

THE REALITY OF HIGHER TAXA AND THE QUESTION OF INTERMEDIATE FORMS

Arthur J. BOUCOT

Department of Zoology, Oregon State University, Corvallis, OR 97331-2914. U.S.A.

ABSTRACT

Emphasis is placed on the fact that forms intermediate between closely related species of diverse genera are well known, that there are far fewer such examples between closely related genera, and almost none between families and higher taxa. The simplest explanation is that species to species level links, evolved in a microevolutionary manner, between families and higher taxa, occur under conditions of very small population size, high endemism, and very rapidly, i.e., quantum evolution. The nature of community evolution indicates that most species level transitional forms will occur within ecological-evolutionary units, whereas almost none will occur during the adaptive radiations characterizing the initial phase of many ecological-evolutionary units. The phyletic evolution so characteristic of community evolution is gradualistic in those cases where an environmentally uniform set of samples is available. Finally, when discussing intermediate taxa it is important to state at what taxonomic level, i.e., is the form intermediate at the specific, generic, familial or ordinal level.

Keywords: Intermediate forms. Quantum Evolution. Microevolution. Taxonomy.

RESUMEN

Se hace énfasis en el hecho de que las formas intermedias de especies próximas, de géneros diferentes, son frecuentes, mientras que son pocos los casos entre géneros y aún menos entre familias o taxones más altos jerárquicamente. La explicación más simple es que a nivel de especies tenemos procesos microevolutivos, mientras que a nivel de familias o más alto se dan en poblaciones pequeñas, con alto endemismo, y muy rápidamente, o sea una evolución cuántica. La naturaleza de la evolución común de las formas intermedias, a nivel específico, indica que mayoritariamente se darán en unidades ecológico-evolutivas, pero que casi ninguna se dará durante la radiación adaptativa característica de la fase inicial de muchas de dichas unidades. La evolución filética tan característica de la evolución de las comunidades es gradualista en aquellos casos en que esté disponible un lote de muestras ambientalmente uniformes. Finalmente, es necesario explicitar a qué nivel taxonómico estamos tratando con las formas intermedias, p. ej.: si es a nivel específico, genérico, familiar u ordinal.

Palabras clave: Formas intermedias, Evolución cuántica, Microevolución, Taxonomía.

INTRODUCTION

Taxonomists have a somewhat different view of certain questions. What questions? The routine decisions regularly made concerning whether or not specimens belong to a new species or an old species, a new genus or an old genus, a new family or an old family, and further up the taxonomic hierarchy, that inevitably convey information of potential importance to our further understanding of how evolution works. The routine assignment of specimens to taxa high and low does inform the taxonomist about certain regularities. It is the nature of these regularities, and their biostratigraphic distribution, that will be considered here.

The Generic and Specific Levels

Let me begin at the base of the hierarchy, at the species level. Most taxonomists, past and present, have employed purely morphologic features when recognizing and defining their species. Today we recognize that criteria other than pure morphology, including bio-

chemical, molecular, behavioral, physiological, ecological, biogeographical, and genetic features should also be employed, but the fact remains that this has virtually never been the case except for that very small number of forms favored by the laboratory scientist, the "fruit flies" of this world. In any event the taxonomist's "species" based chiefly on gross morphology, are commonly considered to be relatively objective units having some reality, utility. One may quibble about sibling, cryptic species and the like, but in practice the species recognized by the taxonomist, identified and described by the taxonomist, are what is actually used now and has been used in the past by the biological community. Rose and Bown (1993) have reviewed many of the problems encountered when one tries more rigorously to define fossil species, while also considering some of the questions posed by biologists. Over the past two hundred years the species of one generation have, it is true, in many instances been split into more than one species, but this does not invalidate the situation. Splitting is a continuing process for which there is no end in sight. My point here is that most taxonomists, and most

users of the taxonomic product consider species to be real, usable units despite their well known problems.

Turning to the genus one confronts an entirely different situation. As with species, during the past two centuries the first recognized genera have been split and resplit many times. But there is a real difference between genera and species. Genera, particularly the speciose genera which tend to be abundant as individual specimens, are the ones commonly most subject to splitting. Genera tend to be considered as subjective units in contrast to the objective nature of species. Why? The following examples illustrate the problem. The well known Silurian brachiopod *Pentamerus oblongus* Sowerby, 1839, is known from most of the warm water Silurian regions of the world. The species is easy to recognize because of its unique trilobate form (Boucot and Johnson, 1979). This is not a case where *P. oblongus* was broadly defined earlier, and has since become restricted in its concept. Since the early nineteenth century many species additional to *P. oblongus* have been assigned to *Pentamerus*, including species that subsequently have been used as the type species for over twenty genera distributed in three major pentameroid and one terebratuloid families! The key character involved in the older assignments was a unique feature, termed a spondylium, present in the ventral valve of all species. Following consideration of additional features these type species ended up as the basis for the twenty genera and suprageneric categories mentioned. My point is that the species have remained relatively stable, with little difference of opinion about what belongs in *Pentamerus oblongus* or the other type species, whereas the concept of the genus *Pentamerus* has changed from a very broadly construed one to a much more rigidly defined one. One could reproduce this situation in group after group of unrelated plants and animals. At the lower, specific level this is also common experience, i.e., that the species concept in group after group becomes more and more narrowly defined as one moves from Linnaeus to the present. Another view of the subjectivity of many generic terms is to review the varied generic assignments that many early nineteenth century species have undergone since their initial generic assignment. Additional evidence of the subjectivity of generic terms is the number of disagreements generated over whether or not particular generic terms are useful. In the Silurian-Devonian brachiopod arena I have been involved in two spirited discussions, over which my splitter tendencies have been challenged by more lumper colleagues (Boucot, 1973; Wright, 1973; Boucot, 1987). Reading these brief statements makes it very clear that the generic category may commonly involve a reasonably high level of subjectivity. Lest the reader now conclude that genera, subjective as they may be, are useless units, let me emphasize that the biostratigraphic, paleoecologic, and behavioral utility among others, of genera are beyond dispute if usage is any indication.

Suprageneric Levels

Having considered the generic level as commonly subjective, in contrast to the relatively objective species, one must now wonder whether or not the suprageneric

taxa are also subjective. Are Felidae and Canidae truly objective taxa or not, and so forth up the hierarchy? Almost all taxonomists opt for the objective nature of suprageneric taxa. Why? It is the common experience of taxonomists that when provided with well preserved, adequate material, they have little difficulty in deciding whether a particular sample belongs to one family or another, or to an undescribed, new family. What is the evolutionary significance of this statement? In largest part it has to do with the latter part of this paper's title, "intermediate forms". The all too common absence of species and genera intermediate between families and higher taxa is what makes it so easy to swiftly and easily discriminate between specimens readily assignable to one family or another, closely related family. The common absence of such intermediate species is what caused Hessler *et al.* (1972) to immediately publish an account of an abyssal Pacific Ocean amphipod that they found to be morphologically intermediate between two families. The common absence of species and genera intermediate between families and higher taxa is what impelled that experienced taxonomist, G.G. Simpson (1953) to define his apology for this absence, Quantum Evolution. The concept of Quantum Evolution posits that the absence of genera and species intermediate between most families and higher taxa can be ascribed in microevolutionary terms to origination of the descendant family and its lower taxa under conditions of 1) very small population size; 2) high endemism; 3) very rapid morphologic-genetic change, all of which ensure that representation in the fossil record will be minimal. It is this absence of intermediate species and genera between families, extant and extinct, that makes these higher taxa so easy to define and recognize, i.e., they are non-gradational with each other at the generic and specific levels despite the conclusion that much of our evolutionary evidence points to ancestor-descendant relations. Now let me turn to further consideration of intermediate forms.

It needs to be emphasized that Simpson's (1953) concept of quantum evolution as an explanation for the absence of genera and species intermediate between families and higher taxa concluded to have ancestor-descendant relations should not be confused with the concept of punctuated equilibria. Both employ allopatry under conditions of small population size and rapid evolution. However, the punctuated equilibrium concept was defined to explain the all too common absence of data indicating morphological transitions between most described species of a genus. I have previously made it clear (Boucot 1978, 1990a) why many practising paleontologists find the concept of punctuated equilibrium false. The chief reasons are summarized below.

Each species occurs within a hutchinsonian hyperspace. Within this hyperspace there are one or more areas of high population density for the species, surrounded by an envelope of lower population density terminating at the surface where the species' abundance diminishes to zero. The one or more areas of high population density occur in at least one community, whereas the peripheral very low population density areas are associated with other communities and other environments, i.e., the cause of the low population density is an environmental situation far less favorable for the

species. Within this peripheral, low population density community, or communities, allopatric speciation can certainly occur, as the proponents of the concept of punctuated equilibrium have stated repeatedly. However, the inference that newly generated, allopatric species have the inherent behavioral-ecological capacity to then disperse successfully back into the area(s) and community (communities) occupied by the high population density occurrences, where they replace the parent species, is unsupported by an evidence from either the present or the past. Peripheral populations are known where allopatric speciation has occurred. Such things include the dwarf proboscidiens and other unguates on offshore islands, and some high montane forms, and the obligate troglobites. In no case, however, have any of these peripheral environments, where allopatry has occurred, served as sources from which the high population density ancestral taxa have been displaced. Additionally, if the punctuated equilibrium concept had any validity it should be relatively easy to discriminate one species from another within speciose genera, i.e., they would commonly have distinct morphological gaps between them, but this is definitely not the case. Also, taxonomists are well aware that when describing new species differences are emphasized, and tend to minimize any overlapping characters that might bring into question the new species. Plus, the all too common absence of intermediate forms between most species of most genera is merely a reflection of the basic sampling problem imposed by the nature of community evolution (Boucot, 1990a; most species belong to rare to uncommon genera, which militates against a solid, continuous sample that would provide a test of the question, whereas the abundant genera and their far smaller number of species seldom show much evidence of species level changes). The interested reader will note (Boucot, 1990a, Table 45; Hoffman, 1982; Boucot, 1978, Table; Levinton, 1988, Table 7.2) the numerical dominance in the many tabulated examples provided of oceanic planktonic microfossils and small mammals (their tiny teeth), as contrasted with megafossils, i.e., there is obviously a sampling problem involved here which suggests that solid evidence favoring gradualism requires good samples, whereas the negative evidence used by the proponents of punctuated equilibrium depends on inadequate samples. In order to test the concept of gradualism one needs, naturally, an environmentally uniform, continuous sequence of beds yielding the same community through time; this situation is, unfortunately, geologically uncommon. Finally, most species described in the past were based on small samples collected relatively randomly with no thought given to the sampling questions that have now been raised. *Caveat emptor!*

There is no denying that one of the major triumphs of the Darwinian concept has been the recognition of intermediate forms, living and fossil. That Amphibia are evolutionarily, morphologically, etc. intermediate between Pisces and Reptilia need hardly be pointed out today, or that *Archaeopteryx* is intermediate between certain gracile coelurosaurs and Aves. However, there is more to the question. One needs, as a taxonomist and evolutionist, to consider what is actually involved in the use of the term intermediate. Let me proceed

while using examples. Most taxonomists are well aware that there are many examples in just about every group of both living and fossil organisms where certain samples are morphologically intermediate between the commonly accepted concept of one species and another of a particular genus. Does this situation necessarily invalidate one of the two species? Does the presence of a morphological intermediate imply that all members of the continuum must be assigned to a single species? *Reductio ad absurdum* would then indicate that should the millenium arrive when we have a complete, total record of all living and once living organisms we would be reduced to concluding that they all belonged to a single species extending from the bacterial to the naked ape (Simpson, 1961, p. 165, pointed this same item out most effectively, as with so many evolutionary questions)! It is unreasonable to conclude that the presence of morphological intermediates between two well defined species necessarily invalidates one or the other of the two (Gingerich, 1985). It is, however, common taxonomic experience to note that such morphologically intermediate samples are common only between those species of the genera which are reasonably abundant as individuals, the same genera that also tend to be both cosmopolitan and eurytopic (Boucot, 1990a). As is so commonly the case in science, sampling problems are involved. In order to obtain the morphologically intermediate samples one must have a relatively continuous stratigraphic record within the same environment, i.e., community type, as emphasized by Bown and Rose (1987), Rose and Bown (1986, 1993) and Gingerich (1980, 1990) for vertebrates, and by myself (Boucot 1986) for invertebrates. This also involves the fact that most genera include only one or a few species and are both relatively endemic and stenotopic (Boucot, 1990a). There is a far lower probability that gradational, intermediate forms will be collected and recognized between the species of an endemic, stenotopic genus, because such genera are also numerically uncommon in most biotas which results in their seldom being collected. Still, most taxonomists are familiar with a reasonable number, albeit a small percentage, of genera which include species having gradational relations with each other. Turning next to the inter-generic level the situation changes, as one might have predicted. Most taxonomists are familiar with some situations where there are species (named or unnamed, based on old or new collections) intermediate between one species of one genus and a species of another genus, where the two genera are closely allied (Rose and Brown, 1984, provide an excellent example from the vertebrates, and Johnson, 1979, from some Silurian marine invertebrates). These are, almost always, the more finely split genera. Here again, the percentage of such genera, those which are both finely split and numerically abundant (also cosmopolitan and eurytopic) is small, resulting in an even lower percentage of intermediate samples and species than one finds between species of such genera. Turning to the suprageneric levels, however, it is clear that such intermediate samples, as well as intermediate species and genera are commonly absent (Hessler *et al.*'s, 1972, amphipod notwithstanding). Here again one appeals to Simpson's Quantum Evolution concept as the explanation. In this context one may emphasize the presence

and evolutionary importance of intermediate forms. One may also make it very clear that at the suprageneric levels such intermediate forms are commonly absent as species and genera forming a complete chain of species and genera leading, without a species level break from one family and higher taxon to another. One may at the same time recognize that there are many such continuous, species-level chains linking some species of some genera, and even some genera together in an evolutionary manner. Turning back to the beginning of this paragraph, it behooves one when designating a particular taxon as intermediate to make it very clear at what taxonomic level the form is intermediate (species, genus, family, order). Being specific does not rob the evolutionarily intermediate concept of its importance or significance, but it does make more evident the nature of the evidence. Finally, one must not be confused by the fact that in situations where there are a large number of missing links in the chain at the generic and specific levels the intermediate family, order or other higher taxon, the *Archaeopteryx lithographica*, is represented by a genus and species, but one that is totally isolated by a large number of unknown genera and species from the presumed ancestral and descendant higher taxa. One cannot leave these considerations without mentioning Gingerich *et al.*'s (1983, 1993, 1994) exciting work on ancestral Early and Middle Eocene whales from southern Asia that are increasingly characterized by post-cranially intermediate characters linking them more and more to terrestrial mammals, not to mention Thewissen *et al.*'s (1994; see also Berta, 1994) material.

AMMONOIDS AND TRANSITIONAL SPECIES BETWEEN FAMILIES AND HIGHER TAXA

In the previous discussion emphasis has been placed on the virtual absence of species and genera intermediate between families and higher taxa. Brian Glenister (written comm., 1994) emphasises that this is NOT the case for ammonoids. He points out that there are a number of situations where there definitely are genera and species truly intermediate in their morphology, at the generic and specific levels, between ammonoid families and higher taxa. He recommends Boardman *et al.* (1994) as an excellent example, using Pennsylvanian ammonoids, of such transitional forms at the specific level between good families. He concludes that the "morphologic complexity and closely constrained development of sutures are the basic factors: you have the gross features of coiling and whorl section that are available from snails and lesser groups, but in addition there is the full ontogeny of the complex suture line that for appropriate functional reasons undergoes disciplined rapid evolution. Add to this at least local abundance, commonly in environments in which the organisms could not have lived, and you have a combination that has attracted detailed attention for the best part of two centuries". Glenister (oral comm., 1994) concludes that for the ammonoids such intermediate genera and species tend to be relatively rare as individuals, in accord

with Simpson's quantum evolution concept, but that these intermediate species need not be endemic. Aside from the ammonoids I am unaware of any other similar example in any kingdom where intermediate species and genera are known between many of the families and higher taxa.

THE NATURE OF SPECIES TO SPECIES TRANSITIONS WITHIN A GENUS OR BETWEEN GENERA HAVING ANCESTOR-DESCENDANT RELATIONS

There has been extensive discussion during the past two decades concerning whether or not species within a genus having ancestor-descendant relations, or species transitional between one genus and another, undergo that transition very rapidly under conditions of very small population size, with little possibility of the transitional forms being preserved in the fossil record (the punctuational view), or whether transitions are more commonly slow enough, involving reasonably large populations capable of leaving a fossil record (the non-punctuational view). Gingerich (1993) has recently discussed the matter, employing Cenozoic mammal samples, and makes an excellent case that the punctuational possibility can be most easily viewed as merely the result of more rapid transitions followed by a more morphologically static situation. Gingerich (1993) has summarized experimental data with living mammals that strongly support his conclusion. Gingerich's (1993) conclusion is that the "argument" between the punctuationalists and their opponents is actually a non-argument, since both rapid rates followed by very slow to null rates are evident from considering his Cenozoic materials. Gingerich's (1993) case is convincing. However, when one considers many of the marine invertebrate megafossils it appears that there is commonly a situation in which samples show evidence for morphologic changes that do not restrict themselves to brief intervals only followed by intervals of morphologic sameness (Sheldon, 1987). Sheldon's (1987) Ordovician trilobite data is one of the best documented for the marine megabenthos, but there are many, many similar examples (see Boucot, 1990a, Table 45, and Levinton, 1988, Table 7.2, for varied examples; there are many more published examples additional to those gathered by Levinton and Boucot). One gets the feeling that within the marine environment the mode is probably closer to Sheldon's (1987) samples than to Gingerich's (1993) terrestrial mammal examples, with this difference probably saying something about modes of speciation within mammals and marine invertebrates that may reflect some basic differences in the frequency and importance of localized dispersal events, locally significant climatic changes, and other biogeographic items that have the capability of affecting the terrestrial environment. All of this adds up to suggesting that the marine environments tend to be far more widespread and uniform, with far fewer major changes, than is the case with what affects terrestrial mammals.

Gingerich (written comm., 1993) emphasizes that

some of the family distinctiveness, based on his work with mammals, may reflect the "hindsight" gained by considering the presently very morphologically distinctive families and higher taxa unduly, while not paying enough attention to the commonly difficult job of trying to discriminate descendant, more modern families from a potentially ancestral family complex. In other words, the past morphological distinctions for potentially ancestral taxa may have been much less distinctive, subfamilial, as contrasted with the more recently developed, familial and higher level distinctions. However, here again this situation is not commonly encountered with marine invertebrates.

WHERE DO INTERMEDIATE SPECIES OCCUR?

Noted above is the fact that intermediate species are virtually confined to species-to-species gradations within a genus, and less commonly to species intermediate between finely split genera, but almost never between families and higher taxa. There is more to the matter. As is commonly the case when considering evolutionary questions at the whole organism level, it is well to think about ecological-evolutionary units and community evolution (Boucot, 1990a, b). When this is done the question of where one may expect intermediate species becomes clear. Intermediate species are most commonly found among the more abundant genera whose species are evolving at a moderate, phyletic rate (Boucot, 1990a, Fig. 409, genera B, C, D). Intermediate species are not found during the initial diversification, adaptive radiation, occurring at and near the beginning of a new ecologic-evolutionary unit, i.e., between new families and higher taxa (Boucot, 1990a). Keep in mind that higher taxa originate at the beginning of ecologic-evolutionary units, not during, except for the abrupt appearance of new, non-level bottom complexes and any newly evolved taxa they contain (Boucot, 1990a, Fig. 417). This paragraph provides the biostratigraphic background for intermediate species and their occurrences through time.

Mayr (1963), in common with most biologists, had no understanding of the community evolution background against which evolution is played out for most of the fossil record, leading ultimately to the modern biota. Thus (Mayr, 1963, p. 589). "Every species is an incipient new genus, every genus an incipient new family, and so forth." This statement flies in the face of the facts of community evolution-biostratigraphy which make it clear that the phyletically evolving generic lineages within community groups are not adaptively radiating to give rise to new families and higher taxa. This ignorance of the evolutionary implications of biostratigraphy (Boucot, 1990b) led to Mayr's curious conclusion that all species have the same potential for generating families and higher taxa ("...and so forth."). Mayr implied that cladogenesis giving rise to new families and higher taxa was a relatively continuous process, whereas biostratigraphy makes it very clear that it is a very discontinuous process. Mayr did not realize that most species

through time do not have the opportunity to participate in adaptive radiations since they are locked into the long term community evolution process which only permits low level phyletic evolution capable of giving rise phyletically to lineal species of the same genus, or finely split subgenera of the same genus, or finely split genera. Also involved here is Mayr's overall implication, never actually stated in any of his publications, that there is a relatively continuous allopatric rate of speciation. When the facts of both historical biogeography and community evolution within the biogeographic units are considered it becomes clear that: 1) The distribution of most modern plants and animals is easily explained by allopatry as Mayr has always emphasized. 2) But, the initiation of that allopatry most commonly took place a long time ago, following which there has been vicariant, community evolution type phyletic evolution rather than continuing allopatry. 3) There is no paleontological or other evidence for an overall, continuous, high rate of allopatric speciation.

WHERE DO INTERMEDIATE FORMS NOT OCCUR?

Throughout this discussion emphasis is placed on the problem of intermediate forms. When a paleontologist mentions "forms" it most commonly means "species". Are there situations where intermediate forms are not to be expected? The best examples I can think of involve heterochrony. Heterochrony in the sense of the omission of specific growth stages, i.e., morphologies. This situation gives rise to species to species evolution, phyletic and/or cladogenetic, in which at least some intermediate forms are missing. Boucot and Wilson (1994) have discussed this possibility, and provided examples. Their examples are capable of explaining family level origination, with an appropriate, family-level morphological gap. This leads to the conclusion that there are two types of families: 1) those originating by strong, directional selection involving quantum evolution (small population, highly endemic, very rapid, little or no chance for being recognized in the fossil record), and 2) those originating merely by heterochronic changes. It will commonly be very difficult to discriminate between these two possibilities, particularly because of the all too common absence of adequate data regarding the ontogenies of most taxa. The importance of trying to obtain as complete ontogenetic data as possible, when studying fossils, cannot be overemphasized!

THE CURRENT SYNTHESIS

Fig. 1. Diagrammatically indicates what is involved in the quantum evolution process of speciation that leads from one species (a) of an ancestral family, to the initial species (k) of a descendant family, through intermediate species (b) through (j). Note that different evolutionary rates are involved in the upper as contrasted

with the lower diagram. The important point is that, following Simpson (1953), the intermediate species virtually always fail to make the fossil record owing to very small population size, endemism and rapid evolution, resulting in a fossil record only recording species (a) of the ancestral family and species (k) of the descendant family. This scheme provides a rational, microevolutionary explanation for the absence of a species-to-species chain linking families and higher taxa concluded on other grounds to enjoy an ancestor-descendant relationship.

It is crucial to also keep in mind that the chances of any once living organism, well skeletonized or not, becoming part of the fossil record are very, very low, even for abundant species, whereas for rare species those chances are virtually nil.

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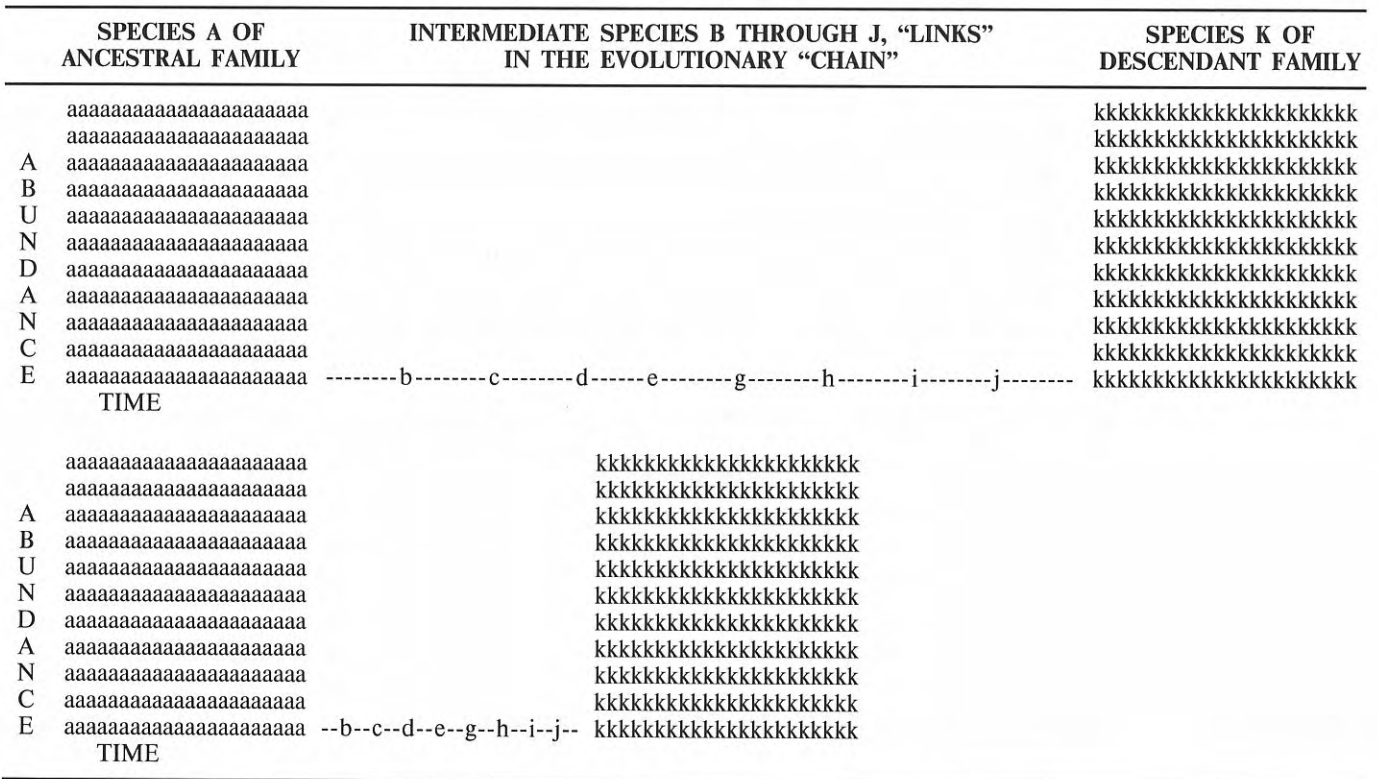


Figure 1. Diagrammatic outline of the relation between population size and rate of evolution between two ancestor-descendant families (indicated by their species/genera a and k), and the genera and species inferred to bridge the "gap" between them (indicated by their species/genera b through j). The "gap" referred to here is the virtually complete absence in the fossil record of such bridging genera and species following Simpson's (1953) conclusion that during such Quantum Evolution the presence of very small populations, high endemism of these "gap" populations, and very rapid evolutionary change essentially precludes a fossil record. Note carefully, that the relative numbers of individuals (diagrammatically indicated by the repetition of the letters for each species/genus, i.e., a, b..., j, k) are far less for a and k, owing to space restrictions, than is the actual case in nature. Evolutionary Time is the Horizontal Ordinate. It is critical to understand that the horizontal time ordinate diagrammed below is "flexible" in that the time from b through j may commonly be far, far less than that from the left hand "a" through the right hand "a" or from the left hand "k" through the right hand "k", although this need not always be the case. In the lower diagram there is less time involved in the quantum evolution change from the ancestral to the descendant family than in the upper diagram.

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