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ABSTRACT: Modeling of morphological evolution is difficult, especially when complex systems are considered. "Complex," as used for adaptive systems, should imply integrations among the components that produce adaptational effects, and their developmental programming, this latter being the most fundamental. Two models of complex morphological change are reviewed and reconsidered. A third (new) model assumes progressive, stepwise (not concurrent) additions of components to an evolving adaptive system. The metaphor employed for the third model is the random laying of flat, irregular stones on a horizontal field. The model relates to conjectures about evolutionary rates and rate changes, the construction of canalized development, and the effect of canalization on future evolution. The same model is possibly useful for ecological considerations of species packing, and of rates of community changes and of species origins. It is suggested that pertinent ecological models may be applicable to morphological evolution.

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Introduction

Many a good science thrives on the proper balance between fact and imaginative conjecture. Too little conjecture and a discipline may risk entombment in a stagnant morass of generated detail that, once cherished knowledge, becomes "old hat" and leads nowhere else. Too much conjecture and speculation bounds so far ahead of hard information that it enters a sort of twilight zone of unreality.

It should be clear that there is no set rule or ratio helping us to decide how much conjecture is justified when given the state of factual knowledge. This will depend on the scientific discipline, or the phase it is going through, and on the person working at it that day. For instance, anatomy is a discipline that can do with more information than has yet been accumulated--most animals are not very well known structurally. But sufficient information has existed long enough to have justified more conjectural approaches such as functional anatomy, adaptive anatomy (usually lumped with the preceding), and various developmental and evolutionary analyses.

Models, in a way, often are the leashes that a discipline's established information holds on conjecture. Then, the model abstracts and repositions elements of knowledge in ways that may be conducive to the birth of new conjectures. Thus, and ideally perhaps, even while being somewhat free of factual confinement, conjecture is reigned in by the intermediate connection formed by the model.

At least some kinds of models seem to work this way. There are other kinds, enough so that the word "model" outside a specific context suggests a very indefinite picture if it suggests any at all. Some are merely descriptive--mental leaning posts that simplify a plexus of information. An example is Waddington's (1957) epigenetic landscape where a rolling marble defines the course of organic development as it traverses a groove whose depth is a measure of the degree of canalization.

Other models are more closely attached to fact and are less surrealistic, such as simple, deterministic population growth equations. These can serve as a calculation tool for measuring or predicting real information in the real world. But

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The parts of the middle ear operationally blend together to perform their function. By its very intricacy, the ear suggests to an observer that no single component can be changed very much before the working harmony among the aggregate of parts is harmed, and the hearing function impaired.

Machine Analogy Model

Animal systems are certainly comparable to machines in many respects. The famous mathematical biologist A. J. Lotka made a crude comparison between animals and artificial machinery in his classic book (1956) where he described an intriguing toy beetle that could scoot about on a table top but had the "ability" to avoid the edges and a tumble to the floor. More recently other writers have considered animals as machines from an evolutionary view, such as Gould (1970) and myself (1975a).
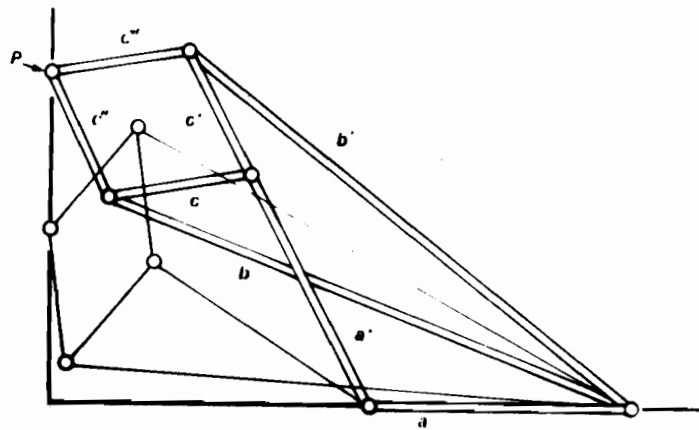

Figure 2. Peaucellier straight-line mechanism showing two positions. Note that point P traces a straight line along the ordinate axis. Text has further explanation. After Frazzetta (1975a).

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Figure 2 shows a linkage that, when flexed, moves point P in a manner to describe a straight line at 90° to link a. This ingenious apparatus--the Peaucellier straight-line mechanism--is constructed so that all members of each family of links (a, a'; b, b'; c, c', c", c'") are of the same length. This construction is confining because any alteration in the length of any link must be simultaneously matched by an appropriate adjustment in several other links, otherwise the line traced by point P will appear to the left or right of the present y axis; or worse, the line traced by P will no longer be straight.

The implication of such a model for structural evolution, insofar as it can simulate adaptive complexes in animals, is that phenotypic alteration of integrated systems requires an improbable coincidence of genetic (and hence, heritable phenotypic) modifications of a tightly specified kind.

Several serious problems adhere to this kind of analogy between the evolution of organic systems and the modification of man-made machines. These difficulties have been dealt with in some detail (Frazzetta 1975a) and will not be repeated here. Perhaps the existence of important disparities between artificial machinery and complex biological adaptations make it seem compelling that the entire analogy be waved off on a permanent holiday. This would not succeed, however, because the connection between working organic systems and machinery is not dismissable. Historically, evolutionary biologists have been most obsessed with how, in the world, can one explain the origin and subsequent major modification of systems that

operate in integrated, machine-like ways.   Despite all the molecular and
quantitative population-biological concerns emphasized now since those old days, the
original curiosity has not been cancelled.   It has broadened.   In the search for
answers at the molecular and population levels, it became apparent that these were
complex entities in their own right.   We are still left with the unabating need to
explain evolutionary changes in systems that have the operational integration
characteristic of the things we recognize as "machines."

The Concurrent Acquisition Model

This model follows from a mercilessly strict acceptance of the implications in
a machine analogy model of the sort just presented.   The underlying assumption is
that components of a system cannot be altered singly without disrupting the vital
integration--hence function--of the adaptive complex.   Hence, in this view, specific
alterations must be made in several components simultaneously to readjust inte-
grative relationships to maintain functional harmony.

As anyone can imagine beforehand this model, because it depends on happenstance
concurrence of rather unlikely events, will predict a low probability of any
evolutionary change at all.   Models of this kind have been around for a long time
offered by a number of authors (including myself in 1975a).   A recent outbreak of
them has come from the hands of the anti-evolution anachronists who, in this latter
part of the Twentieth Century, are still having trouble in accepting the Universe
for what it is. When used in this way, the models seem to serve the purpose of
proving how impossible evolution is.

Some of the major flaws in such models were set out by me in 1975a.   They are
reviewed briefly here, but it must be said that there is no good basis to assert
that concurrence was not a significant beginning to some major evolutionary innova-
tions.   The issue needs some examination.

The reptile-mammal transition provides a possibly adequate example.   If we
consider changes in the middle ear and jaw joint alone (outlined above), it would
seem that our disregard of the rest of the animal is a great simplification.   Still,
the ear and jaw region afford us numerous traits in transition.   The several small
bones at the rear of the jaw (Fig. 1) become diminished, reshaped and, together as a
unit, disengaged functionally from the large tooth-bearing dentary bone in front.
Allin's careful work (1975) has demonstrated these changes, and others: The little
suspensory bone, the quadrate, becomes smaller still and loses firm connection with
the bulk of the skull but retains the contacts with the stapes bone (the ear bone in
terrestrial vertebrates other than mammals) and with the articular bone of the lower
jaw.   (Not every worker is comfortable with the thought of such an adventurous
migration of the eardrum; e.g. Van De Water, et al. 1980.)   While these alterations
are all taking place, the eardrum is provided housing in, of all places, the crook
of the angular bone of the lower jaw.   During these important revisions, and
coordinated with them, the dentary bone begins to produce an increasingly enlarged
extension reaching toward the skull above.   There, at some point in the transition,
a functional joint develops.   As this joint increases in size, strength and
importance, the several bones behind the dentary begin to shift away and upward
toward the skull above, carrying along the angular, its attached eardrum, and the
whole chain of bones that are changing to become the definitive trio of mammalian
ear ossicles.

Accompanying these changes are others: the teeth are less reptilian and
increasingly mammalian, and the means of picking up airborne vibrations for the
function of hearing undergoes continuous, correlated modification (see Allin 1975,
and Crompton and Jenkins 1979).   It is hard to resist going on to point out further
changes, including some less obvious ones.   An argument can be made that the myriad
changes already noted or implied must be coordinated if structure is not to depart
from useful function through time.

The concurrence model supposes that we must combine several particular traits at once before we achieve selection's favor. For example we might estimate that for selection to favor the first step in the series of changes, that step must be the simultaneous appearance in one individual of a certain half-dozen traits (that, for simplicity, are assumed to be located on separate chromosomes). We could stipulate that each is controlled by a single dominant (to be charitable) gene whose frequency is 10^{-3}, far larger than that allowed by most guesses about mutation rates. With no linkage effects, diploid animals provide us 2 chances to randomly choose a given gene from the population's pool of genes. The chance of drawing each gene is 2 X 10^{-3} which is nearly 10.3 X 10^{-3} or about $10^{-2.7}$. Six of these is $(10^{-2.7})6$ and if we estimate the average selection-age population size (Frazzetta 1975a, Frazzetta and Franson in prep.) to be a generously large 10 million (10^7) and the generation time but one year, the chance of concurrence in that year is 10^7 x $10^{-16.2}$ = $10^{-9.2}$. This is a little worse than one chance in a billion. And this is but the first step. After this, selection must come into play, increasing the gene frequencies whenever independent assortment randomly permit those six traits to coexist in one animal.

The errors in such concurrence models are numerous. The effective population size is perhaps much larger than even the 10 million we allowed with such apparent generosity. Probably any of a great number of separate populations, belonging to many related species, were genetically similar enough to have provided the beginnings of this evolutionary transition. As it is, several separate lines of therapsids achieved or closely approached "mammalness" in a number of characters (Hopson and Crompton 1969).

Even if (for whatever reason) six concurrent traits were actually needed to start things off, there is no justification for supposing that this set must be a particular six. There may be many sets of six traits, any of which could have been involved in an initial evolutionary step.

Of course, too, the treatment of these six traits as independent might be unduly severe. The action of regulatory genes could conceivably control changes in several related features while retaining functional harmony among them (e.g. see Valentine and Campbell 1975); or in more general terms, epigenetic interactions during development might mutually guide the formation of characters that appear separate when seen in a static, fossil skull (e.g. Frazzetta 1975a; Rachootin and Thomson 1981).

And finally there is the basic question: is an actual concurrence of structural features really necessary? It seems more than a little possible that certain components in a multifaceted system can be altered singly without necessarily diminishing the system's adaptive level. This will be more likely whenever the fitness topography (sensu Wright 1932) is nearly flat. Mayr has skillfully argued (1960) for a conception of major evolutionary change that does not depend upon concurrence.

Thus it appears that an additive model may fairly represent much of morphological evolution. The model should be framed in a way to properly deal with--or at the very least, avoid--the problems associated with the concurrent model.

Progressive Model

Let us consider a mode where new, evolutionary innovations are added progressively, one at a time. The word "progressive" is not at all intended to suggest an orthogenetic, relentess path of evolution toward some adaptive finish line. It means that despite branching, reversing and sidetracking of the changes in the transition from one type to a significantly different one, the series of all modifications will have been progressive for the particular evolutionary transition considered. In this sense, a random walk seen in hindsight is "progressive" if it leads from one point to another.

It seems intuitively evident that independent innovations cannot be continuously introduced in a system in a completely unordered way. In the very early evolution of a multicomponent system, the components acquired may be fairly independent of each other. But later, a point will eventually be reached where further additions of independent traits are limited.
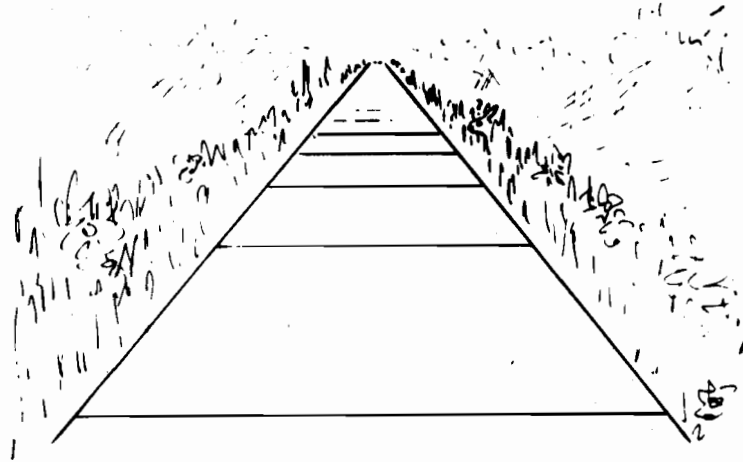

Figure 3. A road with marked, square sections.

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The addition of traits in this model may be seen as modifications of some preexisting structure, or of some capacity, that permit a new, adaptive participation in some functioning system in an organism. When an acquired innovation does not interact with the other components, as may more likely occur in the early evolutionary stages, the incorporation of the new feature is purely additive. Traits introduced later must have to be capable of some interactive integration with the other components if the results are to be selectively favored.

The model is based on a set of metaphors: A road is being constructed by laying down a basic, semifirm matrix into which durable surfacing materials will be pressed. The work is to be done a square section at a time, and sectional boundaries are scored into the matrix layer as shown in Figure 3.

Surfacing material consists of flat stones having irregular shapes and assorted sizes. In the model, the hard stones are to protect the less durable matrix against the potentially damaging effects of rolling vehicles. The stones are picked at random from an inexhaustible pile of mixed stones and are randomly set by dropping them to press them into the matrix. Because both the picking and placing of the stones is "blind," we could imagine a hard-working but not very clever robot performing the task; or instead we could conceive of an inattentive human laborer with his mind on other things.

For any section of road, the first few stones will very likely be successfully placed. This means that the ith stone when randomly dropped onto the section, will not strike another stone, but will fall into the matrix unobstructed. If the ith stone is inadvertently placed over parts of one or more previously set stones, the new stone will be discarded (except as noted later), after which another stone will be both chosen and placed randomly. (The act of discarding an improperly set stone depends upon an acurate assessment of the stone's placement, and thus this part of the process is not random.)

Clearly, as more and more stones are added to the section, there is met increasing difficulty in their (randomly) successful placement. Three factors grow in significance: 1) the size of the ith stone; 2) the shape of it; 3) the stone's location of placement on the section and its orientation when it falls into the matrix.

When many stones already occupy the square section, larger stones cannot be placed successfully unless they happen to be properly shaped to conform to portions of available space. This proper conformation becomes more exactly required as the density of previously positioned stones increases. If, for example, the randomly chosen location of placement of the ith stone has an open, star-shaped space, a large stone would have to resemble a star to be successfully set. A somewhat smaller stone could be less star-shaped, and a very small stone could be of any form. In this model, even a properly shaped stone could be useless if set down in the "wrong" part of the section, or set down in the "right" part if improperly oriented. These random factors are restrictive and reduce the opportunity for continued, nonintegrated additions of large effects (see Figure 4).

first group of stones to be placed (near average size of all stones available in stock pile)

second group of stones to be placed

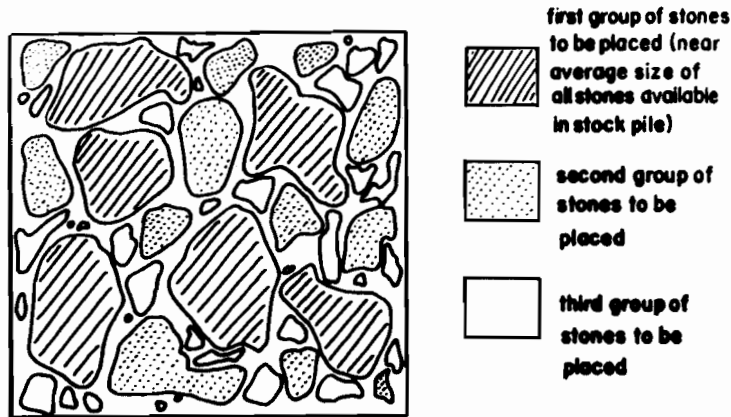third group of stones to be placed

Figure 4. A section of road containing flat, irregular stones. Cross hatched stones were placed first, stones with diagonal lines were set in place later, and unlined stones were positioned last. See text.

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Close conformation of edge shapes, characterizing a tight, mutual accomodation among neighboring stones is the (spatial) integration referred to in the model; it is symbolic of a functional/developmental integration in biological systems.

The model reflects an expectation about additive changes. The stones could represent actual "hard" structural components, a biological process or a capacity of an adaptive system in some imagined species. Continued addition of components makes the biological system complicated--functionally multifaceted--by the sheer number of functional attributes. As this point is approached, it becomes increasingly difficult to maintain the system as a collection of components having a related, functional effect, but which act independently of one another.

From a biological standpoint the origin of new component parts or capabilities would, by dense crowding, force impingements among components that, if not mutually integrated, will tend toward adaptive deterioration of the system. Hence, progressive evolutionary innovation may soon come to depend upon the acquisition of integratable components which, because they are more uniquely specified than other kinds of components, are less likely to appear. Or, alternatively (but not exclusive of the first possibility), evolution can proceed by the nonintegrative addition of ever smaller effects, and this can be more rapid.

The terms of the model would treat these smaller changes as less adaptively strong or versatile--the small stones being more easily sunk or moved about under heavy, diverse traffic than larger ones, especially if the larger stones were integrated by conformation of shape and position. Because of their small size, and the relative unlikelihood that most of a number of very small components will be strongly integrated within the fabric of the system, small components will have little role in defining basic adaptive strategies.

Clearly the harsh restriction on evolutionary change that was imposed by the concurrence model is much relaxed in this stepwise model. Even at that, however, stepwise change is not free from its own set of limitations.

Further Implications of the Road Model

As the model has been presented so far, each biological component to be added could be regarded as being transformed from another one, from another already existing system. The degree of transformation from the entity's form in the original system may range from no change at all to a major change.

A further refinement of the "road" model would permit a sufficiently large stone, when dropped upon one or more smaller ones already set into the matrix, to press the smaller stones into the unhardened road bed, leaving the new, larger stone in their place. As Figure 5 shows, the success of this will depend upon three factors: 1) The fraction of the present stones(s) covered by the new one as it is dropped into place; 2) the ratio of previously uncovered matrix that will now be protected, vs. the amount of matrix that may be reexposed by sinking a preset stone that is not entirely covered by the new stone; 3) the degree of integration existing among the preset stones.
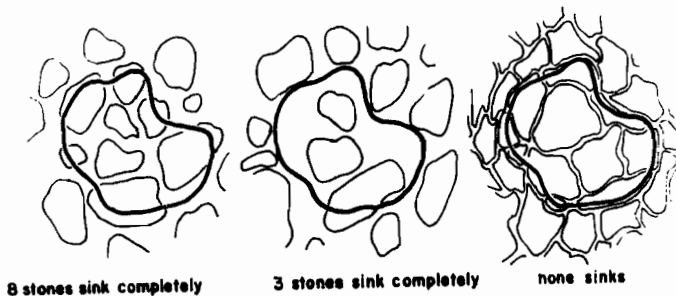

8 stones sink completely   3 stones sink completely   none sinks

Figure 5. Sets of preexisting stones covered by large, new stone (heavier outline). See text for explantion.
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Presumably, some mimimal area of a stone must be covered by the new stone to permit its being sunk. This minimal area will vary according to circumstances—such as those enumerated in the paragaraph above. Clearly, if this method of replacing stones results in a net loss of matrix covered, the effect will be deleterious (in biological terms, and thus rejected by selection). Finally, when the preset stones are well-integrated, their closer, mutually conforming edges gives to the mass of them a cohesive singularity that is greater with increased integration. This factor provides a resistance to sinking of any of the constituent stones in the integrated nexus. (For the model's sake, one might fancy that the closer, conforming edges with their thinner bands of separating matrix are more frictionally bound to one another by the stiff bedding matrix, and tend to resist relative displacements —including sinkings—of the composing elements of any one to another).

The biological meaning of a large component supplanting another—or others—is the effective transformation of one preset component into another. This can occur by the relatively drastic process of a mutation that significantly alters the original component. Or again by drastic mutational effect, an entity—not previously related to the one(s) to be transformed—is modified to operationally enter the appropriate region of this system (the road bed section), and takes over (at least part of) the functional domain of one or more preset components. The components already in place, and which are involved in this process, suffer a disturbance that

prevents their normal full expression, even when not <u>wholly</u> superseded by the new element.   Less drastically the transformation may occur through a preexisting component that, with only minor intrinsic alterations, expands its role in the system, taking over the functions of other components already in place, or at least reducing their capacities.   Although these possibilities are at least subtly different, they all have a similar final effect.

As the square section of road becomes crowded with stones, the most probable means of randomly adding a moderate or large new stone might involve supplanting one or more preset stones, instead of encountering an open space for it.   This method of adding a new stone has unpredictable effects on the overall integration of the system.   It could increase the integrative level in certain instances but disrupt it in others.   The parallel with biological systems having many components may have validity: it will, at some point, be more difficult to add another large component unless a previous component is in some manner diminished by partial or complete substitution; and likely the least difficult method for "adding" a large component is the enhancement of one already in place, that may enlarge to include biological operations that previously were peripheral to it.

The Effect of Integration in the Road Model

By now it should be easy to acknowledge that the two sorts of integrations of primary biological moment are functional and developmental. Without <u>functional</u> integration each organic component would work to produce its adaptive effect separately and purely additively, in considerable isolation from everything else. (This isolation is always imperfect because, after all, all adaptive effects are housed in one and the same individual whose biological success--or lack of it--is statistically ascribable to the totality of its adaptive resources.)   If adaptive effects were always separate, major, magnificently complex adaptive traits would not exist.   And if there is no <u>developmental</u> integration there can be no functional integration either.   Because development can be measured in functional terms (How "good" is the developmental process in producing a "properly" working adaptive system?) developmental programming is pivotal.

As Waddington repeatedly emphasized (e.g. 1957, 1962), the formation of biological systems is not a simple matter of gene action.   In his view, the "strategy of the genes" is the staging of epigenetic interplay: an immense, orderly series of interactions among environments (external and internal) and structural components that are one or more steps removed from the genes.   These thoughts inspired further considerations of epigenetic effects in evolution and development over the past two decades, that included Whyte (1964, 1965), Løvtrup (1974), Riedle (1977, 1978), Frazzetta (1975a, 1975b), Gould (1977), Ho and Saunders (1979), Alberch, Gould, Oster and Wake (1979), Rosen and Buth (1980), Alberch (1980), and Rachootin and Thomson (1981).

The effect of highly organized epigenetic programs is the mutual monitoring, guidance and response among the changing components to produce the ontogenetic continuum.   It seems evident, then, that a "slip" of one component out of its normal pathway will have repercussions among the others.   It is strongly suspected that in many epigenetically integrated systems the repercussive effects are "corrective" in that they provide an ontogenetic outcome that offers a reasonable prospect of individual survivorship and reproduction (e.g. see Rachootin and Thomson 1981).   In Waddington's terms, such systems are "canalized." They possess coherent protections against potentially damaging mutations, environmental changes or happenstance accidents affecting the individual.   Thus canalized systems are largely tolerant of perturbations.

From this recognition it can be hypothesized reasonably that some canalized systems can, occasionally, accept a novel component (a result of genetic mutation) and <u>mold</u> it to fit within the functional and developmental context without greatly decreasing individual adaptation.   If this can occur then, presumably less

frequently, the result of a molding and fitting process can actually be favored by selection, and canalization might thereby increase the rate at which seemingly improbable, complex systems can evolve.
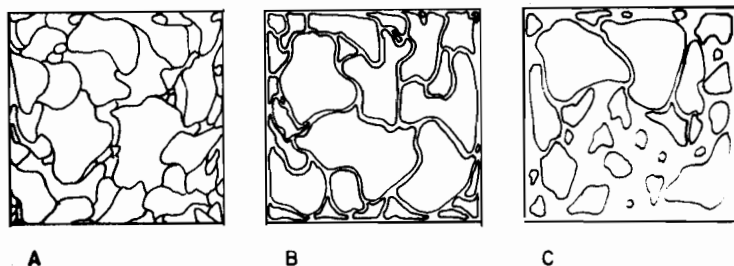

Figure 6.   Three degrees of integration among stones set in square section.
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    The introduction of these views into the road model requires some new conventions. Figure 6 shows several highly integrated stone-inlay patterns. The first of them (A) is the utmost extreme of integration. The second (B) is only a little less strongly integrated while the third (C) shows an uneveness in the strength of integration. In Figure 6, wherever strong integration is indicated, the involved stones tend to form a unit mass (as described in the third paragraph under the previous heading, above). A new stone, dropped upon a sufficiently well-integrated group, may be tolerated and absorbed by the system in the manner already described.

    The new convention, that bends the mechanics of the model to the views of canalization expressed here, is this: a canalized system could accept some new mutations whose deleterious effects can be covered--not phenotypically expressed. Hence, mutations that will go unexpressed may be absorbed to lurk beneath the "surface" of those components involved in the existing canalized integration, and whose own effects are expressed (a view held by Rachootin and Thomson 1981).

    In some instances it is at least imaginable that while some aspects of a new mutation may be unexpressed, a well-adjusted canalized development may permit the less deleterious portions to be revealed to functionally enter and participate in the system.

                    The Road Model and Complex Morphological Change

    Having consciously designed the road model to represent certain views of morphological evolution, we are not entitled to feelings of triumph in demonstrating those views from the model. This model can be used as an illustration of those views; and cautiously, extrapolations from the model can be raised as questions.

    As already considered, the model is consistent with progressive evolutionary change being most rapid during the early stages of the appearance of a new adaptive system, but soon slowing in later stages. Beyond the initial phase, further evolutionary change will more likely involve small, relatively trivial, innovations. Larger changes will come more and more slowly, with increasing statistical difficulty.   Processes that may ease this difficulty include the enlargement of an already present component. Enlargements like these, if too great, might jeopardize the classification of the system as "complex" if they effectively reduce the number of different, interacting parts.

    Presumably, progressive evolution of a system becomes limiting with regard to what sorts of innovations are possible in the future. In some instances canalization can arise (a manifestation of an extremely high level of component integration) and further, significant modification of the system will consequently be either retarded or accelerated, depending upon several factors.

From these thoughts emerges a picture of most potential evolutionary change achieving rather little in the way of basic adaptive novelty; yet rarely, major complex systems will come into existence and, from thereon, for a short while anyway, they may undergo further, rapid modification.

As a purely hypothetical exercise, we may regard some possible attributes of the evolution of the jaw and ear apparatus from reptiles to mammals (see Figure 1 and above description). In appearance, the transition can seem smooth and gradually paced. Figure 7A depicts this view. Genetic changes through time form a uniform series that produces the progressive morphological changes observed.
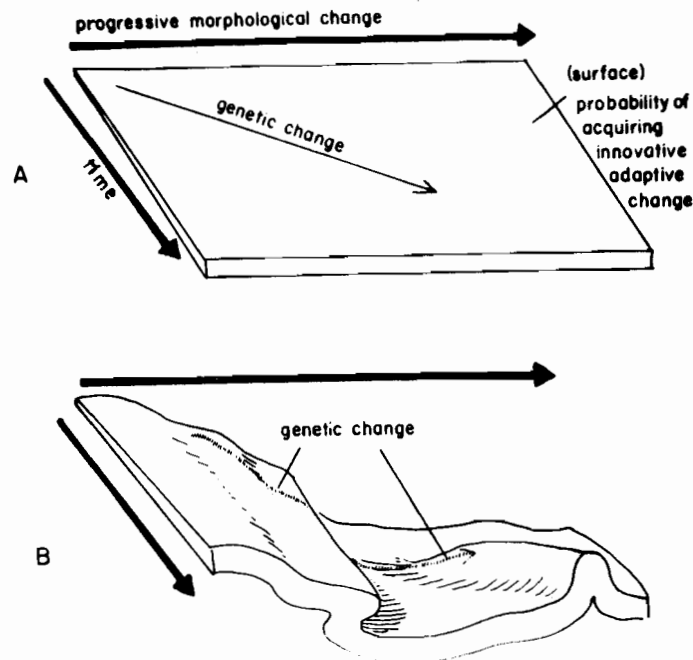

Figure 7. A. Graph depicting progressive morphological changes and the sequences of genetic change that underly them. B. A second model where the probability of the genetic changes is uneven during the morphological progression. Note that the line representing genetic changes tends to follow the highest ridges when the "probability terrain" is uneven. See text for explanation.

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There is the chance, however, that Figure 7B is a better iconograph. Here the smoothness of the structural trend is preserved, but the underlying genetic changes are not aligned as an even series of events. Instead, the genetic changes required to "drive" the progressive morphological change become harder to acquire. Their probability of occurrence falls into a valley and the series of genetic alterations suffers disruptions and discontinuity.

The onset of this "valley" period coincides with an increase in the crowding of elements in the system when (as the model suggests) new, large elements may be accepted only rarely. If difficult periods of accumulating genetic changes occur in the manner conjectured here, the fossil record of progressive evolution may sometimes seem smooth, and thus mislead the observer away from the discovery of underlying, erratic evolutionary events. Where the record is disjunct (e.g. Eldridge and Gould 1972) the causal basis may be similar to that proposed here.

Beyond this difficult period, the system may have gained efficient integration among its parts to have become highly canalized. This canalization may

differentially mask the harmful effects of a genetic change, while permitting expression of less injurious aspects which, thusly, have some greater chance of being tolerated by selection. Correspondingly, Figure 7B shows a rise in the probability of acquiring further innovative change.

The model is consistent with a view that a high degree of canalization does not foreclose further evolution of a system (as is sometimes supposed). Thus canalization may promote continued evolution, although possible evolutionary directions would most probably be harshly limited. The meaning of this seems to be that canalized development results in canalized evolution, if there is any significant evolution yet to take place.

Ecological Analogy to Progressive Model

Addition of irregular, stone tiles to a square section, used to model the acquisition of morphological complexity, suggests itself as a metaphor for another biological problem. If the shape and size of a stone tile can define the qualitative and quantitative impacts a species has in its environment, then competitive interactions can be suggested by the spatial relationships of adjacent tiles. Additional species at the same trophic level may be introduced into the community by fitting new tiles in amongst those already present. However, in the model, the stones are randomly chosen and placed, and adding a new species to the community thus becomes ever harder.

As the community fills up, at any ecological trophic level, the addition of a new species is more likely if it is "small," its members having very restricted resource requirements and being (thus) less likely to engage established species in major, competitive intercourse. In a relatively short time, the community will be nearly closed to further species additions.

The ecological application of the model has some special attributes not present in its morphological employment. A species' impact will partly depend on its number of contained individuals. And this number can expand or contract depending on ecological conditions. Seen in this way, the impact of a species (the size and shape of its representative tile) is plastic to a much greater degree than that of a component in the morphological model. Certainly numerical changes in membership of a species will occur as the community itself is changed. But presumably there is some minimum number, below which the species cannot hold its own, without risking local extinction. The "size" and "shape" of the species' effects on other species, when at that threshold number, may be taken as a fundamental characteristic.

The road model is thus possibly useful in problems of species packing, where considerations of niche overlap (e.g. Pianka 1976, Werner 1977) or the rise of species communities by colonization (e.g. MacArthur and Wilson 1967, Williams 1969) are paramount. There is thus illuminated an interesting correspondance between the addition of species to a community and of morphological features to an individual, developmental system. In both the ecological and morphological models, it is the competitive relationship among the constituents that is the common basis shared between them, and which causes their similarity in dynamics and outcome. Ecological models are numerous and have attained a sophistication beyond what can be rationally anticipated for morphological models—at least for the near future. Where enough similarity exists between ecological and morphological processes, the former may be engaged to suggest models of the latter with, of course, the constant vigilance of caution always required when handling metaphors.

As can frequently be shown for the addition of extant species to a community, the fossil record often shows that in adding species within higher taxonomic units, there is an initial rapidity of species origins followed quickly by stagnation later on (e.g. Stanley 1979). Certain classic examples are well known, and these include lungfish evolution studies by Westoll in 1949 and considered again by Simpson (1953). Westoll, after comparing the earliest with the later lungfishes, could "score" their morphological features as more or less "modern." Figure 8 shows this

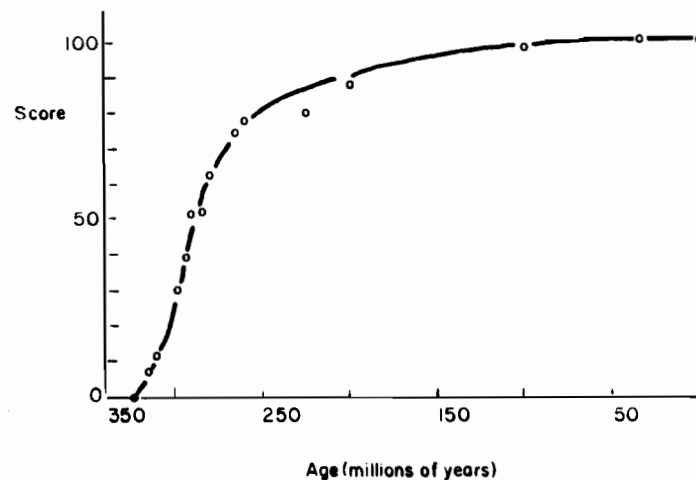Figure 8. Changes in "score" of lungfish morphology. After Westoll (1949).
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score rising very fast in the early stages of evolution, soon reaching a plateau and
changing hardly at all thereafter.   Surely a number of factors might produce this
pattern, but among the possibilities is that new and distinct lungfish species
rapidly arise to fill up the available ecological space. As this space becomes more
crowded, the rate of species addition tapers off as the curve adopts a logarithmic
shape, and further additions depend increasingly upon rare events.

These views are suggested strongly in the temporal patterns of origin of new
taxonomic levels. For many years paleontologists noticed that, beginning with the
Cambrian, when all or nearly all of the known phyla of complicated animals appeared,
the levels of taxonomic rankings of later animal origins declined throughout the
remaining Phanerozoic.   Hence in the Ordovician there are no new phyla appearing,
but many new classes, orders, families, genera and species. Later there are fewer
classes, but some new orders.   Later still, there are few new orders but some new
families can   be found; and so on.

Simpson (1953) and Valentine (1969) see this as a filling up of ecological
space at a declining rate. When the space is wide open, many very distinct animal
groups (large tiles), that will occupy major niche regions, can evolve. But as the
ecological space becomes crowded, only smaller subdivisions of niches are available
for occupancy, and this implies specialized variations on old themes (lower taxon-
omic levels under preexisting higher levels—smaller tiles).

As in the morphological use of the tile model, there is replacement where a new
species may outcompete and usurp the niche space of a preexisting species. Here the
rules of replacement cannot be identical to those in the morphological case.   In
that instance all the components are contained within an organism whose survival is
at stake, and any events that disturb its development are terminated by its death.
Disturbances affecting a community, caused by attempts of a new species to steal all
or part of the niche space of an established form, are not necessarily adverse for
the replacing species.

Moreover, it is not clear to me how a well-integrated (in the sense of the tile
model) community may affect future additions of species.   Such a high level of
integration could suggest stability because of the precisely interlocking demar-
cations of resource space partitions between (or among) the species.   Whether
stability is a cause or an effect of such high integration is not resolvable on any
consideration presented here.   These matters relate to the continuing mysteries of
species diversity differences around the world, as discussed for example by Pianka
(1978). We may note, however, that high stability implies high predictability. A

new species hopeful of joining a highly integrated community may have to shrink
itself to fit within the few, odd, available spaces. With sufficient stability,
the newcomer may survive with part of its adaptive aspect thwarted by competition,
so long as its remaining adaptive substance--that part not in competitive conflict
with an established species--is large enough to resist devastating attrition from
perturbations in community organization.   Perturbations would, presumably, be
reduced in stable ecological systems.
     The tile model was originally composed for the evolution of the development
underlying morphological adaptations. Some extension to analogous attributes of
other biological phenomena--like adding species in an ecological setting--although
potentially productive, should not be made to reach too far. In the ecological
usage it is, after all, a metaphor of a metaphor.

Acknowledgments

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