Intro remarks.
General aspects
+ adaptation

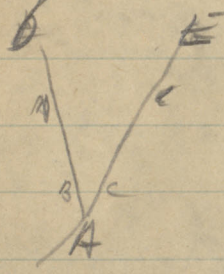
2.

Rather than regarding as today's subject "the divergence model of the origin of higher categories," I'll follow Mayr + regard it as the "synthetic theory of evolution with reference to higher categories," by which we mean in general the extrapolation + magnification of events taking place within populations + species to explain the origin of higher categories: in so doing, we are in essence putting natural selection versus saltation, + perhaps orthogenesis, but not necessarily excluding polyphyly, which some authors at least incorporate into the general divergence scheme, regarding it as a special, or even unusual, means by which higher categories arise, but consistrepresenting basically the same evolutionary processes as in monophyletic evolution. That polyphyly can be satisfactorily subsumed within the general theory will be discussed below: + remains for further meetings of this series to explore the possibility that monophyletic + polyphyletic evolution are in fact qualitatively different in terms of evolutionary process.

In essence, neo-Darwinists view the origin of higher categories, defined as any taxon above the species level within the Linnaean framework, as the assumption by a single species or phyletic lineage progressing on the species level, into a new adaptive zone by the familiar processes of random mutation + natural selection. That such an adaptive shift involves phenomena differing in intensity + scope from those involved in speciation + race formation has led to the adoption of the terms "micro-" + "macro" evolution by neo-Darwinists, along with the saltationist. Such a distinction is one

of convenience only, & probably should be dropped, as Simpson suggested in 1953, to avoid the implication that the evolution above the species level involves ~~the~~ processes essentially diff. from race & species evolution.

The heart of the synthetic view of transspecific evolution lies in the observation, made both by Simpson & Mayr as taxonomists, that a higher category can only be defined ~~exposfacto~~ ex post facto, that is, an early form can only be regarded as a member of a particular higher category in light of subsequent evolution from this form within a new adaptive zone. From this we get the "divergence model" pure & simple:



, where D & E are ~~com~~ recent species clearly separated on, e.g. the ordinal level. Taxonomically, B & C, though perhaps but specifically distinct, are considered in the same order as D & E respectively. Thus, by a ~~quick~~ linguistic ~~of B & C~~ orders can arise before families, families before genera, etc. This is definitely not to be understood that an order exists ~~for~~ ~~a~~ ~~time~~ without families, or families without genera, genera without species, but simply that species B, say, has split from the main lineage & is in the early stages of exploring a large new adaptive zone, such that subsequent radiation within the zone leads us a posteriori to ~~call~~ ~~be~~ ~~re~~ consider B within a new order. Clearly, such a species as B would be considered within the order of E had it become extinct without issue. There is no time now for examples, but a beautiful one exists in Simpson (1953) on the origins of the ~~ten~~ ungulates & carnivores.

Though the generalization has often been made that "the ~~higher~~ ~~the~~ ~~adaptive~~ ~~zone~~, the higher the category that is eventually defined" holds true

In most cases, the adaptive characters of the animal indicative of the particular category as recognized by the taxonomist may vary from many (as in carnivores) to 1, as in bats or rodents. Simpson points out that in such cases as the carnivore, all those characters ~~taken~~ of modern carnivores (I suspect) as a whole ~~as~~ may have (did in this case) arise after the group is phylogenetically distinct, whereas in such cases as rodents, growing incisors may originate before the ~~time~~ group becomes distinct. In such cases it is important to emphasize that the character by which we define the adaptive category of rodent, i.e. growing incisors, which for the sake of argument we ~~can~~ might consider to have arisen in one mutation, does not mean that a new order was created by one mutation, but simply that the means for exploitation was given to a segment of the parent population by which it could exploit what turned out to be a radically new adaptive environmental zone. We can not speak of the origin of a new order by a single mutation because the original mutant still belonged to the parent population. All by normal speciation of one sort or another, with the new adaptive character being selected for, we have a new species occupying a new niche, leading to further species occupying other niches within the zone, ~~such that~~ so that we eventually, ex post facto, recognize the origin of a higher category.

In summary, then, the major points of the neo-Darwinian approach are that "the characters which distinguish higher categories are adaptive and are the same sorts of characters, although commonly greater in degree, as adaptive ~~categories~~ characters involved in speciation." (Simpson, 1953) We are involved ~~with~~ always with the shift into a new adaptive zone. Also, the fundamental unit of evolution is the species. That speciation in its strictest sense, the formation of a daughter species from a parent species (cladogenesis) is not the model, but rather a phylogenetic evolution (or anagenesis) is more probably the more common case is important but not at an essential point here. This observation stems from

the fact that as the record is interpreted by e.g. Simpson, most initial ~~migrant~~ entries into a new adaptive zone leave the parent lineage without any concomitant change in the parent lineage, & progress by phylogenetic speciation directly into the new zone.

Though this model presupposes a monophyletic lineage (as does taxonomy), it is frequently recognized that higher categories have originated polyphyletically, or to quote Simpson (1953) "more than 1 single lineage or specific line crossed the arbitrary boundary as drawn by systematists." Simpson then points out that it is a biological necessity for these lineages to have arisen from a single species, & as such falls within the neo-Darwinian theory. The problems of parallel selection toward & over a threshold can thus be considered as a special multiple aspect of the general phenomenon of phyletic progression into a new adaptive zone. Though to await & later meetings to look over the profundity of the difference b/w monophyly & polyphyly, it is essential to recognize that polyphyly can be satisfactorily subsumed into the general synthetic approach — i.e. saltations are not needed to explain the phenomenon.

I have harped on these few aspects of the neo-Darwinian theory as they seem to me to be the essential concepts vital to ~~acceptance~~ the theory as a whole, constituting essentially the neo-Darwinian response to the saltation approach. It remains to summarize some other aspects of the theory: here, I borrow from Simpson even more freely than I have above.

In general, after initial occupation of a new zone, there ~~is~~ will occur, usually quite quickly, a radiation into subzones & increasing specialization as smaller subzones are exploited. Then a weeding out will occur, depending on the geological vagaries, & whole groups may become extinct.

In general, these points may be considered to contribute to the origin of any particular higher category.

11 higher categories may diverge slowly, or, more usually, divergence may involve an geologically speaking more immediate major change in adaptive status

2. "the adaptive status is generally unusual for its time & may begin in an environment then restricted." This has led to long discussions of "preadaptation," etc. In general, we can say that it is usually true that

3. Rates of phyletic change into the new status are higher. This is based on known successive fossil assemblages & is a general follow through of 11 above.

4. Occupation of a new zone sometimes, at least, represents a breakthrough by one or a few lineages of an earlier group that were divergent & exploratory in some respects but all with some tendency toward prospective adaptation for the new zone.

5. popns. in a breakthrough may be small. Follows from pop. genetics more or less narrowly regional — locus may change. Also from pop. genetics. Don't have to be

Other phenomena have been noted, but as paleontologists with an difficult record of origins of higher categories to explain, these phenomena form for us the crux of the synthetic contribution to evol. theory. Fast phylogenetic change, small popns. & localities are items which are particularly important for us & take note of when we come to examine the record.

If there is time, I would just like to summarize the application of this theory to the fossil record, in the abstract, by one paleontologist - theorist - i.e. Simpson. Simpson's, I think, is the most complete discussion of the problems of fitting the theory & the record, or vice versa, for as we should remember, though the data of paleontology illustrate many features of broad evolutionary processes within a given higher category, the very nature of the evidence only poses the questions, & can usually only supply the evidence, when we come to the problem of the exact mode of origin of the higher category.

First of all, we must realize that known fossil lineages that are sufficiently complete to bear up under the scrutiny - no one would seriously deny, I think, that reptiles arose from amphibians through a gradual process rather than a saltation. It is the sudden appearance, with no immediately ancestral forms, of new higher categories in the fossil record, most noticeably in our own invertebrate record, which must be explained. It is these phenomena which lead to saltationist explanations (see Neal, et al.)

As I said, Simpson's defense is the most lucid & complete, & indeed the following points do seem, when taken together, to account for these sudden appearances. Nothing, though, can be proven - we can only show that the synthetic approach is not necessarily ruled out.

Starting with the formulation observation that only a fraction of the animals capable of being fossilized are actually fossilized, & that paleontologists see only a fraction of all fossils, we note that breaks in the record correspond to periods of time in which organisms were still living & evolving, & that subsequent discoveries open wide geographic areas can often fill in the gaps, & the animals contained. Unconformities have long been the retreat of the neo-Darwinian oriented paleontologist - & detractors of this view have quite rightly pointed out that this explanation by itself is insufficient to explain the totality of events.

Certain aspects of the theory outlined above, though, do tend to supplement the invocation of disconformities.

(1) We noted above that at times, though not usually the case, slowly evolving lineages, with the nature of the enhancement of their phylogeny often leave gaps by the very nature of paleontological sampling

(2) Changes of adaptive zone may simply put organisms moved to quite diff. ecological conditions. Since certain eco. zones are known paleontologically better than others the transition types might be expected to be more difficult to find

The most imp

(3) frequently, newer categories arose by phyletic evol. in small populations, at least part of the time. Reduce. chances of fossil.

(4) transitional forms, in a rapidly evolving lineage (anal tree) have less chance of being found fossil since they are around for so short a time

(5) geographical areas are restricted, since we're dealing @ species of small groups, & limits may change

These last 3, following from the theory itself, are very powerful reasons why we would not expect most transitional forms to be found fossil