A MODEL FOR THE EVOLUTION OF FUNCTIONAL-MORPHOLOGICAL SYSTEMS

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ABSTRACT: A theoretical model is put forth that investigates the evolution of functional-morphological systems taking as its starting point the potential morphospace. By examining the influence of constraints the transition from the potential morphospace to the level of morphological plasticity is traced. The interactions of the form-function complex are discussed by looking at the roles of anatomical variation, functional stabilization, and the formation of functional units. Lastly, the integration of functional units within the organism is explored, as is the possible alteration of functional units. At each level, the model examines the possible interactions with all previous levels. The model is related to earlier work on constraints and rates of morphological evolution, with new ideas concerning the role of constraints, the differential rates of morphological evolution, and the production and consequences of functional integration being presented. Additionally, ideas concerning the evolution of major taxonomic groups will be discussed. Specific testable hypotheses are put forth based on the premises and ramifications of the model.

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INTRODUCTION

The study of vertebrate evolution is an excercise in problem solving using a restricted subset of concrete evidence. Since most vertebrates are extinct, the majority of ostensibly direct evidence pertaining to their evolution is present in the form of fossil remains. Although a number of correlations can relate these fossil remains to the animal's behavior, ecology, or life history, the only direct evidence offered by fossil remains is the morphology of the animal, and then only in part (for similar views on the "restricted" information available from fossils see Kitts, 1974 and Rudwick, 1964). Thus the most reasonable approach to understanding vertebrate evolution in its broad sense is to attempt to understand the evolution of morphological systems.

Given this, it is somewhat surprising that there have been few attempts to model the process of morphological evolution on a large scale. Although morphology is currently going through a phase dominated by experimentation, it remains largely a descriptive not a predictive science. While there have been many mathematical models relating to morphological evolution within certain taxonomic groups (reviewed by Raup, 1972), only four workers (Bock, 1959, 1963, 1965; Frazzetta, 1975, 1982; Lauder, 1981, 1982a; and Schaefer and Lauder, 1986) have put forth wider ranging ideas. Frazzetta's models, especially his later (1982) model, deal almost exclusively with the evolution of complex systems. Lauder's (1981, 1982a) papers treat the subject in a more theoretical framework, and lack the step by step modelling provided by Frazzetta. The work of Bock (1959, 1963, 1965) is the most encompassing of the four, dealing with changing

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rates of morphological evolution and the evolution of complex systems. Unfortunately, none of these published models have received the attention they deserve. The present model attempts to describe how functional-morphological systems evolve. I believe there are four ways in which a functional- morpholoqical system can evolve: 1) a morphological element may change, 2) the function of a morphological element or functional unit may change, 3) the way in which the morphological elements form a functional unit may change, and 4) the way the numerous functional units interact may change. In order to explain these four pathways I will discuss the evolution of functional-morphological systems in a stepwise fashion from the potential morphospace through to integration of the entire organism. Along the way I will explore the role of constraints, the origin and significance of morphological plasticity, the process throuqh which morphological elements stabilize upon a qiven function, and the various pathways and consequences of functional-morphological integration. The reader is cautioned that I am dealing only with models of morpholoqical evolution, not theoretical approaches to studying morphology.

To be most effective, a model of functional-morphological change should proceed in a stepwise fashion and be applicable to any taxonomic group. Additionally, it should offer insights into diverse areas concerning vertebrate evolution. Althouqh a "perfect" theory of morpholoqical evolution could relate to almost any aspect of vertebrate bioloqy, there are certain fundamental problems of vertebrate evolution that any theory must be able to address. These fundamental problems are represented in a general way by these five major questions: 1) how is an animal's evolutionary future affected by its evolutionary past?, 2) why do newly radiating groups often remain in the shadow of their phyloqenetic predecessors for extended periods of time (in that "primitive" forms tend to ecologically dominate the "advanced" forms)?, 3) why do most major radiations occur immediately followinq the establishment of major taxonomic groups?, 4) what is the nature of complexity, and what role does it have in evolving systems?, and 5) is there punctuational change?

It is my hope that the present model for the evolution of functional-morphological systems will be broader than those put forth previously. Yet it is intended to incorporate the insiqhts that made these earlier models useful. Following the description of the model, I will: 1) offer an example of the application of the model; 2) relate the model to the previously posed five questions regarding general trends in vertebrate evolution; and lastly 3) provide specific hypotheses based upon the model.

DEFINITIONS AND CAVEAT

This model is based upon (but does not rely upon) an analogy between the evolution of functional-morphological systems and the ontogeny of cartilage replacement bone. I hope to first draw the analogy and parallels between the ontogeny of cartilage replacement bone and the evolution of functional- morphological systems, then to explore in more detail the siqnificance of each step of the evolution of functional-morphological systems. The reader is cautioned that the ontogeny of cartilage replacement bone serves only as a mental framework; thus although I describe this process first, my emphasis is more upon the significance of each step in the evolution of

functional-morphological systems. While the analogy is intended to better clarify the stepwise nature of the system, overemphasis upon the cartilage replacement bone may obscure the points I am trying to make regarding functional-morphological evolution.

Before developing the model it is necessary to define the terminology I will be using. I will follow Patterson (1977) who defines a cartilage (replacement) bone as "a bone which is preformed in cartilage and first ossifies in ontogeny as a perichondral ring or disk on the surface of the cartilage model." I will also follow Patterson's (1977) definition of membranous bone, being "a bone which ossifies in membrane deep in the mesoderm with no ontogenetic or phylogenetic connection with the ectoderm." I use the term "morphological element" to describe any recognizable, single, anatomically isolatable structure. A "morphological system" is any group of interconnected morphological elements. A "functional unit" is any morphological system whose component parts combine to perform a given function (a function being any action, activity, or change in state).

An illustration is the capitate bone in humans which is a single morphological element. The capitate bone is also part of the morphological system commonly referred to as the carpals, as well as a component of the morphological system of the forearm. The capitate also functions in several functional units including: a proximal-distal unit involving the scaphoid, lunate, and the third and fourth metacarpals; and a lateral to medial unit including the hamate, trapezoid, and trapezium.

There is a clear hierarchy to these definitions. An organism is composed of several functional units, each functional unit is made up of at least one morphological system, and each morphological system is composed of at least one morphological element. There is a tendency for multiplicity to occur at each lower level of the system, thus a single morphological element can be a component in several functional units. Note also that a single morphological system may contribute to several functional units. There is also a potential hierarchial nature to this model as a whole. The tunica media may be viewed as a morphological element with the artery being seen as a functional unit; conversely the artery may be seen as a morphological element with the circulatory system being seen as the functional unit. The exact criteria the individual uses to identify a recognizable, anatomically isolatable structure (and thus a morphological element) will determine the boundaries of this hierarchy.

Also, it must be noted that I have kept all time scales out of this argument. In doing so I hope this model can be interpreted in both an ontogenetic and phylogenetic framework. In this sense I agree with Gould (1970) who, when referring to the tendency to increase in size, wrote: "The presence of similar trends in ontogeny and phylogeny has usually been ascribed to such evolutionary "laws" as recapitulation, but a functional approach might illustrate the mechanical necessity of a given trend as a response to increasing size. It then matters little whether the increase occurs in ontogeny or phylogeny; the trend must proceed in either case." See also Kluge and Strauss (1985) and Zweers (1979) for the interrelationships between ontogeny and phylogeny.

The reader is cautioned that my references to cartilage replacement bone apply best to the long bones of mammals, and that not all cartilage replacement bone follows the full ontogenetic sequence described here. I have made at least two fundamental generalizations

and simplifications in my treatment of cartilage replacement bone. I have treated the cartilage precursor as the initial stage of the process of endochondral ossification. As Burke and Alberch (1985) have shown, the cartilage precursor is preceeded by a great deal of tissue interaction. I have omitted the earlier portions of this process for simplicity as well as to provide a distinct starting point to my model. I have treated bone remodelling as a process separate from bone resorption and bone deposition. I realize that these two latter processes are responsible for bone remodelling, but to clarify a point that I feel is critical, I have elevated them to a status equal to that of bone remodelling.

Any theory that attempts to explain morphological evolution from the theoretical morphospace to the alterations of functional units within an organism, runs into a danger faced by any wide-ranging theory. If it is too restrictive, the theory is weakened by the numerous exceptions that can be demonstrated. If it is too general, it is viewed as not really explaining anything. Even so, such models have value in that they keep attention focused upon the problem of functional-morphological evolution, and the many levels upon which the problem exists.

I have taken my description of the process of endochondral bone formation from the following sources, Bhaskar et al, 1950; Bloom and Bloom, 1940; Kelly et al, 1984; McLean and Bloom, 1940; Watt, 1928.

THE CARTILAGE-REPLACEMENT MODEL

The ontogeny of cartilage-replacement bone can be divided into four basic phases, although not every bone will go through all four phases during its developmental cycle. These phases include the formation of the cartilage precursor, the initial invasion by osteoblasts, the complete ossification of the cartilage precursor, and the later restructuring of the bone.

Embryonic development of cartilage-replacement bone begins with the formation of a cartilaginous precursor of the bone. Shortly after forming, the cartilaginous precursor is encircled by a ring of membrane bone. This bony, encircling collar kills the chondrocytes in its immediate vicinity. Following the death of the chondrocytes the osteoblasts invade the cartilage precursor and begin calcifying the cartilage, thus leading to the formation of true bone. This center of new bone begins to spread toward the proximal and distal ends of the element.

The cartilage at the ends (epiphyses) of the developing bone remains in an active state for a long period of time, and can be functionally divided into several distinct zones: the zone of reserves, the zone of proliferation, and the zone of hypertrophy. The zone of reserves is a relatively inactive layer of chondrocytes the primary function of which appears to be to provide cells for the next level of specialization. The zone of proliferation is where the chondrocytes undergo rapid cell division and the actual thickness of the cartilaginous layer is expanded. The zone of hypertrophy represents the death of the chondrocytes as these cells swell up enormously and then die, leaving large cavities within the cartilage matrix.

The expansion of the primary center of ossification also produces distinct zones within the bone. Two such zones are recognized; the zone of calcification, and the zone of ossification. The zone of calcification occurs immediately adjacent to the cartilage's zone of

hypertrophy. The zone of calcification is characterized by an invasion of vascular elements and osteoblasts, as well as calcification of the cartilage matrix. In the zone of ossification the calcified matrix becomes more organized and takes on the histological appearance of bone.

Even after the bone has become fully ossified, its morphology can still be altered. This alteration takes place in three ways; through alteration of surface features, by resorption, and through the deposition of new bone. Alteration of the bone's surface features is a never-ending process reflecting the bones ability to modify its morphology to better suit its environment. Although bone remodelling is often viewed as being due to the influence of muscle, any physical factor can alter the surface features of a bone. An analogy to a wax figurine, in which rearrangement can be achieved by simply pushing material from one location to another, can not be drawn because the process of bone remodelling is made up of the two separate processes, bone resorption and bone deposition.

Resorption is one of the methods the formed bone uses to maintain a close association with its physical environment. A bony tissue that is not currently serving a functional purpose (i.e. a portion of the tibia no longer exposed to the level of compression it once was) may be reabsorbed and its chemical components incorporated into the bony matrix elsewhere. Most often, the area of resorption is one that is no longer affected by some aspect of the physical environment, or at least not to the degree that it once was. Such was the case with bone resorption in astronauts (Mack and LaChance, 1967).

Deposition of new bone also reflects the interaction of the bone with its physical environment. Bony areas undergoing increased stress from the physical environment will receive additional bone deposits to assist in relieving this extra stress.

The process of endochondral bone ontogeny can be viewed in the following manner, with only a slight degree of interpretation or abstraction. The cartilage precursor is an approximate physical blueprint of the endochondral bone. The "approximate" qualification results from the fact that the bone may not form at all, may form in only a portion of the cartilage precursor, or may form in the entire model and then be subsequently altered to deviate from the model. The ossification of endochondral bone can be characterized by the integration and interaction of two cell populations, represented by the cartilage cells and the bone forming cells. Lastly, the fully formed bone has the chance to alter its morphology to better fulfill its functional demands.

To fully appreciate the evolution of functional-morphological systems one must study all portions of the evolution of these systems. A functional-morphological system has an approximate blueprint, has integration and interaction between two components (in this case form and function), and the final product can be modified to fit a change in the functional demand. The same basic organization seen in the ontogeny of cartilage replacement bone exists in the evolution of functional-morphological systems. By creating an analogy between these two systems a model can be developed to better explain the intricacies of the evolution of a functional-morphological system.

In many ways the evolution of functional-morphological systems is analogous to the ontogeny of cartilage replacement bone. This analogy is based on the recognition of the same basic pattern in the ontogeny of cartilage replacement bone and the evolution of functional-morphological systems. This pattern can be divided into four

CARTILAGINOUS PRECURSOR model from which bone develops	POTENTIAL MORPHOSPACE all possible forms and functions
FORMATION OF MEMBRANE BONE localized death of chondrocytes	PHYSICAL AND EVOLUTIONARY CONSTRAINTS reduces the size of the morphospace
INVASION OF OSTEOBLASTS conversion from cartilage to bone	FUNCTIONAL DEMANDS further reduces the morphospace
ZONE OF RESERVES non-specialized cartilage cells	MORPHOLOGICAL PLASTICITY possible morphological variation
ZONE OF PROLIFERATION replication of chondrocytes	VARIATION IN ANATOMICAL DESIGN expression of plasticity
ZONE OF HYPERTROPHY chondrocyte growth & death	STABILIZATION OF MORPHOLOGY TO FUNCTION form-function interaction
ZONE OF CALCIFICATION osteoblasts invasion	FORMATION OF FUNCTIONAL UNITS coupling of morphological elements
ZONE OF OSSIFICATION conversion into bone	INTEGRATION OF FUNCTIONAL UNITS combining of functional units
BONE REMODELLING change in morphology of bone	ALTERATION OF FUNCTIONAL UNITS WITH STABLE NUMBERS OF ELEMENTS
BONE RESORPTION loss of bony material	ALTERATION OF FUNCTIONAL UNITS BY DELETION OF MORPHOLOGICAL ELEMENTS
BONE DEPOSITION addition of bony material	ALTERATION OF FUNCTIONAL UNITS BY ADDITION OF MORPHOLOGICAL ELEMENTS

Figure 1. Step by step comparison of the processes of cartilage-replacement bone ontogeny and the evolution of functional-morphological systems.

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components: 1) an early condition limiting phase (represented by the interaction of the cartilage precursor and the membrane bone, as well as the potential morphospace and the influence of physical and evolutionary constraints); 2) the initial formulative phase (represented by the early invasion and spread of osteoblasts, as well as the initial influence of functional demand upon form); 3) the phase of interaction (represented by the epiphyseal-plates "race" between cartilage and bone, as well as the formation of complex morphological systems from individual elements and the continual interaction between form and function); and 4) the "terminal" stage (represented by the remodelling of a fully formed bone, as well as the integration of all morphological elements into a functional organism).

The generalized analogy between the two systems is provided below, followed by a detailed step by step discussion of the model. Figure 1 illustrates the basic analogy used for the cartilage replacement model, while Figure 2 provides a flow chart of the course and interaction of the steps postulated to occur during the evolution of a functional-morphological system.
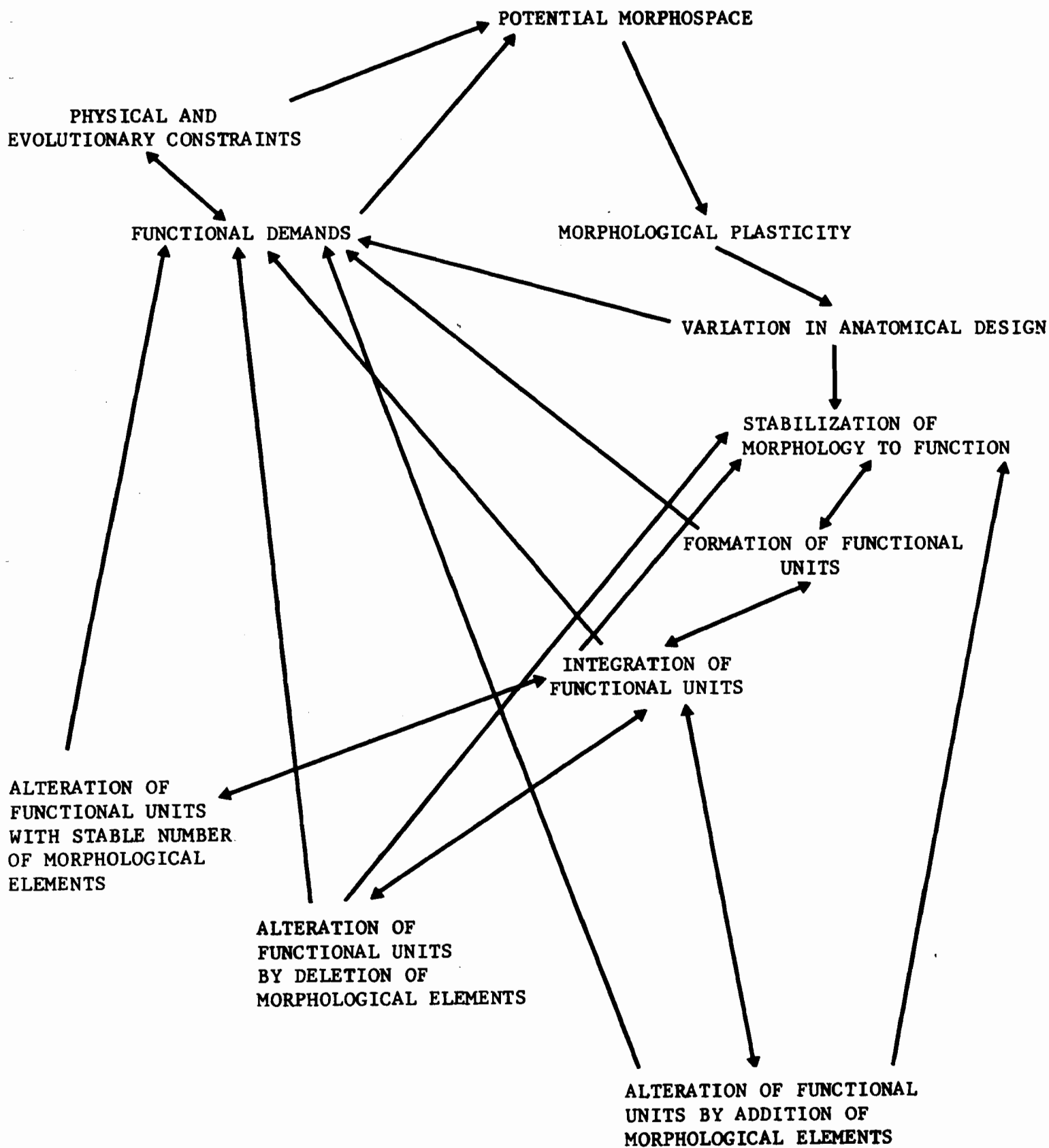
POTENTIAL MORPHOSPACE

PHYSICAL AND
EVOLUTIONARY CONSTRAINTS

FUNCTIONAL DEMANDS   MORPHOLOGICAL PLASTICITY

VARIATION IN ANATOMICAL DESIGN

STABILIZATION OF
MORPHOLOGY TO FUNCTION

FORMATION OF FUNCTIONAL
UNITS

INTEGRATION OF
FUNCTIONAL UNITS

ALTERATION OF
FUNCTIONAL UNITS
WITH STABLE NUMBER
OF MORPHOLOGICAL
ELEMENTS

ALTERATION OF
FUNCTIONAL UNITS
BY DELETION OF
MORPHOLOGICAL ELEMENTS

ALTERATION OF FUNCTIONAL
UNITS BY ADDITION OF
MORPHOLOGICAL ELEMENTS

Figure 2. A flow chart of the cartilage replacement model of
functional-morphological evolution.

CARTILAGE PRECURSOR FORMED= the potential morphospace, a theoretical construct encompassing all possible anatomical structures or functional roles. Both of the elements (the cartilage precursor and the potential morphospace) do not directly contribute anything to the final product (the endochondral bone or the functional-morphological system) but rather represent the "potential" present in each system.

FORMATION OF MEMBRANE BONE= the reduction of the potential morphospace due to the influence of the physical and evolutionary constraints. The membrane bone functions (albeit in a slightly abstract way) as a barrier to the expansion of the cartilage precursor. Likewise, the physical and evolutionary constraints prohibit some of the morphological elements and functional roles that are present in the potential morphospace from being realized in the organism.

INVASION BY OSTEOBLASTS= the functional demands placed upon the morphological system. This step represents the impact of external forces (functional demands or invading osteoblasts) upon the idealized state (the potential morphospace or the cartilage precursor). In the preceeding step the idealized state was limited, but not directly encroached upon. The invading osteoblasts reduce the cartilage precursor to the much smaller zone of reserves. Likewise, the functional demands (in conjunction with the physical and evolutionary constraints) reduce the potential morphospace down to the morphological plasticity. An additional similarity is the increase in number of osteoblasts, which corresponds with the tendency for functional demands to increase over time.

ZONE OF RESERVES= morphological plasticity. The zone of reserves is the remnent of the cartilage precursor following the invasion of the osteoblast. The zone of reserves has a crucial role in determining the final shape of the bone by its relative level of expression. The morphological plasticity is the remnent of the potential morphospace following the impingement of the evolutionary and physical constraints, as well as the functional demands. The morphological plasticity has a crucial role in establishing the parameters for the range of morphological and functional variation expressable in the organism.

ZONE OF PROLIFERATION= the variation in anatomical design. The zone of proliferation represents a specialized subset of the zone of reserves. The morphological variants represent a specialized subset of the morphological plasticity. In a not too abstract sense, both the zone of proliferation and the production of morphological variants represent the transition from a component of a purely theoretical system (in terms of endochondral bone and functional-morphological systems) to a component of a "real" system. In other words, the preexisting "blueprint" becomes materially realized. Both the zone of proliferation and the production of morphological variants represent a deviation from early systems (the zone of reserves or the morphological plasticity) that were remnents of the original "blueprint" (the cartilage precursor and the potential morphospace). The general pattern of production is also similar in that several cells leave the zone of reserves to enter the zone of proliferation, while several morphological variants can occur within the range of morphological plasticity.

ZONE OF HYPERTROPHY= the stabilization of a single morphological element upon one (or a few) distinct functions. The zone of hypertrophy represents the final contribution of the cartilage cells to the developing cartilage replacement bone. One cell at a time

leaves the zone of proliferation and enters into the zone of hypertrophy where its expansion and death facilitates the invasion by osteoblast. Similarly, the stabilization of a morphological element onto a single (or several) functions is the final stage of the purely morphological system. Each morphological variant is tested by selection, until a morphological element is produced that can meet the functional demands. Once an element is present that is capable of meeting the functional demands, new functional demands can be tested upon it, and it can be incorporated into higher organizational levels (i.e. functional units and morphological systems).

ZONE OF CALCIFICATION= the formation of morphological systems and associated functional units from isolated morphological elements. The zone of calcification represents the amalgamation of several regions from within the zone of hypertrophy, into one larger complex. Individual morphological elements never occur in complete isolation, but rather in conjunction with other morphological elements to form functional units and morphological systems. Thus we see in both the zone of calcification and the formation of higher orders of functional-morphological organization a coalescing of previously fully formed units (the zone of hypertrophy and the stabilized morphological elements) into interactive groups.

ZONE OF OSSIFICATION= the incorporation and integration between all of the higher orders of functional-morphological organizations (morphological systems and functional units) into the whole organism. The zone of ossification involves the amalgamation of the different zones of calcification into the endochondral bone. Thus the zone of ossification is the stage in which the individual units are integrated into the whole "final" product.

BONE REMODELLING= the alteration of morphological elements within a functional unit without a change in the number of morphological elements. In this sense, I use the term bone remodelling to refer to that condition where the shape of the bone is changed without a change in the amount of bone present. Thus any alteration in relative proportion, or interconnections between morphological elements would be seen as analogous to this bone remodelling.

BONE RESORPTION= the alteration of a functional unit through the loss of one or more morphological elements. Bone resorption represents the elimination from the endochondral bone of some fully formed bony portion due to an alteration of the functional demand (or other possible causal factors). Likewise, a morphological element that is a portion of a functional unit may be lost due to a new functional demand, or other potential influences.

DEPOSITION OF NEW BONE= the addition of new morphological elements to a functional unit. Bone can change its physical appearance and functional performance through the deposition of new bone. Likewise, new morphological elements can be added to a functional unit producing a change in appearance and functional performance. In both cases (bone deposition and the addition of morphological elements) new components are being added to an already established system (the endochondral bone or the functional-morphological system).

On The Potential Morphospace and Constraints

The cartilage precursor represents the total possible plasticity and adaptability within the developing bone. In this model, the cartilaginous precursor is analogous to the potential morphospace of the organism. The potential morphospace represents all possible

anatomical and functional structures without regard to any physical or evolutionary constraint. Any morphological structure, such as the presence of more than two pairs of appendages on a terrestrial vertebrate, is possible within the realm of the potential morphospace. The realm of the potential morphospace has often been discussed in papers dealing with theoretical morphology (Lauder, 1981; Raup, 1967; Raup and Michelson, 1965) and the overall conclusion seems to be that all known life occupies only a small fraction of the potential morphospace.

The formation of the membranous bone around a portion of the cartilage precursor in essence seals the fate of that cartilaginous precursor by providing an access into the cartilage for the osteoblasts. Immediately following their formation, the bone cells within the membranous collar begin to destroy the cartilaginous cells in their immediate vicinity. In this model, the formation of the membranous bone is analogous to the concept of a constraint on morphological evolution. Just as the membranous collar forms a barrier to the expansion of the cartilaginous precursor, the constraints on morphological evolution limit the expression of the potential morphospace. Note that in one sense the cartilage precursor can be viewed as limiting the membranous bone; perhaps a similar system exists whereby we can only truly define the potential morphospace using those constraints that act upon it. In a simplistic sense it is possible to view these constraints as being of two types, physical and evolutionary.

The physical constraints are quite familiar to us, representing the interaction of a wide range of physical laws upon biological systems. For example, the ratio of surface area to volume is not a linear one but rather the volume increases to the third power of the linear dimensions, while the surface area increases only by the second power of the linear dimensions. The results of these different exponents are that small endothermic organisms tend to loose heat faster through their skin, thus necessitating a much higher metabolic rate. So profound is this differential heat loss and energy requirement, that it appears to place an absolute minimum size limit upon endothermic animals. It is important to keep in mind, however, that size constraints are but one example. For an excellent treatment of physical constraints see Alexander (1985).

The evolutionary constraints are harder to illustrate but probably every bit as important in limiting the potential morphospace. An evolutionary constraint arises with the formation of any new lineage or morphotype. With only rare exceptions the offspring from within a lineage or morphotype inherit a genotype that is strongly correlated with those of their parents, and thus the resulting phenotype is generally related to that of one or both parents (the historical-phylogenetic factor of Seilacher, 1970). In a sense the conservative nature of genetic replication canalizes the phenotypic expression of the offspring (see for example Chapleau, 1986; Lande, 1986; O'Dor and Webber, 1986). This is not to say that there exists no room for change, but rather that the boundaries for the potential change are established early on in a lineage and are rather stable. While birds may form many designs of wing to respond to the environmental pressures experienced by the individual species, the phenotypic expression of a wing is canalized due to evolutionary constraints.

Evolutionary constraints also occur outside of the strictly genetic realm. Examples include epigenetic phenomena, morphogenetic

fields, and the overall integration observed during development. I
classify these examples as evolutionary constraints because I feel
that all have a predominantly genetic basis, and all limit possible
variation. While I do not doubt the reality or significance of these
evolutionary constraints, I believe they occupy a restrictive not
productive role. Like other constraints, they can be overcome under
certain circumstances (potentially with large-scale results). These
particular forms of evolutionary constraints will not be dealt with
separately in this model.

The interaction of the physical and evolutionary constraints
greatly reduces the potential morphospace. However, just as the
formation of the membranous collar does not signal the death of all of
the cartilaginous cells, the physical and evolutionary constraints do
not completely limit the potential morphospace.

Functional Demands and the Interactions Between Constraints

The invading osteoblasts are viewed as being analogous to the
placement of functional demands upon the anatomical system. In the
same way that the invading osteoblasts alter the structure of the
cartilage precursor, functional demands alter the structure and
integration of any anatomical system. There are two additional
similarities between the processes: 1) invading osteoblasts largely
shape the final morphology of the bone by limiting the amount of
cartilage present. Likewise, the functional demands largely shape the
final morphology of the anatomical system by reducing even further the
potential morphospace; 2) The invading osteoblasts tend to
progressively expand the ossified area of the cartilage. Functional
demands also tend to increase in number (as discussed later), which
places more and more selective pressure upon the anatomical system.
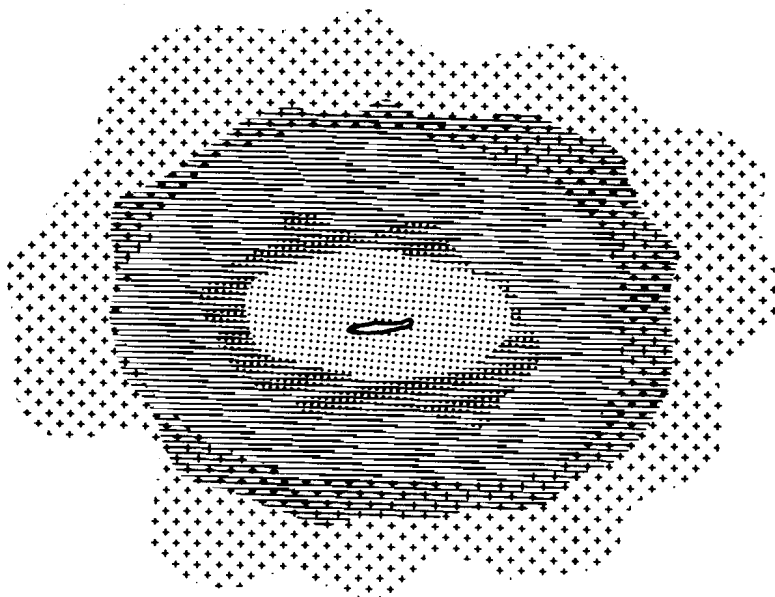The fate of the potential morphospace is illustrated in Figure 3.

Figure 3. The fate of the potential morphospace, which is reduced
by the physical constraints (..), the evolutionary constraints (__),
and the functional demands=constraints (+ +) to leave only the small
realized morphospace of anatomical plasticity. Note that the
constraining levels overlap to a large degree, symbolizing the
boundary softness of their divisions.

   An example of a functional demand is provided by mammalian
dentition. Mammalian teeth are all constrained by the physical
properties of dentine and enamel, yet their external morphology
reflects a wide range of structural characteristics in terms of both
functional subsets (i.e. canines, molars) as well as specializations
for particular diets (i.e. carnassial teeth).
   An example of interactions of the three types of constraints is
offered by the tibia of a terrestrial mammal. One primary functional
demand on a tibia is to support the mass of the animal. The physical
constraints of bone strength and gravity influence how this functional
demand can be met. Once a successful (i.e. one that meets the
functional and physical constraints) tibia evolves it becomes an
evolutionary constraint for the descendants of the organism due to the
nature of gene replication. If a new function becomes important, for
instance an increase in running performance, then a new set of
conditions may occur. Over time, the tibia may elongate as part of its
morphological plasticity, with the result in an increase in stride
length. Note that even if the tibia lengthens it is not escaping from
the original functional constraint of being a compression bearing
element. Suppose the tibia elongates to the extent that fusion with
the proximal tarsal occurs. If this happens, it represents the
escaping of two evolutionary constraints (the presence of a discrete
tibia, and the presence of a joint) and the creation of two new
evolutionary constraints (the presence of a tibiotarsus, and the
absence of the lost joint). Although continual elongation would
constantly increase stride length, this is not possible because of the
physical constraints of how bone responds to compression, a long
column of bone is likely to fail through buckling. Thus the physical
constraint will ultimately check the elongation of the tibia.
   The increase in functional demands is due to the variation within
populations over time, as well as variability of the environment. With
the constant fluctuations that occur in the environment, viable
species must be able to conform to new environmental conditions. Any
stimulus or condition that is novel to the organism will place a new
functional demand upon the animal's system. Clearly not all of these
functional demands will result in morphological change; but the
environmental shifts will occur frequently enough that over time
functional demands will be incurred, hence the tendency toward an
increasing number of functional demands.
   It would be incorrect to suppose from this that functional
demands completely dictate the forms of anatomical systems. Although
the predominance of either form or function has been continuously
debated by morphologists (see the recent review by Lauder, 1982b) it
appears that neither of these factors has the supreme role in shaping
the final morphology. In simple terms, the current anatomy of the
system largely dictates how the functional demands will be met (if
indeed they can) while the functional demands dictate the changes that
are neccessary for the anatomical system to be viable given the
current environmental pressures. This argument may seem rather
circular (although it must be pointed out that the process itself is
circular); it may be clarified somewhat in the following sections.
   To appreciate the intricacies of morphological evolution it is
necessary to further examine this analogy and the step by step process
through which morphological systems are formed. Fortunately it is not
necessary to abandon the cartilage replacement analogy, since the
interaction that occurs between the cartilage and bone at the distal

ends of the developing cartilage replacement bone provides an
illustration of this process.

Morphological Plasticity and Variation

The zone of reserves is analogous to the amount of morphological
plasticity inherent in the system. This plasticity represents the
remnants of the potential morphospace after the influence of the
physical constraints, the evolutionary constraints, and the functional
demands (constraints). Morphological plasticity can be thought of as
the degree of variation allowable within a given morphological element
without producing a change in selective value. For example, how much
variation is permissible within the plumage coloration of birds before
a differential in some selective value (i.e. predator avoidance,
territorial defence, or mate recognition) results? This analogy
produces two important points. The first is that every anatomical
system has within it some potential for variation and evolution
although, as will be discussed later, this does not mean that all
systems have the opportunity to express this variation in the same
manner. The second point is that the nature and range of the possible
variations will differ throughout the morphological system since no
two morphological elements will be influenced by the same combinations
of physical, evolutionary, and functional constraints.

The zone of proliferation is seen as analogous to the production
of morphological variants due to a genetic mutation, or a change in an
epigenetic phenomenon. Just as the zone of proliferation represents a
period of growth and proliferation within the cartilage, the
production of morphological variants represents a "growth and
proliferation" when compared to the normal morphological condition.
For example, the human pinna functions as a sound receptor; the
physical constraints of its component tissues determine to a large
degree the possible size of the pinna (which is always present due to
an evolutionary constraint). The functional demand of sound collection
dictates the size and shape of the pinna. A high level of
morphological plasticity is reflected in the wide variety of pinna
morphology present in humans, whereas a low level of morphological
plasticity is indicated by the low level of variation seen in the
pinna of bats (Henson, 1970). If the morphological variation is large
enough, and if it is expressed (see below), the morphological
variation may produce a "growth and proliferation" of the
morphological plasticity by circumventing previous evolutionary or
functional constraints.

This viewpoint carries with it the assumption that no
morphological element is free from potential variation. This potential
variation is present even in phylogenetically stable elements, as well
as those elements that we view as optimized or constrained. The
production of morphological variation does not, however, guarantee
that these variations will be incorporated within the animal as
functional components (i.e. the variations may be selected against
either during ontogeny or phylogeny).

On Functional Stabilization and Integration

In cartilage replacement bone, the chondrocytes that have passed
through the zone of proliferation will in a sequential fashion enter
the zone of hypertrophy where they increase in size and have a
formative role upon the surrounding matrix. In the cartilage

replacement model of functional-morphological evolution, the
anatomical variations produced are "tested" by the functional demands
of the organism. Each morphological element must perform at least one
function. Some morphological elements may perform multiple functions
(as in some elements of the teleost jaw) while others may perform only
one function (such as the mammalian incus bone).

Just as every chondrocyte hypertrophies alone, it is crucial to
appreciate that every morphological component has an individual
function. The incus bone only functions in hearing on a gross level,
its real role is to transmit forces from the malleus to the stapes.
Likewise each individual carpal, metacarpal, and phalanx has a unique
functional role that is obscured by casually lumping them all together
as a single unit. Because of the function inherent within each
morphological element, many of the anatomical variants produced will
be unsuitable. In the extreme case, we can imagine some elements as
having such specific functional demands that no deviation from the
standard morphology would be tolerated. Such an element would meet the
standard conception of a morphological constraint and would tend to
greatly retard the functional-morphological evolution of the system
possessing it. Even this restriction, however, may have its
exceptions, as outlined later. The method of functional testing must
be clarified somewhat; each morphological element must function in
relation to some other morphological element, thus the functional
testing must always be in relation to the surrounding elements. Note
also that this testing is a continual process, for if the functional
demand is continuous through time, then the morphological element must
be functional in different configurations and with different
relationships.

Once a chondrocyte has hypertrophied it dies and the surrounding
matrix becomes calcified. In the cartilage replacement model this
transition marks the end of the emphasis upon the individual
morphological element, and the establishment of functional units of
interacting components. No morphological element operates in a vacuum
and to one degree or another all morphological elements are components
of functional units. Functional units vary enormously in terms of
their number of elements, as well as the degree of differentiation and
integration between the elements (contrast, for example, the
functional units represented by the three inner ear ossicles, and the
vertebral column).

The formation of functional units involves the linkage of
multiple morphological elements each of which function in a unique
way. This linkage, however, will place additional demands on the
individual morphological elements. As explained earlier, each
morphological element must be able to function within the boundaries
established by the morphological elements with which it is most
closely linked. The necessity of functional compatibility, when
combined with the influences of different degrees of interaction and
variation allow us to categorize morphological units as either
generalist or specialist. For example; the navicular bone may be seen
as a generalist having functional interconnections with the radius,
trapezium, trapezoid, lunate, and capitate; the lower carnassial tooth
is a specialist having only two functional interconnections one with
the upper carnassial and one with the dentary bone. The
differentiation of specialist and generalist morphological elements is
based on the number of functional connections the morphological
element has, as well as the degree of functional integration between
these connections.

The formation of functional units will always decrease the range of morphological variation within the individual elements of the functional unit. This is due to the increased functional demands placed upon each morphological element by its association in the functional unit. There has been a tendency to give too much credence to this decrease, however, and often a view has emerged that "complex" functional units are inherently stable and variation-free. This view cannot be supported by this model. Since each morphological element is a functional entity subject to its own range of morphological variation, and since each element of the functional unit is functionally evaluated in relation to its adjacent elements; there exist the potential for cascading change. If the first element of the functional unit was to undergo a subtle variation that did not effect its functional performance, there is the potential that this small variation in the first element would permit the expression of a variation in the second element that was previously impossible due to functional constraints. This does not mean that morphological change will be as rapid within functional units as would theoretically be possible with an isolated morphological element; only that the view of functional units being stagnated may have been somewhat too restrictive.

Lastly, it is imperative to realize that the formation of functional units from isolated morphological elements carries with it a certain component of chance. Thus a morphological component that was functionally viable in one role may become incorporated into a different functional component where it performs a new functional role. Of course in these cases the morphology of the added element must be compatible with the existing system and there may or may not be compensation within the previous functional unit.

For example, the lower jaw of many diving birds is braced by the presence of a second joint between the upper and lower jaw (Bock, 1960). This second joint appears to have started out as a small bony process for muscle attachment which subsequently elaborated in size until contacting the upper jaw. Eventually this contact between the upper and lower jaw resulted in the development of a fully functional joint. In the terms of this model, the bony process was originally part of one functional unit (that being a portion of the jaw adduction mechanism) but it subsequently became incorporated into a second functional unit (that being jaw suspension). In this case the morphological element retained its place within the original functional unit as well, since the same muscle still attaches to the base of the process.

Integration and Alteration of Functional Units

The zone of ossification is analogous to the incorporation of functional units into the whole animal. Just as the individual zones of calcification unite to form the complete bone, the individual functional units join to form the entire organism (both in ontogeny and phylogeny). An example of the incorporation of functional units into the whole animal is provided by the pectoral appendage of a tetrapodal mammal. Although fairly easy to separate anatomically, the degree of functional interaction between the pectoral appendage and the body is quite pronounced. Clearly it is impossible to fully understand the functional intricacies of the pectoral appendage without looking at the many ways it interacts (functionally) with the whole body. The integration of all these diverse functional units into

one organism will highlight the generalist and specialist nature of
the functional units. The significance of this integration is that
some functional units may experience unpredictable functional demands
due to the cascading effect described earlier for individual units.
This functional integration has implications for the way in which many
morphological studies are pursued. The atomistic approach, that is the
analysis of only one or just a few morphological elements, is the
prevalent philosophical approach to anatomy today. The high degree of
functional integration predicted by the cartilage replacement model
would appear to invalidate the atomistic approach and to illustrate
the necessity of the holistic approach which treats functional systems
in their entirety.

Once the process of cartilage replacement development is
completed the bone is fully formed and little if any cartilage
remains. This lack of cartilage does not curtail changes in the shape
of the bone however, because fully formed bone has the capacity to
remodel its appearance. This remodelling will alter the superficial
and internal morphology of the bone. The remodelling of the fully
formed bone is analogous to the alteration of fully formed functional
units.

There are two possible methods of altering functional units
without changing the number of morphological elements involved; the
alteration of the proportions of morphological elements, and the
rearrangement of the connections between the morphological elements.
The first of these processes is assumed to operate quite slowly since
many of the morphological elements could not accomodate much
variation. The tradeoff to the changes in proportions is that the
resulting function is not pre-determined (as in the emergent
properties of O'Grady, 1984), and thus a novel and unpredicted
function would be produced. The rearrangement of connections between
morphological elements could potentially proceed at a faster pace
since it could potentially occur at only one location. The functional
activity produced by this rearrangement would almost always differ
from the pre-alteration function. Although both of these two forms of
rearrangement are theoretically possible, it must be recognized that
most rearrangements of functional units that do not involve a change
in the number of morphological elements probably incorporate both of
these processes.

It can be seen that the difference between generalist and
specialist functional units will have a profound influence on these
possible alterations. Generalist functional units can be visualized as
having a high potential for rearrangements due to changing connections
because of their many interconnections: this same condition will tend
to reduce the opportunity for alterations due to a change in
proportion. The specialist functional units are rather immune to
change through rearrangment of connections because of their limited
number of interconnections: this same limited number of inter-
connections makes the rearrangements due to changes in proportion more
likely.

Bone remodelling results from the differential deposition of new
bone and resorption of old bone. It is possible that the analogous
situation, the alteration of functional units, can occur without
changing the number of morphological elements (as discussed above).
However, alterations involving the number of morphological elements
within a functional unit must also be addressed.

Bone resorption involves the elimination of select portions of a
previously formed bone, the analogous situation in this model would be

the elimination of an anatomical element from a functional unit. In theory this process could also occur at a higher level, that is the elimination of a functional unit from the whole organism, but for the sake of simplicity the earlier process will be discussed here.

The elimination of a single morphological element from a functional unit is illustrated by the evolution of the dermal components of the pectoral girdle, specifically the fish to amphibian transition. In the placoderm fishes the dermal portion of the pectoral girdle had two distinct roles; to support the fin, and to brace the head. These functions were performed by a solid band of dermal bones extending from the postero-dorsal portion of the skull all the way around to the ventral midline. That this connection was a functional one is demonstrated by its specialization in the arthrodires where a large joint connected the dermal pectoral girdle to the skull (Patterson, 1975). In early amphibians the connection between the dermal pectoral girdle and the posterior portion of the skull is lacking. In terms of this model, a single morphological element (the connecting element) has been removed from the functional unit. The results were rather significant, in that the removal of this single morphological element produced greater mobility of the head, as well as greater movement and evolutionary plasticity of the pectoral girdle. The evolutionary plasticity was increased by freeing the pectoral girdle of the major constraint of attaching to the skull, thus enabling many "new" morphological systems to form which were previously impossible.

Like bone resorption, the addition of new bone is a rather selective process; so too is the analogous situation in this model, the addition of new morphological elements to an existing functional unit. The classic example of this process is the evolution of the lower jaw support between the therapsid reptiles and the early mammals. In the therapsids the functional unit responsible for jaw suspension was composed (in a simplistic sense) of two elements; the quadrate and articular bones. In the transition to the mammalian lineage another bone, the squamosal, is included within the functional unit responsible for jaw suspension. This inclusion appeared to happen progressively and is beautifully illustrated by the fossil Diarthrognathus which has a functional unit of jaw suspension composed of the quadrate and articular bones, as well as the squamosal and dentary bones. This inclusion of a new anatomical element (although actually the dentary bone is also a newly included element in terms of jaw suspension) resulted in biomechanical changes in the jaw by moving the joint more anteriorly, and by having only one bone anterior to the joint. An additional result of this inclusion of new elements was a freeing of the constraints upon the squamosal and articular bones, which produced a situation in which these bones could enhance their function as sound conducting elements (Allin, 1975).

There are, then, four different methods whereby preexisting functional units can be modified (as illustrated in Figure 4): 1) alterations of the proportions of morphological elements within a functional unit, 2) rearrangement of connections between the morphological elements of a functional unit, 3) addition of a new morphological element to a functional unit, and 4) the loss of a morphological element from a functional unit. Clearly (as was discussed earlier for rearrangements within a functional unit) these different modes of modification of functional units will be more likely in some forms of functional units. It would appear that the addition or loss of anatomical elements would be more likely within a
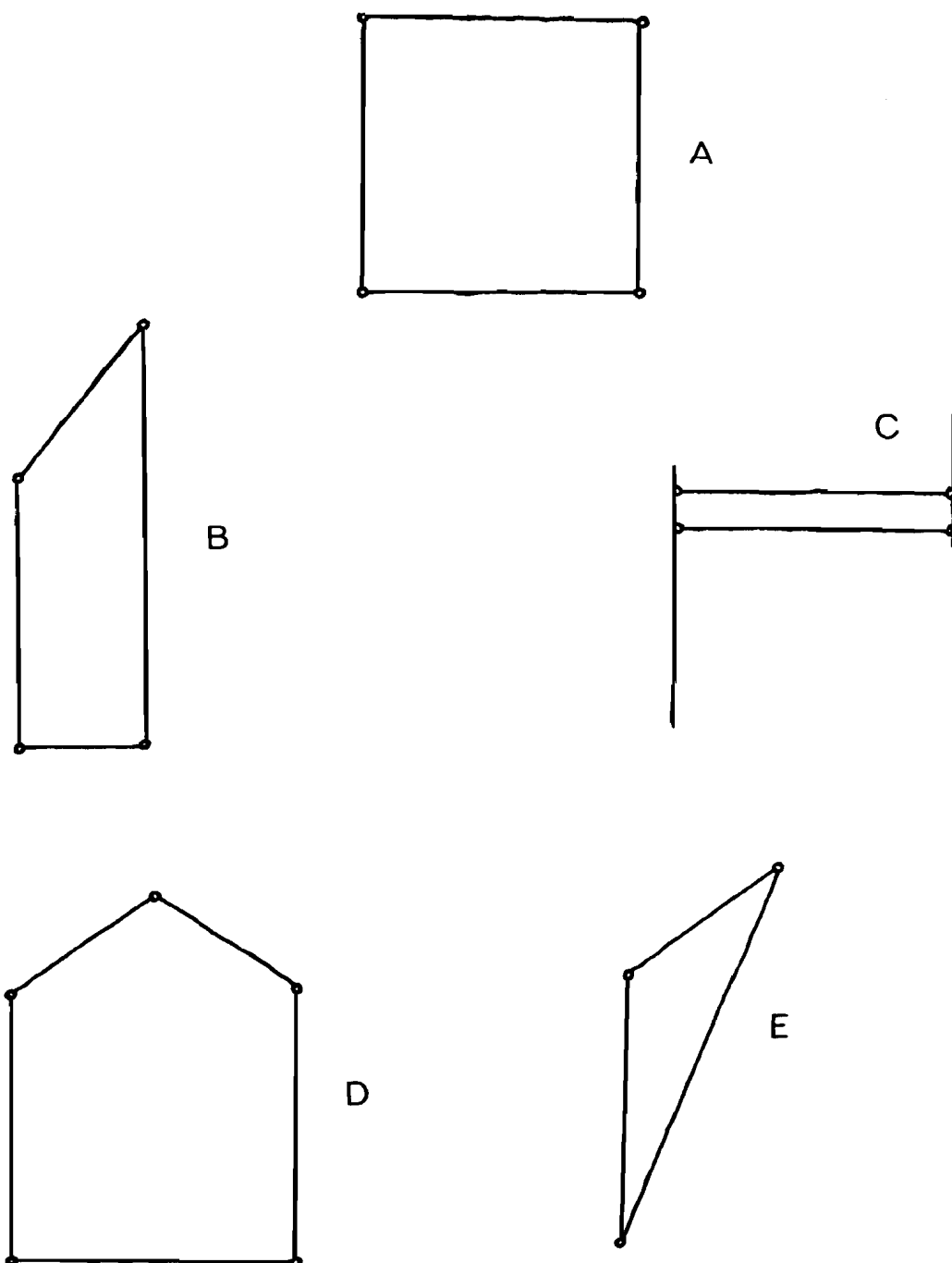
Figure 4. The rearrangement of a functional unit using the four possible methods. A - initial functional unit, B - functional unit following a change in proportion of morphological elements, C - functional unit following the change in connections between the morphological elements, D - functional unit following the addition (or inclusion) of a new morphological element, E - functional unit following the deletion of a single morphological element.

*   *   *

generalist functional unit since this type would have more interconnections established after the removal of an existing element. This does not mean that these methods of alteration could not occur within the specialist functional units, only that they are more likely within the generalist functional units. It is also important to realize that these four forms of alteration of functional units can be

arranged in a hierarchy from least likely to most likely as follows; addition of a morphological element to a functional unit, deletion of a morphological element from a functional unit, rearrangement of the connections between morphological elements within a functional unit, and the change in proportions of morphological elements within a functional unit.

IMPLICATIONS OF THE MODEL

A generalized example of how this model would work is presented for the cetacean pectoral limb. The condylarth ancestor of the cetaceans was a terrestrial herbivore, structurally similar to the modern ungulates (Barnes, 1985). The evolution of the cetaceans is thought to have progressed through an amphibious stage before reaching the fully aquatic stage. At some point in its evolutionary history, the cetacean pectoral appendage was relieved of two major constraints; a physical constraint of gravity (which was eliminated by the buoyancy of water), and the functional demand (constraint) of providing propulsion (which was eliminated by the development of the fluke). The removal of these constraints may have allowed for a great deal of plasticity within the morphological elements of the pectoral limb, but immediately a new functional demand (that being hydrodynamic directional control) began influencing the system. The functional role of each element in the pectoral limb altered in response to this new functional demand, and thus their morphology was modified. Examples of this modification include the shortening of the humerus and its concurrent loss of bony processes, the loss of a moveable joint at the brachial-antebrachial connection, the loss of mobility between the ulna and radius, the loss of flexibility in the carpals and metacarpals, and the elaboration and addition of the phalanges.

Each element of the system had an increase in morphological plasticity (due to the removal of the constraints) from which a new morphological design was molded to meet the changed functional role. The main constraint that remained in place during this transition appeared to be an evolutionary one, represented by the architectural plan of the pectoral limb, for the majority of the cetaceans the same basic arrangement of bony elements was maintained. It should be noted that the distal elements of this functional unit changed more than the proximal elements did. While a component of this differential change might represent the increased functional demand at the distal end (where the majority of directional control occurs), it may also represent the idea of cascading morphological changes within the functional system (as described earlier).

The evolutionary future of an organism is largely determined by its evolutionary past. The evolutionary past of an organism determines the constraints that will be placed upon that organism's morphology. Thus the morphology of the organism will largely be determined by constraints, yet the morphology the organism currently possesses establishes the constraints upon the next generation. Constraints have been treated by several authors in a general sense (Alberch, 1985; Carroll, 1986; Gould, 1980; Jacob, 1977); but not in the sense of stasis or circularity that is envisioned here. The circularity is produced by the constraints acting on the organism which itself produces the constraints that the next generation must deal with. Another aspect of circularity comes in the definition of physical, evolutionary, and functional constraints; it must be recognized that the way in which one generation meets the physical constraints establishes the future evolutionary constraints. The result of the circularity of constraints is a relative stasis in functional-

morphological evolution as was seen by Clutton-Brock and Harvey, (1979); Gould, (1984); Thomas, (1976); and Wake et al, (1983). The most persuasive work for the presence of a potential morphospace and the constraints acting upon it comes from the work of Raup (1960, 1967, 1972) and Raup and Michelson (1965).

No constraint (save some of the more fundamental physical constraints) is permanent. There is always the chance that a rearrangement of an established functional unit, or the interaction between functional units, could be modified (as outlined in this model). This modification will effectively eliminate the constraint (or constraints) that the specific functional unit was exposed to; of course in doing so new constraints are established. Other constraints can be circumvented by a major environmental shift.

The primary factor determining a functional unit's ability to be modified is related to its own morphological structure; the generalist and specialist ideas put forth in this model. Frazzetta (1975, 1982) defines a complex structural system as "a system containing a number of components which possess an operationally integrated relationship among themselves". I find this definition unsatisfying (as well as the numerous other definitions of "complex", see Lauder (1982)), as I believe that all functional units have operationally integrated relationships. I prefer to differentiate functional units based on the number of, and degree of integration between, the component parts.

The concept of functional-morphological stasis leads to questions regarding the rate of functional-morphological evolution. If alterations of functional units are necessary for the majority of morphological evolution to occur (as this model would suggest) then it is necessary to reexamine the rates at which these modifications can occur. Because of the constraints on the system, morphological stasis will clearly be the normal condition, being violated during periods of modifications of functional units. Of the four types of modifications described in this model, three occur in rapid form. This rapid rate occurs in the addition of new morphological elements, the deletion of morphological elements, or the rearrangment of morphological elements due to functional demands. All three of these modes of modification can occur following a change at only one location (hence can procede faster), and can be pictured as all or none rearrangements. The remaining method of modification, the change in proportion of the morphological elements of the system, will occur at a slower pace.

This dichotomy of rates clearly suggests that the normal pace of functional-morphological evolution is one of slow change, interspersed with periods of rapid, large scale, change. This same pattern of evolution has been postulated before under the term "punctuated evolution" (Gould and Eldredge, 1977); and in fact the possible influence of morphological "complexity" upon the rates of change has been put forward (Lauder, 1981; Schopf et al, 1975). In terms of this model however, categorizing a system in terms of stasis or punctuated change may be a gross simplification. A function can change on a punctuated scale due to a gradual shift in morphology, and in fact a punctuated functional change can occur following only a very minor change in morphology: possibly the converse of these relationships is also true.

There exists the possibility that a constraint can be escaped by either a drastic change in the environment, or a functional shift that eliminates a preexisting evolutionary constraint. The escaping of a constraint will have two primary effects: 1) a production of a new morphological arrangement, and 2) for a brief period of time, an

increase in the plasticity of the system (until it is fully reined in by the new constraints). The potential for constraints to both limit functional- morphological change and to promote it has been discussed before by Roth and Wake (1985). The important point here is that the escape from a constraint increases the plasticity of the lineage, leading to the evolution of new morphological and taxonomic groups (Alberch, 1980; Bock, 1959; Gould, 1970; Gould and Lewontin, 1979; Mayr, 1960; Roth and Wake, 1985; Schaeffer, 1965; Vermeij, 1973).

The increased plasticity that results from escaping a constraint will be reflected in the functional units of the organsims. This plasticity will be passed on to the separate functional units, and then on to the component morphological elements (recall the cascading effect of change within the morphological elements discussed earlier, see also Urbanek (1960)). Thus it can be seen that the change in a morphological system will be a hierarchial one, with a differential level of plasticity observable at different levels of organization. The hierarchial nature of evolutionary processes has been treated previously (Alberch, 1980; Arnold and Fristrup, 1982; Gould, 1980; Simon, 1962; Vrba and Eldredge, 1984).

My point is that this increased plasticity may account for the tendency for a new evolutionary lineage to give rise to most of its major groups immediately following its appearance. The time lag envisioned before the system is once again brought under control by constraints may also explain why there is often a time lag between successive forms in an evolutionary hierarchy (i.e. advanced forms live in the shadow of their predecessors).

In my view, the primitive forms have less integrated functional systems, and thus stabilize much faster following the increase in plasticity. Each more advanced form "experiments" with its functional units for a longer period of time (i.e. the heirarchy expands further into the morphological system) which means that it will take this more "advanced" animal longer to outcompete the more "primitive" form, simply because the "advanced" form has not developed its functional systems to their full potential (which is not to say that they are non-functional in the meantime). It must be kept in mind, however, that this hierarchial time lag would only account for a portion of the time of evolutionary dominance. But the head start given to the "primitive" form may be adequate to allow it to fill enough ecological niches that its displacement becomes harder once the "advanced" form achieves its functional potential.

Ideally, since this model attempts to explain evolution it should be applicable to the by-product of evolution, the phylogenetic lineage. In figure 5 I have attempted to demonstrate how this cartilage replacement model could be represented as a cladogram. Since the cartilage replacement model has a certain "hierarchy" (i.e. from variations of a single morphological element to interactions between functional units) these different levels should be convertable to a cladistic format. If my model is plausible, and if figure 5 is a correct representation of my model, then the branching system depicted in figure 5 could be utilized to depict the relationship of a given functional- morphological system within a taxonomic unit. Note however that figure 5 includes all three forms of rearrangments of existing functional units, none of which must necessarily occur, although presumably at least one of the three would.

PREDICTIONS

The cartilage replacement model of functional-morphological evolution contains certain assumptions and ramifications that
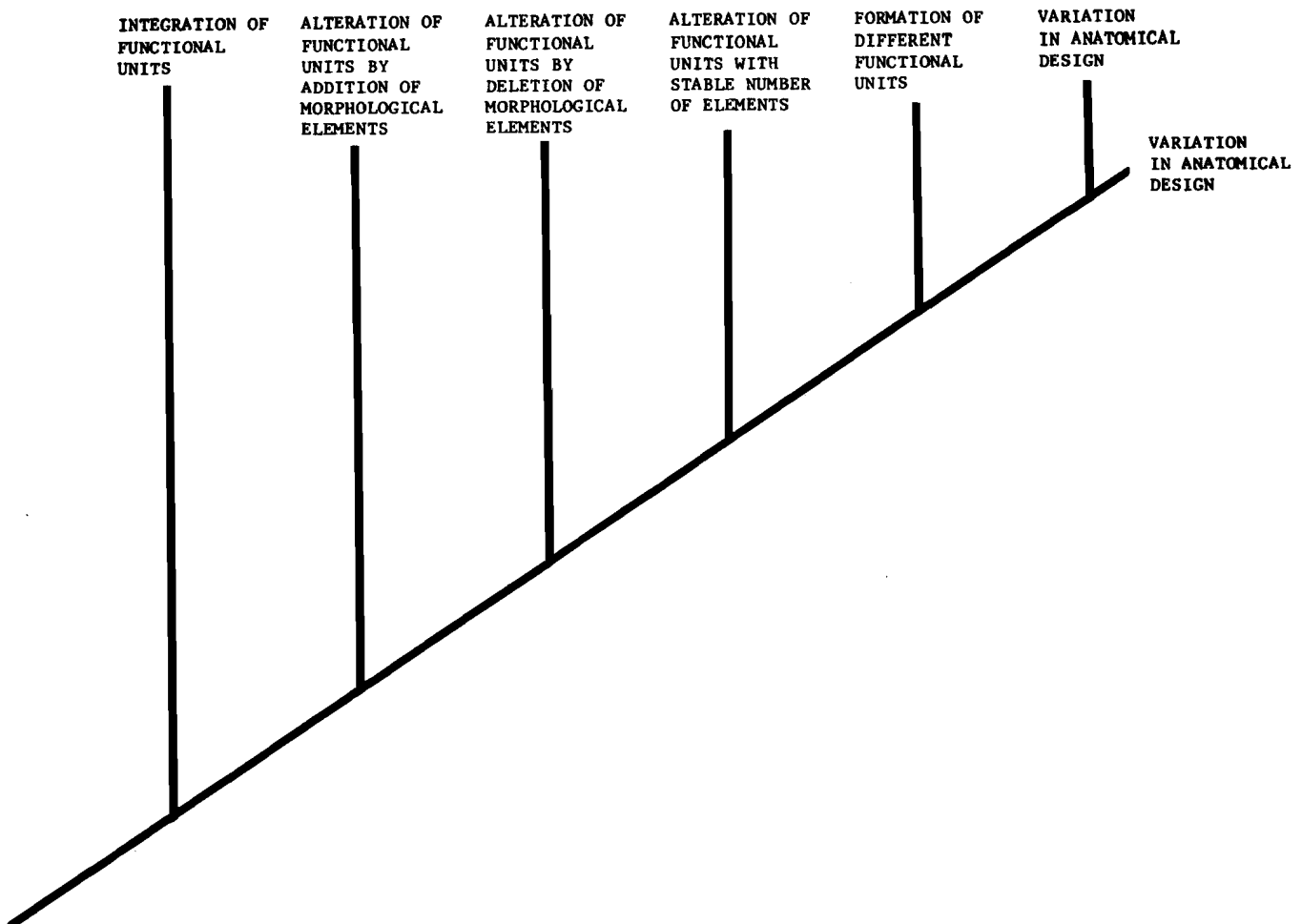
INTEGRATION OF FUNCTIONAL UNITS	ALTERATION OF FUNCTIONAL UNITS BY ADDITION OF MORPHOLOGICAL ELEMENTS	ALTERATION OF FUNCTIONAL UNITS BY DELETION OF MORPHOLOGICAL ELEMENTS	ALTERATION OF FUNCTIONAL UNITS WITH STABLE NUMBER OF ELEMENTS	FORMATION OF DIFFERENT FUNCTIONAL UNITS	VARIATION IN ANATOMICAL DESIGN

VARIATION
IN ANATOMICAL
DESIGN

Figure 5. A cladogram showing the hierarchial arrangement of the cartilage-replacement model of functional-morphological evolution and the possible applications to taxonomy.

                    *   *   *

can form the basis of testable hypotheses. If the cartilage replacement model is realistic, then the following six conditions should be true:

1) All morphological elements within a species will have some inherent variation. The only exception will be elements that are subject to extremely high levels of constraints. If these constraints are present then every other species within the genus (or possibly family) will show the same lack of variation. If one species within this larger taxonomic group has crossed a major environmental gradient it would then be expected to show morphological variation.

2) Due to the cascading effect of functional-morphological systems, a change in the morphology of one element will produce morphological changes in the related elements. Given this, we should never observe a functional unit where only one morphological element has been modified (when compared against the sister group).

3) The evolution of major vertebrate groups will always be associated with a modification of existing functional units, or the creation of "new" functional units.

4) Highly integrated functional units will typically evolve through rapid morphological rearrangements, as opposed to gradual

accumulation of morphological change in the same pattern.

   5) Within a given evolutionary lineage no "novel" structure will occur in a stable environment; in other words a substantial shift in environments will be correlated with alterations of the physical and functional constraints on the organism (an exception could occur in the case of large scale genetic changes).

   6) All morphological elements will be components of functional units, the only exception being those elements that have recently been deleted from a functional unit. In this case, these morphological elements would represent true "vestiges" whose evolutionary history would demonstrate their prior interaction with a given functional unit.

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