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BONE AS A SKELETAL STRUCTURE AND AS A MINERAL RESERVE

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The Evolution of Bone as Tissue and Organ

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If a symposium such as this had been held 50 years ago, it is certain that a contribution on the evolution of bone would have differed greatly from the present one. In those days ideas about the origin of bone and the early history of the vertebrates had reached a condition of relative stability in which available facts and current theory were harmoniously blended. It was believed that the vertebrates were descended from some lowly type like *Amphioxus*, with no differentiated head or jaws, and with a skeleton composed of a few simple, cartilaginous rods. From these were descended the jawless cyclostomes, creatures rather like the modern lampreys, and from these, shark-like fishes with jaws and well-developed skeletons of cartilage. The next step in the rise of the vertebrates was thought to be due to an evolutionary novelty, the appearance of bone. This made possible very strong and well-articulated skeletons capable of withstanding the stresses of an active life in the water, or of bearing the weight of a heavy body on land.

On the whole the fossil evidence was in agreement with this evolutionary picture. Then too, theoretical zoology was dominated by Haeckel's biogenetic law, which states that ontogeny recapitulates phylogeny. And since the skeleton of a vertebrate embryo is composed at first of cartilage, it followed that the skeletons of ancestral adult vertebrates were similarly constituted.

In recent years both theory and fact have been greatly modified. The biogenetic law has been heavily attacked by such authorities as Garstang (1922) and De Beer (1951). The researches of these and other workers have shown that embryos and larvas evolve no less than adults. The presence of some distinctive anatomical feature in an embryo is more likely to be an adaptation to present developmental needs than a reminiscence of past adult structures. Thus cartilage may simply be an adaptation to the need of the embryo for a skeletal tissue that is capable of rapid interstitial growth (Romer, 1942).

Once this approaches its final size, cartilage would give way to bone. It has, of course, been long known that cartilage is not a precursor of bone. Bone may develop in the absence of cartilage, and never develops from cartilage, though often replacing it.

Modern palaeontological discoveries accord well with such views. The earliest known vertebrate fossils are those of small, heavily armoured, fish-like creatures called ostracoderms, whose remains are found in rocks of Ordovician, Silurian and Devonian age. Thanks to the classical researches of Stensiö (1927), we know a good deal about the anatomy and biology of the ostracoderms. Their skeletons were made of bone, and in some of them the dermal armour was remarkably massive. The earliest known vertebrates possessed true bone, and some of them had a great deal of it.

The internal skeleton of the ostracoderms was sometimes cartilaginous, and sometimes more or less ossified, but the exoskeleton was always bony. It is interesting to note that both endochondral and membrane bone are to be found in the earliest vertebrates, whereas it was formerly believed that membrane bone was an evolutionary novelty of comparatively recent date.

The earliest ostracoderms were rather small, ranging in length from several inches to a foot. Each species had its characteristic size, and examples deviating much from the norm are unknown. It is believed that they passed through a larval phase in which the skeleton was entirely cartilaginous, and when the larva had grown to the adult size it underwent a metamorphosis in which a bony skeleton and dermal armour were acquired. In the same way the brook lamprey has a long larval period followed by a metamorphosis when it is almost full-grown, although it never acquires a bony skeleton. No remains of these hypothetical larval forms have been found, but it is not to be expected that soft, embryonic cartilage would often be preserved. In the sharks, in which the skeleton is permanently cartilaginous, it becomes more or less calcified with age, and skeletal remains of sharks are often found as fossils.

The available evidence, then, suggests that, in the earliest vertebrates, the skeleton was entirely cartilaginous during development, and almost entirely bony in the adult condition, and that once maturity was attained growth almost or quite ceased.

The dermal armour of these early vertebrates consisted of three layers, a thin outer layer of hard dentine, a thick middle layer of vascular bone, and an inner layer of lamellar bone. Dentine, too, is found in the earliest known vertebrates, and it covered the whole exoskeleton. It is interesting to compare this armour-plating with that of modern tanks and battleships. Here the same three layers are employed, a thin, case-hardened outer layer, a softer, but very tough middle layer, and a somewhat harder inner layer.

In the existence of this hard outer layer may perhaps be found one of the reasons why the early ostracoderms never grew after metamorphosis. Ordinary bone grows by external accretion, but dentine is laid down from within, so that the outer surface is definitive. As the armour of the head region consisted of a few relatively large plates solidly welded to the endoskeleton, growth at the sutures seems to have been ruled out.

Some of the heavily armoured vertebrates which immediately succeeded the ostracoderms had lost the dentine layer of the exoskeleton, even the teeth being made of ordinary bone. These fish-like creatures were capable of continued growth, and some of them, the coccosteids for example, attained a very large size, up to 20 ft. in length. At the other extreme, the sharks and rays have lost all bone except the dentine layer, which is represented in the teeth and the spiny denticles. This lack of bone in sharks was once considered to be a primitive feature, and they were, therefore, thought to represent the ancestors of the bony vertebrates. As a matter of fact, sharks are the last of the major groups of fishes to appear in the fossil record, so they are not entirely primitive. Many other groups of fishes show a tendency towards loss of bone, or rather towards its non-development. Thus the modern lung-fishes have very little bone, although the fossil lung-fishes were very well ossified. The sturgeons are completely cartilaginous except for a row of bony scutes along each side. Thus the condition in sharks is not unique.

In the evolution of the bony fishes the exoskeleton tends to break up into a number of small plates or scales, and dentine is generally confined to the teeth. In some of the fossil fishes the dentine layer was retained all over the body, being periodically resorbed to allow the bony skeleton to grow. In others, the so-called ganoid fishes, a few species of which still survive, the outer face of each scale is covered with an enamel-like substance called ganoin, which is laid on from without; thus continuous, concentric growth is possible. As a rule, however, modern bony fishes show a tendency towards reduction in the external armour, the scales become thin and papery, and in many species they disappear altogether. Only the bony plates covering the head remain, but these lose much of their original protective function, serving instead for the support and movement of the jaws, breathing apparatus and pectoral fins. Here the bones never become closely knit together, but preserve a great deal of freedom of motion. The fish skull is not a solid structure like that of a terrestrial vertebrate, but a mechanism of quite surprising complexity. Terrestrial vertebrates show a generally opposite evolutionary trend, the skull tending to become a compact, bony box. Only in birds and some reptiles do the skull elements show some power of relative movement.

Some mention may be made here of the comparative histology of bone. Certain evolutionary trends seem indicated here, although there are still many gaps in the account. The bone of the ostracoderms contained no osteocytes, and this condition is also found in the more advanced of the bony fishes. In these, once a skeletal element has become ossified, further growth is by concentric accretion, and there is little or no formation of secondary bone within. This, and the fact that growth is continuous, make it possible to tell the age of a fish by examination of the cementing lines and growth ridges in suitable bones and scales. This method of age determination would not be possible in a mammal, where growth eventually stops, and the periosteal layers are eventually replaced by secondary bone.

The more primitive of the bony fishes, however, have cellular bone, and this is of some interest, as these fishes are allied to the ancestors of the terrestrial vertebrates. The arrangement of the lacunae is not very regular, and canaliculi are few, sometimes entirely lacking. Even when numerous, the canaliculi form few connexions with those from neighbouring cells. It follows that, as the bone increases in thickness, the deeper osteocytes are gradually deprived of nourishment. Eventually they die and disappear, leaving empty lacunae. Thus the deeper bone comes to consist largely of non-living tissue, rather like the heart-wood of a tree.

The amphibia show, on the whole, a more regular arrangement of the osteocytes, the canaliculi are more numerous, and more interconnected, and there are fewer empty lacunae. The diaphyses of the long bones are composed entirely of periosteal bone, and the osteocytes show a concentric arrangement, as though the diaphysis were a single large Haversian system. In some of the more primitive salamanders, however, the cellular arrangement is hardly more regular than in the bony fishes.

Conditions in the reptiles are interesting, inasmuch as they exhibit a series of intermediate stages in the evolution of the mammalian type of bone structure. In all reptiles the inner part of the periosteal bone becomes excavated and replaced by secondary bone. This replacement is never complete, and as a rule the cellular arrangement in the secondary bone is very irregular. In the tortoise, however, the secondary bone is laid down in Haversian systems. As with other reptiles, replacement is incomplete, cellular arrangement in the periosteal bone is irregular, and there are many empty lacunae (Crawford, 1940).

Finally, mammalian bone is characterized by great regularity in the cellular arrangement. Most of the periosteal bone is replaced by secondary bone arranged in very regular Haversian systems. Osteocytes are well interconnected, and empty lacunae are rare.

So far the evolutionary account seems fairly straightforward; actually there are a good many gaps and contradictions. Mention has already been made of the coccosteids, large fish-like creatures with peculiar jaws and bony teeth, which lived in the Devonian era shortly after the ostracoderms. The head and thorax were very heavily armoured, and this armour shows secondary bone arranged in Haversian systems. Gebhard (1907), who described this condition, only published a preliminary announcement without any illustrations; the complete account which he then promised does not seem to have appeared. Nothing is known of the bone structure of the Mesozoic and late Palaeozoic reptiles and amphibia, and one would think that a comparative study of these would be most rewarding. Up to the present, however, more is known about the evolution of bones as organs than of bone as a tissue.

SUMMARY

The possession of bone is one of the most ancient vertebrate characteristics, and its primary function seems to have been protective. The function of support seems to have been of less importance, since a tendency for the bony endoskeleton to revert to cartilage has appeared in many groups of fishes. The dentine layer, which at first covered the whole of the armour, became confined to the teeth (except in the sharks), the body plating became reduced to thin scales, and even these have disappeared in many species. The plating of the head acquired new functions in connexion with the mechanism of the jaws, breathing apparatus and pectoral fins.

With the appearance of terrestrial vertebrates bone acquired a new importance in connexion with the problem of supporting a heavy body on land. Except in very small animals, cartilage becomes largely a juvenile and embryonic tissue. The central vacui-

ties of the bones become the site of haematopoietic tissue, and in the higher vertebrates bone is known to act as a storehouse of mineral salts.

In its finer structure, too, bone shows a progressive evolutionary change, although here the account is far from complete. In the earliest vertebrates the bone is acellular. In the primitive bony fishes the bone is cellular, although the arrangement of the lacunae is very irregular, and the osteocytes do not long survive. In the advanced bony fishes the trend has been once more toward the acellular condition, but terrestrial vertebrates show a trend toward greater regularity, longer survival of the osteocytes, and the appearance of nutrient canals and secondary bone arranged in Haversian systems. These trends reach their culmination in the bone tissue of modern mammals. There is, however, some reason to believe that some of the most ancient fish-like vertebrates had also a very regular type of cellular arrangement.

Knowledge is lacking of the histology of bone in many extinct vertebrate groups, but the fact that bone structure is known to vary so greatly between the different groups studied suggests that this knowledge would be well worth having. Even less is known about the reasons underlying this variation. The problem of correlating the evolution of bone structure with that of bone function remains one for the future.

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Bone as a Skeletal Structure

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Bone has provided absorbing problems for biologists for many hundreds of years. A fascinating account of the early history of this subject is to be found in *Menders of the Maimed* by Sir Arthur Keith (1919), a new edition of which is to be published shortly. The point of interest has varied from time to time but the basic problem is still the properties of bone as a supporting structure; this is the practical aspect of bone physiology which is most obvious to the man with a fractured femur, or to the surgeon who looks after him. I reviewed the information, such as it is, on the healing of bone some years ago (Bell, 1945) and I propose to confine my attention here to what might be termed engineering problems. These are, firstly, the search for the factors determining the shape of a bone and, secondly, the measurement of the physical properties of bones.

In the embryo the earliest cartilaginous rudiments possess the characteristic shape of the future bone, for example the head, trochanter and condyles of the femur can be recognized; furthermore, femora removed from 5½- and 6-day-old chick embryos, and