the prenasal at the lateral narial border.

Trajectories originate from the most anterior teeth and converge on either the prenasal or the maxillary ornament. A second group of trajectories run parallel to the more posterior teeth (past the sixth tooth). These parallel trajectories converge on the jugal ornament (lateral orbital border) and originate from the main ornamented area at the anterior portion of the maxillary. More trajectories from this maxillary ornament run anteriorly to the prenasal ornament and posteriorly to the jugal ornament (medial orbital border). The medial skull trajectories deflect toward the maxillary ornament and run parallel between the orbits and radiate out into the heavily ornamented squamosal (skull table).

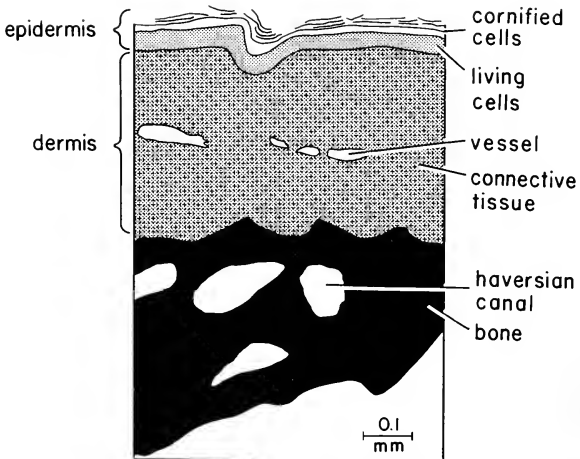


FIG. 2.—Cross section of *Caimon sclerops* maxillary showing the relation of ornamented bone to dermal and epidermal vascularization.

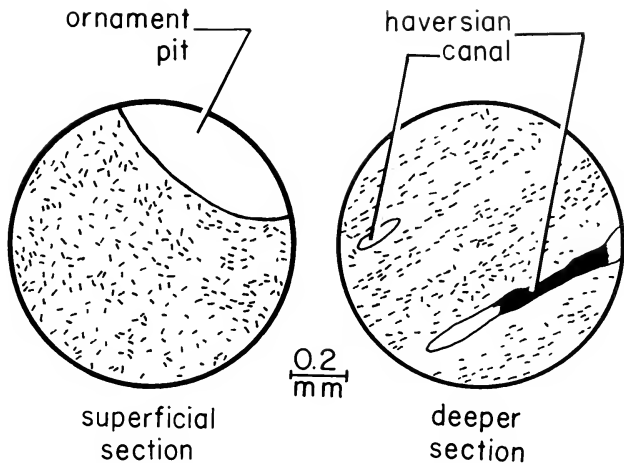


FIG. 3.—Thin sections of *Eryops* dermal bone fragments showing the orientation (small dashes) of lacunae within the bone.

The histological sections of the ornamented maxillary (Fig. 2) and squamosal exhibit four important features. The bone has very large Haversian canals in what Bystrow (1947) calls the middle layer. Above and below this layer no canals are present. The vascularization of the subcutaneous connective tissue and smooth muscle above the bone is slight. Finally, above the epidermis lies relatively thick cornified epithelium. The cells are flattened, compact, and apparently dead throughout this layer.

Thin sections of ornamented dermal skull roofing bone in *Eryops* (Fig. 3) show different collagen fiber orientations according to bone depth. Collagen fibers themselves cannot be seen. Their orientation is inferred from the long-axis orientation of the bone lacunae. In the lower and middle layers, collagen fibers parallel one another. Where ornament interrupts the upper layer, the collagen fibers are non-parallel and random.

Ornament rugosity within different labyrinthodont lines shows a general trend relative to the ratio of skull height to skull width (measured at the occiput), and shape of the subtemporal fossa (Table 1). Two trends are present: (1) with wider and longer subtemporal fossa the ornament is usually more rugose; and (2) with a smaller height/width ratio of skull the ornament is most often better developed. These trends are not apparent in individuals of only slightly differing characters. However, large differences in the

TABLE I.—CHARACTER STATES OF VARIABLES OF LABYRINTHODONT SKULLS.

	Height/Width of Skull	Intensity of Ornament	Size of Sub-temporal Fossa; Size and Depth of its Anterior Emargination	Width of Inter-pterygoid Vacuities	Degree of Kinosis	Length of Skull
<b>Ichthyostegids</b>						
<i>Erpetosaurus</i>	1:3	moderate to well developed	wide; deep wedge	$\frac{3}{4}$ palate width	moveable	8cm
<i>Colosteus</i>	1:3	moderate to well developed	wide; deep wedge	$\frac{3}{4}$ palate width	moveable	10cm
<i>Ichthyostega</i>	1:3.5	moderate to well developed	oblong; no emargination	none	moveable	21.3cm
<b>Loxommid</b>						
<i>Macreripecton</i>	1:2.3	moderate	very wide; shallow emargination	none	moveable	10cm
<b>Primitive Rhachitomes</b>						
<i>Trimerorhachis</i>	1:3	moderate to well developed	moderate; deep, broad emargination	$\frac{3}{4}$ palate width	moveable	15cm
<i>Saureripecton</i>	1:3	well developed	very wide and long; no distinct emargination	$\frac{3}{4}$ palate width	moveable(?)	6.5cm
<i>Edops</i>	1:5	well developed	wide; well developed emargination	$\frac{1}{2}$ palate width	moveable	61cm
<b>Typical Rhachitomes</b>						
<i>Cucops</i>	1:1.6	moderate to well developed	wide, very long; deep, wide emargination	$\frac{3}{4}$ palate width	fused	15cm
<i>Parioxys</i>	1:2	moderate to well developed	wide; wide, shallow emargination	$\frac{1}{2}$ palate width	fused(?)	10cm
<i>Acheloma</i>	1:2.5	moderate to well developed	wide; wide, shallow emargination	$\frac{1}{2}$ palate width	fused	14cm

<i>Melosaurus</i>	1:3(?)	moderate	very wide; very slight emargination	$\frac{1}{2}$ palate width	moveable	20cm
<i>Broiliellus</i>	1:3	moderate to <i>well developed</i>	well developed; very deep emargination	$\frac{1}{2}$ palate width	fused	8cm
<i>Eryops</i>	1:3.1	moderate to well developed	wide; well developed emargination	$\frac{1}{2}$ palate width	fused	40cm
<i>Chenoprosopis</i>	1:3.1	well developed	wide; deep emargination	$\frac{1}{2}$ palate width	moveable	30cm
<i>Stegops</i>	1:3.1	well developed	wide; deep emargination	$\frac{1}{2}$ palate width	moveable	7cm
<i>Dissoroplans</i>	1:4	moderate to well developed	moderate; moderate emargination	$\frac{1}{2}$ palate width(?)	fused	17cm
<i>Zatrachys</i>	1:4.6	very well developed with horns	moderate; well developed, deep emargination	$\frac{1}{2}$ palate width	fused	11cm
<i>Trematops</i>	1:7.8	very well developed	wide; shallow emargination	$\frac{1}{2}$ palate width	fused	8.5cm
<b>Capitosaur</b>						
<i>Capitosaurus</i>	1:3.6	well developed	wide; moderately deep emargination	$\frac{1}{2}$ palate width	fused	28cm
<i>Parotosaurus</i>	1:6	moderate to well developed	moderate; wide, shallow emargination	$\frac{1}{2}$ palate width	fused	25cm
<b>Trematosaur</b>						
<i>Trematosaurus</i>	1:2.8	moderate to well developed	moderate to wide, long; wide wedge shaped emargination	$\frac{1}{2}$ palate width	fused	27cm
<i>Lyrocephalus</i>	1:3.4	moderate to <i>well developed</i>	moderately wide; wide, deep wedge shaped emargination	$\frac{1}{2}$ palate width	fused	17cm
<b>Neorhachitome</b>						
<i>Benthosuchus</i>	1:3.0	moderate to well developed	wide; moderate deep emargination	$\frac{1}{2}$ palate width	fused	17cm

	Height/Width of Skull	Intensity of Ornament	Size of Sub-temporal Fossa; Size and Depth of its Anterior Emargination	Width of Inter-pterygoid Vacuities	Degree of Kinesis	Length of Skull
<b>Stereospondyls</b>						
<i>Eupelor</i>	1:5	well developed	wide; wide, deep emargination	$\frac{3}{4}$ palate width	fused	61cm
<i>Getrothorax</i>	1:10	very strong but unique columnar bumps	moderate to wide; wedge-shaped, moderately deep emargination	$\frac{3}{4}$ palate width	fused	13cm
<b>Embolomeres</b>						
<i>Palaeogyrinus</i>	1:2:3	slight to moderate	very long, narrow; no distinct emargination	none	moveable	16cm
<i>Archeria</i>	1:3:2	slight(?)	wide and long(?); emargination unknown	none	moveable	20cm
<i>Pteroplax</i>	1:2-1:3	slight	very wide; wide, shallow emargination	none	moveable	17cm
<b>Seymouriamorphs</b>						
<i>Scymouria</i>	1:2:8	moderate	wide; thin, long emargination	none	moveable	10cm
<i>Kotlassia</i>	1:3:2	well developed	wide, long; wide, very deep emargination	none	moveable	11cm

above characters show these trends to be predictable in widely different lines of labyrinthodonts. Ornament rugosity seems to be independent of other variable skull features such as length of skull, relative proportions of cheek and snout, degree of kinesis, and width of inter-pterygoid vacuities.

## DISCUSSION

The histological sections show that cutaneous respiration is impossible. The top layer of ornamented bone is free of the large Haversian canals as is the subcutaneous connective tissue above. Hence, the blood supply below the living epidermis is meager, at best, and could not serve for efficient gas exchange. Furthermore, the cornified epithelium prevents any possible exchange that could take place between the living epidermis and the poorly vascularized connective tissue below. Frogs, which do respire through their skin, lack this outer cornified layer so that gas exchange can occur. Also, the alligator has, at the bottom of many ornament pits, an opening like that seen in some labyrinthodont ornament. Bystrow (1947) interpreted these to be openings in the bone for blood supply to a respiring skin. Clearly, even if these foramina are associated with blood vessels, they can not be related to skin respiration. All these factors, then, indicate an alternate explanation for the occurrence and function of ornament.

The results of the histological study must be interpreted cautiously. The dermis of the ancient amphibians could have been arranged quite differently. In the case of the modern alligatorids, the ornament shows no correlation with cutaneous respiration. Therefore, the histological evidence, being negative, is only indirect.

The split-line technique might offer a mechanical explanation to ornament. Parallel fractures along smooth bone indicate the general orientation of the collagen matrix in a particular region. Because the collagen fiber orientation is an indicator of stress direction, the stress is clearly shown to run from either the tooth row to an ornamented region or from one region of ornament to another. The fact that the fracture lines run antero-posteriorly between ornament demonstrates the overall stress direction over the skull. With the origin of stress at the posterior attachments of the jaw musculature and at the more anterior teeth, one would expect the fracture lines to run in a general antero-posterior direction.

Within the ornamented region the disorganized non-linear fractures demonstrate a random collagen orientation. The simple round punctures indicate that the collagen fibers are oriented perpendicular to the skull surface. Round punctures would occur in the walls of ornamented pits and small foramina. The non-oriented collagen on the other hand, shows stress is diffused throughout that region of bone. Hence, the ornament acts as a reinforcement against stress

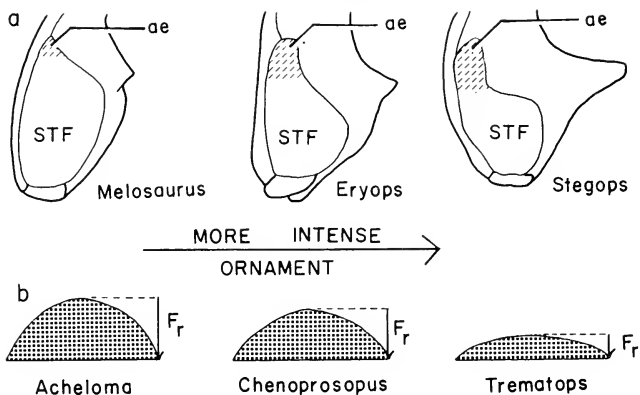


FIG. 4.—Trends seen within the labyrinthodonts concerning skull profile, jaw musculature, and ornament intensity; (a) shows increasing area of anterior adductors from *Melosaurus* to *Stegops*; (b) shows lower skull profiles (occipital view) from *Acheloma* to *Trematops*.

by diverting the stress down into thicker bone and by diffusing stress throughout the ornamented area. Since stress converges on ornament, fractures cannot form where stress is best defined.

The thin sections of *Eryops* dermal bone demonstrate a structural mechanism for diffusing stress throughout ornamented areas. Individual collagen fibers propagate stress because of their greater organization and density different from the bone mineral. In lower layers of ornamented bone the collagen fibers are oriented parallel to one another and stress direction is well defined. This is seen in the smooth areas of alligator bone, where the fractures are straight or gently curving and parallel. In the upper layers of *Eryops*, however, the collagen fibers are random, as were, presumably, the stress directions. Ornamented areas in the modern alligator show the same random stress directions by the split-line technique. In labyrinthodonts the ornament is distributed over the entire dorsal skull surface. Thus, ornament could diffuse stress wherever it occurs on the skull. Therefore stress could not form in preferred areas.

The random pattern of collagen fibers should be expected in ornamented bone. Exostosis produces sculpturing on bone surfaces in modern frogs (Trueb, 1973). In this process resorption, secondary deposition, and subsequent modification of sculpture patterns produce all three basic ornament patterns. Because of the extent of reorganization involved one would expect a more complicated collagen fiber arrangement than in simple bone. In smooth bone, layer after layer is laid down in simple sheets without differential



growth to create ridges or resorption to produce pits. A simpler but familiar model of sculpturing is seen in the production of Haversian canals. Resorption and secondary deposition create a more complex collagen fiber arrangement adjacent to a canal than in the surrounding bone.

Trends of greater ornament rugosity with larger subtemporal fossa and/or lower skull profile indicate a correlation of ornament with labyrinthodont jaw mechanics. Labyrinthodonts have a distinct jaw musculature which is termed by Olson (1961) as the kinetic-inertial (K-I) system. In this system there are two main divisions of the adductor muscles, anterior and posterior. The anterior adductors exert the greatest force at maximum gape. At occlusion the anterior adductors exert no force since the adductor fossa and subtemporal fossa are on nearly the same plane. The posterior adductors are most important in holding jaw position and have some importance in adduction.

The subtemporal fossa often has an anterior emargination (Fig. 4, a) variably developed. Olson interpreted the anterior emargination of the subtemporal fossa to be a slot over which the tendon of the anterior adductors passed. However, in many forms this anterior emargination is wide and deep, indicating that it also accommodated better developed anterior adductors.

In reptiles, the adductor musculature is divided into three parts—anterior, middle, and posterior. The middle and posterior adductors become differentiated, whereas the anterior adductors are emphasized. The anterior adductors are small or absent. Olson termed this as the static-pressure (S-P) system. In this system maximum adductor force occurs at or near occlusion. Because the adductors are differentiated over the K-I system, the S-P system is more susceptible to evolutionary modification. The crocodylians are such an example. They have a secondarily derived K-I system.

Concerning adductor muscle insertion, the K-I system has a longer and more powerful lever arm than does the S-P system (Fig. 5a). The resultant angular acceleration is much greater in the K-I system, as seen in the following analysis (also see Fig. 5c):

$$\text{K-I: } a = \frac{x_1 F_1 \sin \psi + x_2 F_2 \sin \psi + x_3 F_3 \sin \psi}{I}$$

$$\text{S-P: } \acute{a} = \frac{x_1 F'_1 \sin \psi + x_2 F'_2 \sin \psi + x_3 F'_3 \sin \psi}{I}$$

where  $a$  and  $\acute{a}$  = angular acceleration.

$x_1, x_2, x_3$  = distance from the jaw articulation to the point of muscle insertion on the lower jaw (= lever arm length).

$F_1, F_2, F_3$ , and  $F'_1, F'_2, F'_3$  = forces of the adductor muscles.

$I$  = moment of inertia

$\psi$  = angle at which the adductor muscles attach to the lower jaw.

From figure 5, b and c, one sees that  $F_2 = F'_2$ ,  $F_1 = F'_3$ , and  $F_3 = F'_1$ . All other variables are assumed to be equal for simplicity (see below for further comment).  $F_3$  and  $F'_1$  represent the maximum adductor force. In this simple model the muscles differ only in position of insertion. Therefore, the difference in angular acceleration will be directly related to  $x_3/x_1$ . Examination of table 1 indicates that the anterior emargination of the adductor fossa in some labyrinthodonts is quite deep. This suggests that the main adductor force ( $F_3$ ) has a large value for  $x_3$ . In both the K-I and S-P systems the posterior adductors are reasonably close to the jaw articulation;  $x_3/x_1$ , then, would be reasonably large. The result is a significantly greater angular acceleration,  $a$  at occlusion in the K-I system.

Stress is defined as force per unit area. Because force is directly related to the angular acceleration, the stress exerted on the skull also will be significantly greater in the K-I system. This force will, of course, be greater in those forms with better developed anterior adductors. Greater stress created with a better developed subtemporal fossa might explain the trend toward more intense ornamentation.

The skull profile is also important in ornament intensity. The flatter skull is more susceptible to both compressive and tensile stress. The type of profile determines the resistance offered by the skull roof to the occlusal force of the lower jaw (Fig. 4, b). With a smaller height/width ratio, there is a smaller vertical component of the resistance force. This bears on the trend of stronger ornamentation with flatter skulls. If ornament diffuses stress and strengthens bone, then more intense ornament may be necessary to compensate for such a small resistance by the skull roof. Tensile stress is generated by raising the skull roof relative to the lower jaw. Watson (1951) stated that there is a dependent corollary in a large retroarticular process with flat-profiled skulls. This process serves

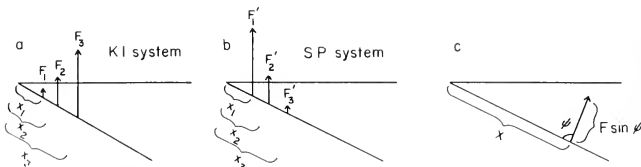


FIG. 5.—Different adductor muscle forces (a,  $F_1, F_2, F_3$ ; b,  $F'_1, F'_2, F'_3$ ), and lever arm lengths ( $x_1, x_2$ , and  $x_3$ ) of the K-I and S-P system, and force exerted by an adductor muscle (c,  $F \sin \psi$  for any angle of muscle insertion,  $\psi$ , where  $\psi < 90^\circ$ ; for  $\psi > 90^\circ$  read  $F \sin (180^\circ - \psi)$ ).

as an origin for the *depressor mandibuli* which inserts on the occiput as high as possible (nearest to the skull table). This muscle is responsible for raising the skull. Because of the short lever arm distance between the end of the process and the jaw articulation, the muscle must act at a great mechanical disadvantage. The force needed to raise the skull then must be large. The result is a large tensile stress imparted on the skull table behind the orbits. In the alligator, which has a well-developed retroarticular process, the skull table is one of the most heavily pitted regions of the skull.

In forms with large height/width ratios, ornament would not need to be as well-developed, because a large vertical resistance to the occluding jaw is present. The change of skull profile and ornament intensity also can help to explain the reduction of ornament in the cotylosaurian reptiles. The anthracosaurs (labyrinthodonts) have high skull profiles and only slight to moderate ornamentation. The captorhinomorphs and procolophonids, with narrower and higher skulls, finally dispose of ornament except for a few forms (*Captorhinus* and some paraesauurs, for example). It should be added that these cotylosaurs had acquired a S-P jaw musculature.

Drawing conclusions from ornament intensity and trends in skull parameters is tentative. Because many of the skulls could only be examined by photographs, any direct measurements were impossible. Only 30 genera of labyrinthodonts were observed; thus, the trends described here are not necessarily conclusive. Because a dead system is being studied, only qualitative differences and comparisons among and within the different jaw mechanisms can be made. Other problems exist in comparisons between the two jaw mechanisms. In many forms which have a S-P jaw musculature, there is also a reasonably well-developed coronoid process. A coronoid process lengthens the effective lever arm of the lower jaw. This reduces the difference between the S-P and the K-I systems. However, the S-P jaw musculature is also characterized by differentiation of the adductors for lateral and antero-posterior movements (Olson, 1961). The result is a decrease in vertical adductor force (lower value for  $\sin\psi$  in the equation above). By dividing the adductor force into different components in the S-P system, the resultant stress on the skull is less than if the adductor force were directed vertically (K-I system). Thus, there are conflicting factors which make comparisons between labyrinthodonts and reptiles ambiguous. The trends of ornament intensity have been restricted to the labyrinthodonts where trends in jaw musculature conform to the K-I system.

Many of the conclusions concerning ornament function in labyrinthodonts have involved the crocodilian skull. A comparison of sculptured bone in the two groups is warranted. In the labyrinthodonts ornament is evenly distributed over all the skull roof. The ornament in modern crocodilians is widespread over the skull but

is distributed unevenly; the more rugose regions are usually associated with thicker bone. Similar irregularities exist in only a few labyrinthodonts (*i.e.*, *Intasuchus*). Also the crocodylians have relatively long, non-linear ridges and furrows unlike most of the ancient amphibians. However, the random pits and ridges are similar in both groups. The uneven distribution of ornament over the skull and its slightly different form in crocodylians might imply a function different from that in the labyrinthodonts. However, the differences in ornament between the two groups are in degree, not in kind.

There is also the possibility that ornament ridges may act to reinforce bone in a girder fashion, as mentioned by Fox (1964). Trueb (1973) also suggested that the ornamentation in modern frogs may reinforce bone. In all long-snouted labyrinthodonts longitudinal ridges occur in the snout region. Orientation of these ridges is not a developmental artifact. Ornament is added onto bone surfaces at early but separate stages. In *Branchiosaurus* (Credner, 1883) radial ridges appear from the earliest stages of growth to maturity. The same process of sculpturing is seen in the modern alligator. Random sculpture appears in localized areas first; at later stages longitudinal ridges appear in the snout region and persist in later growth stages. Trueb (1970), studying casque-headed tree frogs (Hylidae), observed that ornament initially is localized and then spreads over the bone surface. Olson (1951) showed bone growth in *Diplocaulus* to occur at different rates. However, the ornamented surface is uniform with random pits and interconnecting ridges. Because ornament patterns are not due to differential bone growth of perimeter relative to center, the patterns may necessarily act to reinforce long dermal bones by resisting stress in a general antero-posterior direction. Stress exists in this general direction, as is seen in stress lines (trajectories) of the alligator (Fig. 1), which is also long-snouted. The same reinforcement of bone may be acting in radial ridging.

Another possible function of ornament is to prevent microscopic surface fractures from spreading. Currey (1962) examined thin sections of partially cracked bone. He found that fractures stopped at bone lacunae more often than would be expected from a random fracture pattern. Alexander (1968) stated that stress is concentrated at the end of a crack. This stress can be blunted if the crack ends in a rounded cavity. Stress would be redistributed and diffused around a much larger surface area (the surface of the lacunae). This same principle may act at the surface where dermal pitting occurs. Any fracture that starts at or near the surface immediately would run into a pit. The leading edge of the crack would be transformed to the larger surface area of the pit. Hence, stress would be less concentrated because of the larger surface area. Parts of automobile engines which are under stress are often pitted (shot-

peened) in order to stop fractures from spreading along the surface and into the interior.

By assigning a strengthening function to ornament, one can explain its presence on any structure. As mentioned previously, ornament appears on widely different structures, including the pectoral girdle (most prominent on the interclavicle) and dermal plates capping the neural arches. The interclavicle has a wide contact with the clavicles. From this contact, torsion (stress) from the limbs would be transferred to the interclavicle via the clavicles. The unusual dermal caps are assumed to lend rigidity to the vertebral column. This allows the vertebral column to support the weight of the animal on land. In this case stress would be applied to these elements through the vertebral column and by adjacent plates. Of course, whether the forces involved would warrant the ornament is speculative.

### SUMMARY

This paper presents possible explanations for the function of ornament on dermal skull roofing bones of labyrinthodont amphibians. Ornament is ubiquitous within the Labyrinthodontia and appears in essentially three forms: random pits and ridges, and longitudinal and radial ridges and furrows. Previous interpretations of ornament function have proven either inadequate or incomplete. The histology and morphology of sculptured dermal bone in both ancient amphibians and modern crocodylians show that ornament may strengthen bone by reinforcement and diffusion of stress. Study of the vascular system in modern crocodylians contradicts previous interpretations of function of ornament. Trends in skull proportions and jaw musculature as they relate to skull mechanics correlate with changes in ornament types and relief. These trends imply a positive association of ornament with a bone-strengthening function.

### SPECIMENS EXAMINED

The following is an alphabetical list of most of the specimens examined in this study (see Appendix I for other specimens studied through the literature). The specimens show the dorsal view of the skull unless otherwise noted. "AMNH": American Museum of Natural History; "KU": University of Kansas Museum of Natural History.

*Acheloma cummingsi*.—AMNH 4205. *Archegosaurus*.—AMNH 5704. *Broiliclus texensis*.—AMNH 1824. *Capitosaurus uasatus*.—AMNH 5744. *Chenoproscopus melleri*.—AMNH 1831. *Colosteus scutellatus*.—AMNH 6916. *Edops craigi*.—AMNH 7614. *Erpetosaurus radiatus*.—AMNH 6924, 6927. *Eryops*.—AMNH 4175, 4183, 4901 (palatal view), KU 695. *Eupelor browni*.—AMNH 1832. *Gerrothorax*.—AMNH 3868. *Ichthyostega*.—AMNH 1058. *Macrerpeton huxleyi*.—AMNH 6944, 6834. *Parioxys ferricolus*.—AMNH 4310. *Parotosaurus peabodyi*.—AMNH 2001. *Saurerpeton tabulatus*.—AMNH 6837. *Stegops divaricata*.—AMNH 6952. *Triuroclachis*.—AMNH 4591, 4557. *Zatrachys*.—AMNH 7501.

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## APPENDIX I

The following references were used for data on skull measurements and photographs. This list does not cover all genera mentioned in this study, but is supplemental to specimens studied directly. There are a few specimens, however, which were studied completely through the literature.

*Acheloma*

OLSON, E. C. 1941. The family Trematopsidae. *Jour. Geol.*, 49:149-176.

*Archeria* (*Cricotus*)

CASE, E. C. 1911. Revision of the Amphibia and Pisces of the Permian of North America. *Publ. Carnegie Inst. Washington*, 146:1-176.

*Broiliellus*

WILLISTON, S. W. 1914. *Broiliellus*, a new genus of amphibian from the Permian of Texas. *Jour. Geol.*, 22:49-56.

*Cacops*

WILLISTON, S. W. 1910. *Cacops*; new genera of Permian vertebrates. *Bull. Geol. Soc. Amer.*, 21:249-284.

*Chenoprosopus*

LANGSTON, W., JR. 1953. Permian amphibians from New Mexico. *Univ. Calif. Publ. Geol. Sci.*, (29) 7:349-414.

*Colosteus, Macrerpeton*

ROMER, A. S. 1930. The Pennsylvanian tetrapods of Linton, Ohio. *Bull. Amer. Mus. Nat. Hist.*, 59:119-126.

COPE, E. D. 1875. Synopsis of the extinct Batrachia from the Coal Measures. *Geol. Survey Ohio, Paleont.*, 11:349-411.

*Dissorophus*

WILLISTON, S. W. 1910. *Dissorophus* Cope. *Jour. Geol.*, 18:526-536.

*Ereptosaurus, Saurerpeton, Stegops*

STEEN, M. 1931. The British Museum collection of Amphibia from the Middle Coal Measures of Linton, Ohio. *Proc. Zool. Soc. London*, (B), 1930 (1931):849-891.

*Eugyrinus*

WATSON, D. M. S. 1940. The origin of frogs. *Trans. Roy. Soc. Edinburgh*, 60:195-231.

*Lyrocephalus*

SAVE-SÖDEBERG, G. 1936. On the morphology of Triassic stegocephalians from Spitzbergen, and the interpretation of the endocranium in the Labyrinthodontia. *K. Svenska Vetenskapskad. Handl.* (3), (16) 1:1-181.

*Melosaurus*

EFREMOV, J. A. 1937. Notes on the Permian Tetrapoda and the localities of their remains. *Trav. Isnt. Pal. Acad. Sci. URSS*, (8) 1:1-44.

*Parotosaurus*

PIVETEAU, J. 1955. *Traité de Paléontologie*. Masson et Cie, Paris, 5:1-1113.

*Seymouria*

HOTTON, N. 1968. The Evidence of Evolution. *Amer. Heritage Publ. Co.*, 160p.

*Trematosaurus*

WATSON, D. M. S. 1919. The structure, evolution, origin of Amphibia—the orders Rhachitomi and Stereospondyli. *Philos. Trans. Roy. Soc. London* (B), 209:38-41.

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