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## Problems of Origin and Early Development of the Vertebrates: Skeletal Tissues

By GEORGE M. ROBERTSON

For the past thirty years one of my major interests has been Organic Evolution, and coupled with that for most of this period has been Vertebrate Paleontology, with special emphasis on the earliest vertebrates. Taxonomic study of these primitive forms has been bound to lead to phylogenetic speculation, and of recent years that aspect has dominated my interest. At the same time I have become increasingly concerned with problems of the mode or modes of occurrence of evolutionary changes. Merging these two has given rise to some serious problems.

Study of the mode of occurrence of evolutionary change involves genetic concepts. Study of the phylogeny of particular groups depends largely on morphology of fossil forms. How to bring the application of genetic concepts specifically to bear on paleontological data is an especially difficult problem. We rather glibly write or lecture to our classes about the occurrence of mutations, their incorporation in the "gene pools" of our population genetics, the influence of differential survival on gene frequencies within these pools, with consequent change in the characters of the species; a somewhat more sophisticated way of stating Darwin's theory of Natural Selection. That being out of the way, we may go ahead with accounts of the evolution of plant and animal life, with general phylogenies based on morphological and embryological data. For more specific examples we turn to the horse or to *Micraster* or some other classical case, and sometimes proceed to show how such evolution might have been brought about by mutation plus selection.

This is probably valid reasoning, but philosophically I am somewhat disturbed. Where is the specific tie-in between our genetic knowledge and our paleontological data? Perhaps it is asking the impossible, but one would like to have more such definite knowledge than we have available. I read studies on the phylogeny of various structures based on careful and detailed morphological analysis of fossil and recent forms, always with the assumption that if you find three conditions of some structure and if one of these is intermediate between the other two it follows either that one of the extremes gave rise to the other through the intermediate one or that the intermediate represents an ancestral condition which gave rise to both extremes. How far does our knowledge of mutation justify such speculations? Do we not have cases in which independent mutations of different genes produce similar results, or in

which a single mutation may produce a condition more extreme than that produced by another mutation of the same gene? The phenomenon of "Phenocopies" also presents possibilities, i.e., environmentally induced structural features which simulate known genetic combinations.

Thirty years ago our speculations regarding vertebrate phylogeny were dominated by the idea that the cartilaginous fishes were persistently primitive and that ossification came later in phylogeny. It was further assumed that these cartilaginous forms were preceded by "soft-bodied" animals, and that therefore we were probably faced by a gap in our knowledge of actual ancestors, a gap which could only be filled on the basis of embryological and comparative anatomical data. The disturbing fact that the earliest vertebrates of which we had any record were bony forms, Ostracoderms, was explained as an accident of preservation. Cartilage is less resistant to decay than is bone. Thus not only the soft-bodied ancestral stages but also the cartilaginous ones which had given rise to this aberrant group of phylogenetic nuisances had simply left no record.

During the past thirty years our information on Ostracoderm structure has become much more adequate, and it now appears to be the consensus of workers in early vertebrate phylogeny that Ostracoderms do include the stem forms from which other vertebrates have been derived. Moreover, as our knowledge of Silurian and Devonian "fishes" has become greater, it has become apparent that sharks may well represent a separate off-shoot from the Acanthodians, an off-shoot in which bone was lost, and that the shark structures which appeared to fit them for an ancestral role had been shared by their Placoderm ancestors. This change in the phylogenetic status of the Chondrichthyes on the one hand and the Ostracoderms on the other has re-opened the question of the origin of bone, or perhaps better the origin of the process of ossification.

Six years ago (Robertson 1949) and again two years ago (Robertson 1953) I suggested the significance of attempting to determine something further regarding the origin both of ossification and of chondrification. In the latter paper I went on to suggest "it appears possible that any unarmored ancestor of the vertebrates as a whole may have been at an invertebrate level, and that the mutations necessary for ossification of connective tissue preceded or were contemporaneous with the other chordate characters."

I wish to reiterate that suggestion. We are learning more regarding the mode of evolutionary change. It now appears that in the gene pool which is the genetic species many mutant genes may accumulate but not come to significant expression until (1) other mutations occur and come to be included in genotypic combinations with these "latent genes," or (2) they chance to enter into

genotypic combinations with appropriate gene groupings already available in the gene pool, or (3) environmental conditions arise, either due to environmental changes or due to migration, which make adaptive some characters which had not previously been so. If ossification is dependent on the action of a number of genes it could well be that their gradual accumulation in the gene pool finally reached the point at which all could become incorporated into one genotype, with resultant "sudden" appearance of ossification.

There are certain questions regarding both chondrification and ossification which are fundamental here and to which we do not seem to have answers, or at least adequate answers. Among these are:

(1) What factors are concerned in chondrification and in ossification? We know something of enzyme roles in ossification and suspect that enzymes are also concerned in chondrification. Much of our information on the ossification process has been derived from regeneration work. We need to trace its embryonic development in physiologic terms rather than in histogenic terms only.

(2) Why are chondrification and ossification limited to certain tissues? Here also some studies have been made, but more need to be carried out. We may gain some information from ectopic chondroses and ostoses, such as occur in various soft tissues. Their occurrence, when they do occur, is frequently in a number of areas in the same subject, as though, perhaps, there were available the necessary mechanism for ossification except for some single factor, and when this appeared the process set in. For example, Ipponsugi (Ipponsugi 1927) reported results of an autopsy in which ossification had occurred heterotopically in 27 skeletal muscles, pineal body, kidneys, brain, colonic mucosa, splenic arteries, and the ground substance of the trachea.

(3) Why do not all chondrifications ossify in bony forms? What is the physiological significance of ossification patterns?

(4) What is the genetic basis for chondrification and chondrification patterns, ossification and ossification patterns? Here we meet the handicap which hinders us in our attempts to determine the genetic basis for other major evolutionary changes, the handicap which led Goldschmidt to suggest that there is a qualitative difference between the "micromutations" which we see in our cultivated plants and domesticated animals and which we study so intensively in the genetics laboratories, and the "macromutations" which have real taxonomic significance. Our only direct information as to the genetic basis for any character is derived either from results of controlled matings or from population analysis in random mating groups. The only direct evidence that a character has a gene basis is the finding of an allele for that gene. If a species is homo-

zygous for a gene and no mutation of that gene is found, we have no way of proving the existence of the gene in question.

Here, then, is one of our major problems. Is there an indirect approach? If so, what? This is not a rhetorical question. I do not know an answer. My hope is that someone may be able to suggest a feasible one. If it should prove to be the case that ossification and its patterns have gene basis, and if, as we suspect, genes act primarily through control of enzyme production, we might find some such scheme as this: a gene or series of genes for chondrification, a gene or series of genes for ossification, genes for susceptibility of any tissue to chondrification and to ossification, genes for chondrification and ossification patterns, etc.

Actually we would not expect to find any simple scheme. The process of ossification itself probably involves a number of genes. Ossification patterns characterize not only Classes but also lower categories. There are numerous genetic factors which we know to affect bone, and the very fact that ossification patterns are characteristic of taxonomic groups would seem to imply genetic bases for them.

The order in which mutant genes arise appears to be random. The genetic basis for ossification could have arisen in forms lacking those which determine susceptibility to ossification and under these circumstances have had no ossification influence. Similarly others of the series could be assumed to have arisen independently. Their presence in the gene pool of the group would practically assure that eventually they would appear together in individual genotypes, resulting in ossification as a phenotype character. We know of no form in which the ossification is or was completely without pattern, and presumably, as stated above, this too is dependent on genetic factors.

It could thus be that our very first vertebrates with tissues likely to fossilize would present a very "sudden" appearance. The series would be, so to speak, set up in the gene pool by accumulation of the various mutations over a considerable period of time. Various combinations might occur, but in the absence of the entire series no ossification would appear. Once the final element was added there it would be, pattern and all, without necessarily any previous hints of its imminence. This is one aspect of "pre-adaptation" which may be of major significance in the evolution of those adaptive changes which have so puzzled us when we have thought of them as arising "gradually", i.e., each step in the alteration being phenotypically present in what we could recognize as a stage toward the attainment of the final manifestation.

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