

TESTS OF SOME MATHEMATICAL MODELS  
OF TAXONOMIC DIVERSITY

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## ABSTRACT

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The number of species per genus of any large taxon, when plotted, forms a characteristic curve called the 'hollow curve'. It has the same shape as the curve for the number of individuals per species in an ecological community. These curves are called the genus-abundance and species-abundance curves respectively. They are the starting points for the study of taxonomic and ecological diversity. It has been suggested in the literature that the mechanism or mechanisms producing both curves is the same. The literature on genus-abundance is reviewed.

The genus-abundance curve for the amphibians is shown not to be an artifact of taxonomic processes, such as splitting and lumping or taxonomic philosophy. By extension, it is considered that this is true also of other large taxa.

It is shown that there exists genus-niches and intergeneric competition. On this basis, four biological hypotheses are considered: random niche boundaries leading to a broken-stick distribution of genus-abundance, niche preemption leading to a logseries distribution, many random factors leading to a lognormal distribution and a queuing theory hypothesis leading to a modified logpoisson

(ii)

distribution.

The observed genus-abundance curves for birds, mammals and amphibians are found not to fit the expected curves of these distributions on the basis of a non-null hypothesis.

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## INTRODUCTION

If one takes any reasonably large taxon above the level of genus, say one containing several hundred species, and lists the number of genera containing one species, two species, three species, and so on, a very characteristic pattern emerges. Many, perhaps more than half of the genera, will contain only one species. About as third as many will contain two species. The number of genera with three, four and more species will fall-off rapidly. But the distribution will have a long tail; there being usually a few large genera.

Willis (1922) was the first to call attention to this distribution. He called it the "Hollow Curve". He showed that it was a characteristic of plant taxa. Williams (1964) showed that it is also a characteristic of animal taxa. Both authors showed that it is also a characteristic of species per genus in any geographic area and for genera per family and families per order.

Williams also recognized that the hollow curve of species per genus had the same shape as the curve for individuals per species in an ecological community - the 'species-abundance' curve. We can, by analogy, use the term 'genus-abundance'. Williams also implied that the same mechanisms might be operating to produce both curves, that is, ecological diversity and taxonomic diversity were two 'aspects of the same process. The terms 'species-abundance'

and 'genus-abundance' will be used interchangeably with 'ecological diversity' and 'taxonomic diversity' in this thesis where no ambiguity will result.

While there has been little investigation of the genus-abundance curve there has been a great deal of investigation of the species-abundance curve, because it is the starting point for the study of community diversity (Pielou, 1975; Cody and Diamond, 1975). Pielou has stated the central problem: "Given a stable many-species community, how have its constituent species come to share the same habitat and how do they maintain themselves and interact with one another? What determines the number of species that can live together and their relative proportions?"

Generally, if a process is postulated to operate, then we should be able to write descriptive equations, and from these equations we can generate theoretical abundance curves which can be compared with the observed curves.

Specifically, three biological processes have been postulated in the literature to account for the species-abundance curve. First, the environment is, in some sense, pre-divided into niches of various sizes. This is the "broken-stick" distribution hypothesis of MacArthur (1957). Informally, one can say that the environment 'decides' the size of the niches. Second, the various species sequentially pre-empt a fraction of the exploitable resources. This is the logseries distribution hypothesis whose strong-

est proponent is Williams (1964). Informally, one can say that the species 'decide' the sizes of the niches. Third, the factors affecting the sizes of the niches are so many and so varied that their distribution is essentially random. This is the lognormal distribution hypothesis of Preston (1962).

Now if genus-abundance and species-abundance are homologous, that is they are both generated by the same mechanisms; then if we can make meaningful statements about species-abundance, we can also make the same meaningful statements about genus-abundance.

It is generally held that species-abundance is determined by the distribution in the sizes of niches (however defined) and is mediated through interspecific competition. Therefore, in order for species-abundance and genus-abundance to be homologous, there must exist a genus niche and intergeneric competition. Williams (1964) and Mayr (1963) hold that there exists a genus niche and Mayr, Linsley and Usinger (1953) and Van Valen (1971) hold that there exists intergeneric competition.

Therefore, it is legitimate to test genus-abundance in the same way species-abundance has been tested since the same mechanisms presumably dictate the shape of both curves.

There are two other postulates in the literature which do not require consideration of niche size or competition. Koch (1966) has describes a hypothetical process

of species formation which should lead, by implication, to a logpoisson distribution of genus-abundance. Finally, Chamberlin (1924) and others have suggested that the curve is an artifact of the process of taxonomy.

This thesis reviews the history of the concept of taxonomic diversity and examines the postulated homologies between species niches and genus niches and between inter-specific competition and intergeneric competition. It then develops theoretical distributions from the broken-stick, logseries, lognormal and logpoisson models and tests these against the observed distributions for birds, mammals and amphibians. There is also an extended discussion of the hypothesis that the observed distribution is an artifact of the taxonomic process itself.

## HISTORY OF THE CONCEPT OF GENUS-ABUNDANCE

The literature on diversity is now of enormous quantity. It divides naturally into three clusters, according to Anderson (1974): (1) the British phytogeographers, whose works center about J.C. Willis, (2) the British entomological ecologists, in particular C.B. Williams, and (3) the American animal ecologists, of whom Robert MacArthur is the chief figure.

Most of these investigators deal with species-abundance rather than with genus-abundance. The literature on genus abundance, in the strict sense, is very much more limited. The chief references are, in order, Willis (1922, 1940), Chamberlin (1924), Yule (1925), Wright (1941), Mayr (1963), Williams (1964), Koch (1966), Raup et al (1973) and Anderson (1974).

Surprisingly, many of the leading students of evolution scarcely consider genus-abundance. Simpson in two major works, Tempo and Mode in Evolution (1944) and The Major Features of Evolution (1953), does not deal with it at all and deals with it only peripherally and qualitatively in Principles of Animal Taxonomy (1961). Sokal and Sheath in Principles of Numerical Taxonomy (1963) note the genus-abundance curve and note that it has never been satisfactorily explained, but judge that the lack of objective criteria for genera, families and higher categories is the major obstacle to understanding. Hennig in Phylogenetic Systematics (1966)

also does not deal with the phenomenon. Mayr in Principles of Systematic Zoology (1969) adds nothing to his 1963 discussion.

Willis and Yule and their critics: 1920's to 1940's.

Since Willis appears to have been the first to call attention to the phenomenon of genus-abundance, and all subsequent studies have started with him, it is worthwhile to examine his views at some length.

In his book Age and Area (Willis, 1922), he demonstrates without any ambiguity that the plot of the number of species per genus for the fauna and flora of any moderately large area forms a 'hollow curve' - the genus-abundance curve- and that this is also true for the world as a whole. On a world-wide basis in 1922, 4853 genera of the known 12,571 genera of flowering plants and ferns were monotypic. He also claims that, on the basis of his data, species and genera of small range are phyletically young, species and genera arise more or less mechanically and regularly and geographic dispersion in related groups occurs at a nearly constant rate. Willis gives no very firm reason for his conclusions.

Willis' conclusions appear to me to be identical to those of Guppy (1906) [cited by Lawrence, 1951, page 161] which were based on an unsupported premise that for terrestrial plants there had been an era of nearly uniform environment: "... of great atmospheric humidity, when per-

sistent cloud-covering blanketed the globe and where the same equitable temperature everywhere prevailed."

Anderson (1974) says that Age and Area has a "curiously archaic flavour". Willis is an avowed anti-Darwinian. He states in his preface: "I have endeavoured - with what success this book will show - to free myself from the trammels of natural selection theory." In a contributed chapter, Hugo de Vries concluded that: "The general belief in adaptation as one of the chief causes of evolution of specific characters is thus contradicted by the statistical studies of Willis, ...".

It is very difficult to discover exactly what Willis' basic argument is, why he feels that selection is an inadequate explanation for evolution, and how the actual shape of the genus-abundance curve is generated. He attempts to explain further in a second book (Willis, 1940). Some of the statements in this book just plain do not make sense whether taken in or out of context. For instance (page 191): "Evolution and natural selection are probably to a great extent independent, and they work at right angles to one another, with (in plants at any rate) little mutual interference."

In his 'Final Summary of Conclusions' (1940, page 191), Willis says: "Evolution most probably goes on by definite single mutations, which cause structural alteration, which may, but by no means necessarily must have some

functional advantage attached." He holds that both species and higher categories arise abruptly. "Mutations tend to be divergent, especially in the early stages of a family. The family, consisting probably of one genus and one species, is probably created by a single mutation, whilst later ones are usually less marked than the first and give rise to further genera and species. ... Evolution goes on in what one may call a downward direction from family to variety, not in the upward direction required by the theory of natural selection. ... Varieties are the last stages in the mutation and are not, as a rule, incipient species."

Thus evolution is wholly dependent on the chances of mutation and is saltational - that is, new forms differing sufficiently to constitute a new higher taxon arise spontaneously and breed true. But then Willis goes on to say that: "The process of evolution appears not to be a matter of natural selection of chance variations of adaptational value. Rather it is working upon some definite law that we do not yet comprehend. The law probably began its operation with the commencement of life and is carrying this on according to some definite plan. ... Evolution is no longer a matter of chance but of law. It has no need of any support from natural selection."

Willis was not a mathematician. His statistics referred to by de Vries (Willis, 1922, page 227) consist of raw data, graphs of raw data and simple averages. He



appears to have been unaware that a log-log plot of a hyperbola gives a straight line and expresses his indebtedness to G.U. Yule for this 'deduction' (1922, page 241). Nowhere in his work is there a test of significance.

Yule (1924) discussed and developed some of Willis' ideas mathematically. He was also an anti-Darwinian. He based his formula on the assumption that: "... the chances of the formulation of a new species from another within the same genus is, in any assigned interval of time (an hour, a year, or a century), the same for all species within the genus considered, and is constant for all time." He then claims that this generates the general formula for the genus-abundance curve:

$$\log S + m \log n = k \qquad \text{Equ. 1.}$$

where S is the number of species, n the number of genera and m and k are constants.

Yule fits a logseries curve to his genus-abundance data and there is no significant evidence against the hypothesis that the fitted curve and the data differ on the basis of a chi-square test, that is, the chi-square alpha values are less than 0.95. Nevertheless, equation 1 is not the equation of a logseries.

Willis immediately came under severe criticism by many leading plant taxonomists who disputed his claim that his data led to his conclusions (see, for instance, Gleason

(1925), Sinnott (1924), and Fernald (1924)).

Batson (1923) attributed most of Willis' anti-Darwinianism to the influence of de Vries. He says that the evidence that de Vries adduced from his study of Oenothera and which led him to propound the theory of mutation is clearly the evidence which Willis had at the back of his mind. But de Vries' mutations, according to Batson, are not genuine illustrations of the origin of species by variation. He says: "Had de Vries grasped the implication of Mendelian analysis he could never have interpreted the [mutations] with any confidence."

Chamberlin (1924) summarized Age and Area and subjected it to "an orthodox Darwinian refutation. He felt that the quality of the systematic work, including its relative completeness, might affect the observed pattern of genus-abundance. He also recognized that a taxonomist had, in a sense, a random sample of the real classification and that this would approach the real as the taxonomist collected more species. In fact, Chamberlin could detect no difference in the shape of the genus-abundance curve generated by 'old' and 'improved' classifications. (Later work by Williams (1964, page 131) has shown, for instance, that there is no change in the shape of the curve for birds between the classification of Linnaeus of 1758 and that current in 1909.)

Like Willis, Chamberlin assumed the genus-abundance

curve to be hyperbolic and concluded that the "ideal" curve was:

$$XY = K$$

Equ. 2.

where K is the square root of the number of species in the taxon and Y is the number of genera containing X species.

The reason why Chamberlin felt the hyperbola to be "ideal" is because the genus-abundance curve looks hyperbolic: "In the first place, the hyperbolic appearance of the curve suggested the simple formula  $XY = K$  would satisfy the conditions. ... The second [place] was deduced from purely theoretical conditions." He goes on to claim that if an original genus gives rise by mutation to a new genus for each time interval and the same rate also applies to the daughter genera, then a geometric progression results. This claim, as stated, is correct if and only if new genera arise absolutely regularly, not probably as assumed by Yule.

Chamberlin also noted that the sizes of cities in California, the distribution of wealth and other non-biological data also yielded a hollow curve, that is, had an apparent hyperbolic distribution. What he was noting was the lognormal distribution which Aitchison and Brown (1966) have shown to be followed by wealth distribution and much other demographic data.

Walters (1961) is a very belated critic of Willis. The fact that, forty years after the publication of Age and

Area, taxonomists still find it worthwhile to criticise the book illustrates its great influence.

Walters examines the pre-Linnaean origin of our family, and generic concepts. Modern botany took shape in Europe and the existing Angiosperm families and genera are the product of early botanical thought in Europe from the beginning of the sixteen-hundreds on. In fact, most of the largest families and genera were defined a century before Linnaeus. Walters asks: "What reason have we to think that the demarcation of the largest Angiosperm families would look approximately like the one we use (with very little dispute) at the present day, if Angiosperm taxonomy had been born in, say, New Zealand, instead of Europe?"

He implies that our classification would be very different. The late appearance in the literature of small and monotypic genera, which make the genus-abundance curve, is the inevitable product of the growth of taxonomy, according to Walters, since the exotics do not 'fit' into our concept of Linnaean and post-Linnaean taxa. He feels that, if we could "wipe the slate clean", a very different taxonomy would result (and by implication perhaps abolish the 'hollowness' of the genus-abundance curve).

It is very difficult to take Walters seriously. He does not seem to realize that the very new and depauperate post-glacial European flora would consist naturally of species from large and wide ranging genera. Nor does he

offer any hints on what a New Zealand-type plant taxonomy might look like.

Wright (1941) points out that Willis has fallen into two errors. First, Willis has assumed that if natural selection is not an adequate explanation, then the only alternative is his own view. Second, Willis has assumed that conformity of data proves the hypothesis without considering that there might be other hypotheses which also fit the data. (Chamberlin (1924) also makes this criticism.)

Wright then puts Willis' theory into perspective by classifying evolutionary theories according to the rôle allowed chance variation:

(A) Evolutionary theories which eliminate or minimize chance.

(1) Evolution preordained: Orthogenesis.

(2) Evolution as an extension of individual physiology: Lamarkianism.

(B) Evolutionary theories in which chance plays an important rôle.

(3) Evolution determined by the selection of chance variation: Darwinianism:

(4) Evolution determined by single mutations, that is, in which chance is all there is: The Position held by Willis and de Vries.

Wright says that Willis in 1922 seems to hold to 4, by 1940 he attempted to combine 1 and 4.

Wright then considers alternative formulae to Willis' to generate the genus-abundance curve. Like Sokal and Sneath (1963), whose formulation will be discussed, Wright arrived at a poisson distribution but from different initial conditions. He considered a taxon "... in which the total number of species remains constant, new species being balanced by extinction. For a given interval of time there is a certain probability that it [a genus] has one, two or a larger number of descendants [species]. By choosing the appropriate interval of time, the variance of this array of probabilities may be made 1 and therefore equal to the mean of the array. Genera containing  $n$  species (whose fates are assumed to be independent) should show a distribution of generic sizes after the chosen interval such that the variance is  $n$ , again equal to the mean of the generic size. These conditions ensure that the distribution will be at least approximately of the poisson type. In the long run the frequencies,  $f(x)$ , of generic size,  $x$ , should reach a certain equilibrium form. [Wright uses  $f(x)$  to mean the frequency of  $x$  and not function.] The class of genera with  $n$  species is dispersed after the chosen interval of time but receives recruits from each other class ( $x$  species) according to frequency  $f(x)$  and to the appropriate terms in the poisson distribution,  $e^{-x} x^n / n!$ ."

In explanation, if a genus has, say, 10 species at time  $t_0$ , it is in the tenth interval at time  $t_0$ . Later, at

time  $t$ , this same genus may contain less or more than 10 species depending upon the chances of extinction or speciation. Perhaps it will move down to, say, the eighth interval or up to the thirteenth, but, if equilibrium has been reached, its place in the tenth interval will be taken by some other genus moving either up or down the intervals. Some genera will become extinct in the time interval but the occasional origin of new genera replaces them.

Wright has not followed up his insight in any subsequent studies.

There has been little criticism of Yule (1924).

Williams (1964, page 121) points out that the formula Yule gives to generate the genus-abundance curve (see equation 1 on page 9) does not agree with his data. Sokal and Sneath (1963, page 245) have a much more serious criticism. They restate the conditions that Yule gives to generate his formula as: If the branching of an evolutionary dendrogram occurs at random, it is the same thing as saying that there is an equal chance of each stem giving off one or more side branches in a given interval. This is indeed what Yule said; it is also the conditions under which the side branches will obey a poisson distribution. Yule's data does not fit a poisson distribution either.

The British ecological entomologists: 1940's to 1960's

The general review paper of Fisher, Corbet and Williams (1943) is adequately summarized and incorporated into Williams (1964). However, it inspired Kendal to make two theoretical studies. One (Kendal, 1948a), on modes of growth leading to a logarithmic series distribution which he ~~generalized to include genus-abundance~~, was used by Williams (1964). In the second paper (Kendal, 1948b), he considered very generalized origin-extinction processes which Anderson (1974) has followed up.

Williams presented an enormous quantity of data in his Patterns in the Balance of Nature (Williams, 1964). Most of it is relevant only to species-abundance but one chapter and part of his conclusions are devoted to genus-abundance.

Williams presents much of his data raw and where data is plotted it is usually done so on y-axis probability paper with the x-axis logarithmic. If the plot is more or less a straight line, the data are considered to be log-normally distributed. Other data are plotted log-log and if the plot is roughly a straight line, it is considered to be a hyperbolic logseries. A surprising feature of the book is that it does not give any tests of significance - and this is especially surprising because Williams was a close collaborator of R.A. Fisher.

Williams (page 142 and following) discusses the



difference between taxonomic 'splitters' and 'lumpers' and whether the genus-abundance curve is an artifact of the taxonomic process. Splitters will allow genera to be separated on the basis of characters which lumpers consider too small or too recent in origin to be justification for separation. Lumpers will allow division of genera only on characters which have a much more distant origin in time, and are thus more 'fundamental'. For a given number of species the splitters will allow more genera than the lumpers. The splitters produce a classification of high generic diversity; the lumpers' one with a low diversity.

'High diversity' is defined as a genus-abundance curve with a low mean number of species per genus, that is, many genera, most with one or few species. 'Low diversity' means few genera, most with many species.

Williams cites Kirby's classification of the world's mantids as a classification that closely approaches a log-series. (In fact it does not - as will be shown - but this does not vitiate William's argument.) One might be inclined, says Williams, on this account to say that the log-series was the 'correct' interpretation of the mathematical structure of the genus-abundance pattern in the mantids and that Kirby had given a correct interpretation. But it might be better to say that Kirby had been consistent rather than correct. Instead of classifying 800 species into 200 genera - as he did - he might have classified them into 400 genera

had he been an extreme splitter or 100 had he been an extreme lumper. Had he been equally consistent in both extreme cases he would have produced a logseries. All three classifications would have been equally sound in so far as they express the evolutionary relationships.

Williams confesses that his original opinion was that 'species', as described by taxonomists, were about 90% real biological interpretation and about 10% matters of convenience - with the percentages the other way around for genera. But when his work showed the same patterns appearing when grouping individuals into species and species into genera, he began to consider that genera might be as real or as unreal as species. Furthermore, when both splitters and lumpers produce the same mathematical pattern, needing only a change of constants, Williams asks whether they may not be equally truthful interpreters of what has happened in the process of evolution.

To this he answers: "Yes". He constructs an imaginary set of twenty-three species having a logseries resemblance to each other in each time era but with the resemblance diverging with time. A splitter, who takes these species and is prepared to accept the present divergences as generic differences, would produce a logseries genus-abundance pattern with a high generic diversity. Lumpers, who probe more deeply into the past, will produce a logseries genus-abundance pattern of lower diversity. But

they will both produce a logseries pattern.

Where a 'wrong' pattern is produced, that is, a pattern that is not consistent regardless of splitting and lumping, is where the taxonomist probes more deeply into the past at one point and less deeply at another. This is to be both a splitter and a lumper. Williams suggests therefore that a composite publication by several authors would be, generally, less reliable than one individual's work.

In his summary (page 294 and following), Williams speculates that the close fit of the logseries to the data may not be a departure of the data from lognormality but is owing to the sample being too small to distinguish critically between the two distributions. In his discussion of the possible biological origin of the logseries distribution he cites Fisher (Fisher, 1941) who showed that a sample taken from a population distributed according to a logseries would itself show a logseries distribution. It follows, therefore, that if the sample is actually logseries distributed, then so is the population. Williams also cites Kendal (Kendal, 1948a) who considered (1) the probability of a species splitting into two, (2) the probability of a new species arriving from the outside and (3) the probability of a species disappearing. Kendal then showed that if, at some particular time, we start with a series of genera each with one species, their distribution after time 't' would be a geometric series with an abnormal zero-class. But since

different genera will not start at the same time, the final result will be a logseries.

The balance of evidence indicates to Williams, with much reservation, that the logseries is the closest to the real genus-abundance pattern.

The American animal ecologists: 1960's to 1970's

Mayr (1963, page 586 and following) appears to have been the first ecologist to discuss at length the phenomenon of trans-specific evolution - that is, evolution at the genus level and higher - in an ecological context and as a homologous extension of the phenomenon of species evolution. It is useful to consider his views at length because of his enormous influence on present-day ecological and evolutionary thought.

Mayr notes the basic difficulty: Genetic differences between populations can be analyzed experimentally by fertile hybrids; analysis of the differences between higher categories is in most cases impossible by this method. [Since Mayr wrote, the technique of electrophoretic protein analysis has to some extent solved this problem. See, for instance Salthe and Kaplan (1966) on the rates of evolution of higher categories in the amphibians.]

Mayr also notes that evolution is not primarily a genetic event - it is a selection. Furthermore a character is not normally the product of a single gene. Trans-

specific evolution is, in his view, the selection of whole coadapted gene complexes. Orthogenetic trends are owing to the fact that evolutionary changes of phenotype are limited by the original gene complex selection. 'Evolutionary inertia' of certain characters is owing to the large number of genes controlling the character and the unlikeliness of the genes of the complex as a whole being strongly selected.

'Evolutionary stagnation' (Mayr instances Lingula, Limulus, Triops) is not caused by a 'depletion' of genetic variability but by a superb adaptation to an unvarying environment.

[Mayr's suggestion that there is no genetic depletion in evolutionary conservative species has been recently confirmed. Ayala et al (1975) found that deep-sea asteroids, which live in an exceptionally stable environment, show high genetic variability. Selander et al (1970) found that the horse-shoe crab, Limulus polyphemus, is just as variable genetically as other organisms and he concluded that slowly evolving lines have not an unusually low mutability.]

Mayr also says that the fossil record shows that the regularities in the rise and fall of higher taxa, which some evolutionists claim to see, are largely absent. [See further in this thesis, the discussion on this point by Raup et al (1973).]

Mayr claims that all evolution is owing to the accumulation of small genetic changes, guided by natural selection, and trans-specific evolution is nothing but an ext

rapolation of what takes place within populations and species. The key rôle that the species plays is because every species (1) is a different aggregation of genes which controls a unique epigenetic system, (2) occupies a unique niche, having found its own specific answer to the demands of the environment [the teleological and volitional vocabulary is Mayr's own], (3) is to some extent polymorphic and can thus adjust to changes and variations of its total environment and (4) is ever ready to bud off populations which experiment with new niches. Entire species or separate populations of species may, at any time, (5) develop a new combination of genes, a new epigenetic system, which constitutes a novel and more successful adaptation to the environment, or (6) shift to a new ecological niche which is so favourable that it becomes an entirely new adaptive zone, and (7) every population that makes such a shift to a new adaptive zone is an evolutionary pioneer and may become the founder of a new higher category. Thus, according to Mayr, every species is an incipient new genus and every genus is an incipient new family. The same is true on the ecological side, there is an insensible gradation from the new niche to the new adaptive zone. The broader the zone, the higher the taxonomic category when fully developed. [Words underlined italicized in Mayr's original.] The concept of 'adaptive zone' will be discussed further in the section of this thesis "The Problem of Taxonomic Diversity".

The process of speciation, even a very active multiplication of species, does not necessarily signify great evolutionary activity. Mayr instances speciation in such stable types as Drosophila and Culex. But, with few exceptions, a breakthrough into a new adaptive zone is followed by two events: a colossal speed-up in the rate of evolutionary change and a period of adaptive radiation. He cites several of Simpson's works which show how rapidly a new type may reach a new/phylogenetic 'grade' to remain essentially stable afterwards (t.f., bats, which were 'modern' by the middle eocene).

The second aspect of every major and most minor break-throughs is the great development of many minor types in the new adaptive zone. For instance, on the adaptive plateau 'bird' there are numerous minor peaks that can be occupied. The fossil record indicates that many 'experiments' were made which had no lasting success. Aberrant types produced during such periods of adaptive radiation disappear as rapidly as they appear. If there is no serious competition or predators even rather improbable genotypes may have a chance to survive for a while. They inevitably give away to more successful types in related branches.

The origin of discontinuities (speciation), evolutionary divergences (adaptive radiation) and extinction have the greatest effect on the size and structure of the

taxa and thus the genus-abundance curve:

(1) If a taxon speciates actively without much adaptive radiation, it will have many species per genus,

(2) If a taxon radiates actively (developing strong evolutionary divergences), without much speciation, it will develop many monotypic genera.

In most taxa there will be a mixture of both tendencies. Thus, according to Mayr, the independence of these two processes, and also that extinction and speciation tend to balance each other, is the main reason for the shape of the genus-abundance curve.

Nevertheless the existence of monotypic genera, so important a factor in determining the shape of the genus-abundance curve, troubles many taxonomists, such as Platnick (1976). He would allow them only when it is known that the other sibling species in a dichotomous branching has become extinct. Mayr (1963, page 342) is somewhat ambiguous in that he implies that there are too many monotypic genera yet tends to create proportionally more by his taxonomic revisions. He says: "An additional benefit of the adoption of the polytypic species is that it has contributed to the reevaluation and simplification of the generic classification. [Of birds] For instance, as soon as the 19,000 nominal species of birds were grouped into polytypic species, it became evident that many of the then accepted genera were monotypic. Each such genus was



nothing more than a designation for a morphologically distinct species. The genus, thus defined, coincided with a polytypic species and failed to perform its true function, namely, that of indicating relationship between species. To restore the balance a lumping of avian genera on a vast scale became necessary, reducing them from between 6000 and 7000 (the number recognized by several authors around 1920) to about 1700 or 1800 (the number currently recognized). In the course of reevaluation of the genus it was possible to show that "morphological" differences distinguish almost any two species (except sibling species) and that mere morphological difference is therefore a useless generic criterion. Indeed, rather striking morphological differences can sometimes be found even among different sub species of a single polytypic species. Defining the genus as a group of related species permits considerable simplification of the genus concept."

Paradoxically, after reevaluation was completed (Mayr and Amadon, 1951), fully 41% of the genera of birds were monotypic (Gruson, 1976), an increase from 31% before the recension.

While Mayr made no suggestion as to the actual shape of the genus-abundance curve, Koch hypothesized that it should be lognormal. In two papers (Koch, 1966, 1969), he noted that in much biological data skewed frequencies are the rule rather than the exception. He gives the

number of species per genus as one of his examples. When many biological skewed frequencies are plotted on semilog paper, a frequency curve results which is called the lognormal curve.

The lognormal curve has been little used and much misunderstood. Although it has many of the properties of the normal curve, it differs in many important respects (Aitchison and Brown, 1966). Where the normal curve arises by the addition of a large number of small, independent, random variables; the lognormal curve arises by the multiplication of a large number of small, independent, random proportionate variables. A comparison of the normal and lognormal equations points to another important difference:

Normal curve:

$$y = \frac{1}{\sqrt{2\pi V}} \exp\left[-\frac{1}{2}V(x-\bar{x})^2\right] \quad \text{Equ. 3.}$$

Lognormal curve:

$$y = \frac{1}{x\sqrt{2\pi V_L}} \exp\left[-\frac{1}{2}V_L(\log x - \bar{x}_L)^2\right] \quad \text{Equ. 4.}$$

where  $\bar{x}_L$  and  $V_L$  are the logarithmic mean and variance respectively. Note the factor  $1/x$  in the lognormal curve which ensures that the curve is skewed even when plotted on semilog paper - that is, the lognormal curve is not usually a curve in which the logarithm of the random variate  $x$  is normally distributed (where  $x$  is not).

Koch claims that the lognormal generating process arises logically in the process of classification and results in a lognormally distributed genus-abundance independent of any historical evolutionary processes. That is, the genus-abundance curve is an artifact. According to Koch, each taxon may be divided into species in which constant proportions have one or other characteristics. If the proportion does not depend on which taxon is under consideration and if there are enough characteristics used in the classification, then the conditions will be met such that the lognormal distribution results.

This hypothesis is examined in the section of this thesis 'Hypotheses of Artificiality'.

Koch makes a second suggestion for a mechanism to generate the genus-abundance curve. First, he discusses how a lognormal curve results from an autocatalytic process:

$$\ln N_f = \ln N_i + \lambda t \quad \text{Equ. 5.}$$

where  $N_f$  is the number of entities finally present,  $N_i$  initially present,  $\lambda$  the growth rate and  $t$  the duration.  $N_f$  is lognormally distributed if  $\lambda$  or  $t$  is normally distributed (but not both) or  $N_i$  is lognormally distributed. Arguing from the normally distributed lag in the germination of seeds, Koch then generalizes to any normally distributed lag process, replaces  $t$  by  $t-L$ , where  $L$  is lag.

and:

$$\ln N_f = \ln N_i + \lambda t - \lambda L \quad \text{Equ. 6.}$$

He gives several examples where this relationship obtains, then he says: "It is possible that the evolutionary time during which radiation of species takes place is normally distributed, and thus the number of species per family, order, etc., is lognormally distributed."

Koch can only mean that there is a lag between the opening of an evolutionary opportunity and the evolution of a species adapted to exploit this opportunity and the lag is logarithmically distributed. I can find no evidence for this intriguing suggestion. A mathematically equivalent situation is to allow the evolutionary time to be logarithmically distributed. Preston (1969) suggests that such a time distribution is not uncommon biologically. I think Koch is wrong in suggesting that such a situation would lead to a lognormal genus-abundance curve. Opening of time 'gates' with 'processing' is a queuing process (Morse, 1965) and a logarithmic parameter of either arrival or processing (but not both) would lead to a logpoisson genus-abundance distribution.

Simberloff (1970) considered the average number of species per genus on an island compared to the adjacent mainland. Williams (1964) had determined the expected average by placing chips for species with numbers on the

chips for genera in a box and withdrawing  $N$  chips. Simberloff did it by generating random numbers on a computer. With the large numbers available it was easy to compare a set of species found on a real island with the distribution of sets of species drawn randomly from the source area, that is, the adjacent mainland.

One of his conclusions is relevant to this thesis, viz, taxonomic splitting or lumping or size of the source area had little effect.

Simberloff's study may seem peripheral, but it may be regarded as the same problem reversed. For Simberloff: Given a selection from a source genus-abundance distribution, what theoretical genus-abundance distribution might be expected; for this thesis: Given a real genus-abundance distribution, what might be the theoretical 'source' genus-abundance distribution?

Simberloff (1972) and his associates (Raup et al., 1973) try to answer the central question: "Can the processes resulting in local equilibria in ecological time also be used to predict events in evolutionary time?" and "... whether an equilibrium pattern of phyletic radiation can exist and if so what its characteristics would be?"

They tested by computer modeling. The details of the programme are peripheral to this thesis, but the constraints are relevant.

An arbitrary time scale was established and a

single 'ancestor' was entered at the beginning of time. The ancestor was made to advance through time and as it advanced its fate was controlled by generated random numbers. At each time unit the lineage could become extinct or persist to the next time unit or persist to the next time unit with branching. The probabilities of these three fates were supplied as input constants. Branches became subject to the same randomly controlled development in time.

If the probability of branching is consistently higher than the probability of extinction, then the number of lineages will increase beyond bounds. A temporary increase was allowed by the programme but a control was included for controlling diversity. The equilibrium diversity was preassigned and when it was reached the branching probabilities automatically dropped to the extinction probability. Diversity thus oscillated randomly about the equilibrium value. The oscillation was damped by increasing or decreasing the probability of branching in proportion to the deviation of diversity from the equilibrium value.

[The control of diversity is biologically realistic. Much modern ecological theory is concerned with the mechanism and extent of such control (MacArthur and Wilson, 1967; May, 1975; Pielou, 1975). For historical examples involving intercontinental faunal interchange, see Simpson

(1969).]

There were, of course, no morphological data and so a cladistic approach was used for subdividing the simulated phylogeny. Routines were added to the programme to define subunits ('clades') automatically.

The results of the programme were reminiscent of the phylogeny diagrams made popular by Romer (1966) showing the relationships, numbers and distribution in time of various taxa. All the real evolutionary histories are simulated: long-lived lines that never really flourish, small ephemeral groups, rapid early radiation and extinction, multiple radiations in time with near extinctions between, flourishing groups that meet with sudden extinction, flourishing groups with long drawn-out extinction, late developing groups which dominate the diagram at the 'end'.

Raup et al note that: "When faced with such variations in evolutionary patterns, paleontologists are inclined to suspect or even to postulate that the organisms involved are inherently different - that the various taxonomic groups differ from one another in evolutionary potential because they differ in population structure, reproductive systems, mutation rates, dispersal systems, and so on. But the simulation modeling shows that two or more groups operating under identical constraints - that is, having the same evolutionary potential - can behave very differently. We do not rule out that such differences in

the real world may be due to inherent biological differences. We can only contend that the observed variation does not in itself demand such an explanation. Above all, the simulation should be a warning against using patterns of diversity as the major evidence for differences in evolutionary potential." [Underlined words italicized in the original.] As noted, this is also Mayr's (1963) conclusion.

Of great interest is a 'survivorship curve' plotted for 158 computer lineages from one run. The lineage duration in computer time units is plotted on the x-axis and the number of lineages surviving for x time units is plotted logarithmically on the y-axis. The data approximate the slope of a line equivalent to the average extinction probability to time x, but there are too few 'old' taxa and too many 'middle-aged' taxa. A similar result is obtained from a plot of real data from 141 extinct reptile lineages. These curves are reminiscent of some of Williams (1964) logseries results (c.f., his table 60, page 137) and one could be tempted into thinking that this is the genesis of the genus-abundance curve if it could be shown that in the real world the ephemeral clades consist of only one or two species while the 'middle-aged' and 'old' clades have an intermediate and large number of species respectively. However, this does not seem to be true.

Anderson (1974), in a major paper, Patterns of Faunal Evolution, has reviewed almost all of the relevant



literature on genus-abundance. He claims that the various explanations offered for the pattern of genus-abundance are idiosyncratic of the theorist and are related to the historic interplay of stochastic and deterministic philosophical concepts. Furthermore, he claims that ecological and evolutionary theorists commonly have been biased towards deterministic models or components of models and have tended to neglect stochastic models. They also fall into the 'reductionist' fallacy: by studying the parts alone one can understand the whole.

He says that it was just such a deterministic bias that was the reason that Willis so repeatedly used the term 'mechanism' and why Williams (1964, page 121) found it "very difficult to accept [Yule's]... assumptions" of probabilistic species formation. I think that here Anderson is misinterpreting Yule, who is as much or as little a mechanist as Willis, and one can only applaud Williams' good sense in rejecting Yule's regular and mechanical generation of species. As for Willis, no one has ever been able to determine what he meant by 'mechanism'. Anderson is on firmer ground in accusing Chamberlin of a deterministic bias. Chamberlin accepted a theory of "regular dichotomous generic increase" because "there is required just some such basic theory of as fundamental nature as this to furnish an adequate reason for the curve's actual occurrence."

MacArthur's (1957) broken-stick model necessitates

three assumptions according to Anderson - but MacArthur made only two. First, the total number of individuals in the sample is equivalent to the occupancy of the whole environment. This is the assumption of continuous niches. Second, the species are equivalent to the niches. This is the assumption of non-overlapping. But, according to Anderson, because of MacArthur's deterministic bias he omitted the assumption of randomness in drawing conclusions from the model of non-overlapping niches of random sizes in a completely utilized environment. Thus, there should be a third assumption: the functional community is broken randomly into these continuous non-overlapping niches. The third assumption is not mentioned by MacArthur nor was any biological premise given for assuming a random breakage. Anderson says: "The first two assumptions, being by definition determined by the sample, could not show disagreement in comparison of model and data. Hence agreement of model and data provide evidence only for randomness and not for continuity or non-overlapping of niches."

I believe that Anderson is mistaken in this criticism. If agreement provided evidence only for randomness then the random variate - biomass or individuals - would approximate a known central-limit type distribution, as held for instance by Preston (1962). It was just such a failure of 'ordinary' randomness which led MacArthur to

formulate the broken-stick model. Pursuing this point further leads to consideration of ecological diversity and not taxonomic diversity. Hairston (1959, 1969) reviews the problem.

Anderson calls attention to the 'dearth' of discussions of frequency distributions of genera and species that is one of the major patterns of faunal evolution. He claims that an aggregate of only about four pages in Simpson, Sokal and Sneath, Hennig and Mayr (op. cit.) refer to the rôle of 'mere chance'. This dearth compares to the hundreds of pages devoted to "relatively reductionist and deterministic concepts" - mutation frequencies, natural selection and adaptation in populations in smaller groups. He admits to the importance of these concepts but denies that they will lead to an understanding or prediction of the major pattern.

He notes that Williams (in a series of pre-1948 papers summarized in Williams, 1964) says that the log-series can be applied to a great variety of biological problems in which 'n' is variously the number of species per genus, the number of genera per family, the number of parasites per host and even the number of research papers per biologist published in a particular year. He also notes Kendall's (1948a) statement: "It is hard to believe that a single mechanism will be found to explain the relevance of the logarithmic series to all these problems..."

Anderson cites Kendall (1948a, 1948b) as the type of study required to elucidate the mechanism leading to the genus-abundance distribution. These two papers, in which Kendall follows up Fisher, Corbet and Williams (1943), describe several discontinuous Markov processes which lead to distributions of negative binomial and logarithmic series form. Kendall's stochastic processes operate in a hypothetical population where numbers fluctuate with mortality, binary reproduction and immigration.

Anderson suggests that Kendall's equations can be applied to faunal evolution by letting births equal species splits, deaths equal extinction, and applied to ecological communities by letting immigration equal the arrival of new species.

Anderson sees a "poignant" [sic] struggle between the taxonomists and nature in the matter of monotypic genera. He quotes Lynch (1977, page 19) who discusses the "need" to recognize monotypic genera in a recent complete revision of the leptodactylid toads. At the same time Lynch says that monotypic genera had been recognized in the past because taxonomists did not know their relationship, that is, monotypic genera are a symptom of an incomplete classification. Anderson also quotes Mayr (1963, page 236) who states that: "Excessively large genera as well as an excessive number of monotypic genera reduce the usefulness of a classification for information retrieval."

Anderson comments rather acerbically that: "The universe does not seem to have been designed by an information retrieval specialist."

Anderson examines the genus-abundance curves for higher taxa for mammals, birds, amphibians, reptiles, Hymenoptera and Chironomidae. The data are new. The mammal data are from an unpublished synopsis prepared by a team of graduate students and staff at the museum of the University of Kansas and not, apparently, from his own and later Recent Mammals of the World (Anderson and Jones, 1967). Anderson does not give explicitly his source for birds except "as classified by recent workers". It is probably from Peters (1931+). The amphibians and reptiles are also a group effort - an unpublished synopsis prepared by another team of graduate students and staff.

Anderson plots the data on a log-log graph. He notes that the hollow curve results from an arithmetic plot of a frequency histogram. He says: "The similarities in cumulative frequency distributions produced by studies proceeding from different taxonomic premises reduces the likelihood that the pattern is imposed by the examiner rather than the properties of the universe being studied." He then makes the acute observation that non-consistent classifications may be self correcting. Taxonomists have various biases and one bias is against taxa of either very large or very small size. Thus the splitters will split

large taxa while lumpers will lump small taxa - both thereby contributing to the centrist tendency.

He purports to give several instances of this tendency from the data he plots. For instance, the Linnaean classification is truncated at both ends, there being few monotypic genera while the larger taxa are relatively smaller than in post-Linnaean classifications. He also cites a numerical taxonomic study of megachilid bees by Michener and Sokal (1957). The smallest genus allowed by these authors contains 18 species. But the numbers (in a numerical taxonomic sense) clearly show according to Anderson that there should be eight monotypic genera and therefore Michener and Sokal are biased against small genera.

Neither of these particular examples is particularly valid. The criticism of Michener and Sokal merely illustrates that numerical taxonomists and numerical taxonomy are as subjective as classical taxonomists and classical taxonomy. Besides this, Sokal, who is the inventor of the technique, has never been accused of, or demonstrated such a bias before or since.

["Numerical taxonomy is the evaluation by numerical methods of the affinity or similarity between taxonomic units and the employment of these affinities in erecting a hierarchical order of taxa." It is claimed that the technique is: "...objective and repeatable, both in evaluation of taxonomic affinities and in the erection of

taxa..." as opposed to the "...intuitive approach of the past." Sokal and Sneath (1963, page viii).]

In his criticism of Linnaeus, Anderson clearly shows that he has completely misunderstood the nature of Linnaean genera. Linnaean genera are close to what are now considered to be orders (Cain, 1956) and there are proportionally fewer monotypic orders than monotypic genera. This would account for the lower-end truncation. The top truncation is simply that Linnaeus did not know enough species to fill up his genera. For instance, in the twelfth edition of Systema Naturae (Linnaeus, 1766), Linnaeus puts all the 17 species of frogs and toads that he knew into Rana. Gorham (1974) recognizes nearly 3000 species of frogs and toads distributed among 350 genera in the order Anura.

Anderson discusses three possible evolutionary models and their resulting genus-abundance curves. The first and second are limiting cases and are not realistic. Both assume an initial number of species, all in one genus in the first case and one genus per species in the second case. In the first case the genus splits and the subgenera split, the probability of splitting being a function of the size of the subgenus. In the second case the genera merge under the same conditions. Both models lead to a broken-stick abundance distribution.

The third model is a generalized birth-and-death

model based on Kendall (1948b). An approximate equilibrium would be reached if the number of species splitting into two species is equal, in genera of size  $x-1$ , to the number of species becoming extinct in genera of size  $x$ . The equilibrium frequency is:

$$n_{g,x-1} = (n_{g,x}) \frac{1}{x-1} \cdot \frac{\mu_x}{\beta_{x-1}} \quad \text{Equ. 7.}$$

where  $n_{g,x-1}$  is the number of genera containing  $x-1$  species,  $n_{g,x}$  is the number of genera containing  $x$  species,  $\mu_x$  is the extinction rate for species in genera of size  $x$  and  $\beta_{x-1}$  is the rate at which species are generated in genera of size  $x-1$  species.

The model makes several assumptions: (1) All species have an equal probability of splitting. (2) All species have an equal probability of extinction. (3) The model is not really an equilibrium model since if  $\beta > \mu$  the number of species will increase and if  $\beta < \mu$  the number of species will decrease. (4) The number of taxa should decrease with time since (in this model) monotypic genera have a probability of 0.5 of extinction when hit with an evolutionary event ( $\beta = \mu$ ). Nevertheless, the number of taxa in the middle of the size range will tend to be in equilibrium, except for a probability gradient leading to a slow drift towards smaller groups because of the one-way gate at the bottom.



It is unfortunate that Anderson did not carry this interesting model to its obvious conclusion and include a 'new genera' generating function which would replace the monotypic genera lost by extinction. Since every genus must (logically) contain only one species at first and only one species at last, a new genus generating function might account for the large number of monotypic genera.

Despite this model, Anderson concludes that the best description of the genus-abundance curve is the inverse power function:

$$y = c/x^m \quad \text{Equ. 8.}$$

or:  $\log y = \log c - m \log x \quad \text{Equ. 9.}$

Anderson is correct. But the power function can be used to fit any inverse hyperboloid curve and thus offers no insights into the mechanism generating the genus-abundance curve, that is, it has no theoretical justification. Furthermore, as will be shown, within the numerical limits of a log-log plot of the genus-abundance curve, equation 9 will nearly always give a significant fit; even to a set of purely random numbers if they are ordered from largest to smallest.

A paper by Kissinger (1963) cannot be fitted into any historical perspective. Kissinger is a beetle specialist. He seems to have worked in total ignorance of all

previous work on genus-abundance. He gives only three references, one to a beetle catalogue and two to papers on beetle ecology. I can find no entries to his paper in the 'Citation Index'.

Kissinger has amassed an enormous quantity of data. He has recorded the number of species per genus for three beetle families - 72,075 species in 7286 genera - and tabulated them by genera with  $2^0$ ,  $2^1$ ,  $2^2$ ,  $2^3$ , ... ,  $2^n$  species. The expected frequency in each  $\log_2$  class was calculated using the grouped data as a base and each of the twenty plus subfamilies was compared by a chi-square test. Kissinger then tried to explain the significant deviations by reference to the ecology of the deviant group.

## THE PROBLEM OF TAXONOMIC DIVERSITY

Simberloff (1972, and in Raup et al., 1973) asks two important questions: (1) "Can the processes resulting in local equilibrium in ecological time be used to predict events in evolutionary time?", and (2) "... whether an equilibrium pattern of phyletic radiation can exist, and if so, what its characteristics would be?"

Simberloff implies that if the evolutionary equilibria resemble ecological equilibria, then the same processes may be operating. In particular, does the close resemblance between the species-abundance curve and the genus-abundance curve imply similar generating processes? It is generally agreed that the species-abundance curve is generated by a process which divides the available resources between species, each of which occupies a distinct niche. Despite this general agreement there is much controversy regarding the actual dividing mechanisms, which are variously postulated to range from equitable sharing to extreme pre-empting (see references and discussions in May, 1975; Pielou, 1975; and Whittaker, 1972). But all hypotheses which are realistic subsume Gauss' rule of competitive exclusion - no two species with identical ecological requirements can coexist in the same ecosystem. The resources exploited by one species are not available to another. Further, the number of individuals or biomass of a species

is a direct function of the total amount of exploited resources.

A second requirement of all the hypotheses is that the system must be undisturbed long enough to come to equilibrium.

Therefore, to answer Simberloff's questions we must first assume that competitive exclusion exists between genera (and other trans-specific taxa), that is, a 'generic niche' exists, no two genera with identical ecological requirements can coexist in the same ecosystem, the resources exploited by one genus are not available to another and the number of species in a genus is a direct function of the amount of 'generic resource' exploited. Second, we must assume that genera and species are long-lived enough to allow the genus-abundance curve to come to equilibrium.

#### Adaptive zones and the genus niche

The literature on generic competition is ambiguous. Mayr, Linsley and Usinger (1953) claim it exists; Van Valen (1971) is not so certain.

Van Valen discusses primarily ordinal adaptive zones. What he says is validly extendable to subordinal and supraordinal and other higher and lower adaptive zones.

The term 'adaptive zone' (Simpson, 1944), 'adaptive plateau' and 'adaptive peak' are used by Van Valen (1971), Mayr (1963) and Mayr, Linsley and Usinger (1953) in

an ecological sense as synonyms for 'niches' of taxa higher than the species. Dobzhansky (1951) uses peaks, valleys and plateaus in a genetic adaptive sense. The concept traces back to Wright (1923).

According to Van Valen, adaptive zones in the sense of Simpson (1953) and Van Valen (1963) have two independent components: use of resources which are part of a lower trophic level and resistance to predation and parasitism which are aspects of a higher trophic level. He says: "Competition occurs within adaptive zones, at the same trophic level." He further states that we can envision the physical and biotic resources of the world, or any community, as constituting a bounded multidimensional 'resource space' in which "...there are strong differences in density that correspond to the degree of development of the adaptive zones in each region of the resource space, whether or not these zones are occupied." Van Valen defines an adaptive zone as the niche of any taxon, especially a supra-specific one. According to him both terms - resource space and adaptive zone - sometimes refer to the aspects of the environment and sometimes to interactions of members of a taxon with the environment. This latter use excludes the possibility of an empty adaptive zone. Van Valen then says: "I therefore restrict 'adaptive zone' to its environmental meaning, i.e., some part of the resource space together with relevant predation and parasitism, and intro-

duce as 'a technical term way of life (original in italics), with its everyday meaning for the interaction. 'Way of life' is also broader than 'adaptive zone' in that the competitive interactions are included. We must exclude the latter from the concept of adaptive zone, or else we can't even consider the possibility of two taxa competing within the same adaptive zone."

This is ambiguous, and perhaps understandably so, since Van Valen is struggling with a concept that has hardly yet been considered by ecologists. He may be calling what is an adaptive zone in the sense of Mayr a 'way of life, thus raising the everyday meaning of 'way of life', which is usually applied to species and applying it to trans-specific categories, while at the same time redefining adaptive zone. It is not clear, however, whether the competition allowed in the 'way of life' is species-species interaction - and thus orthodox Darwinianism - or is trans-specific interaction, that is, between taxa higher than species but at the same trophic level - and thus a new hypothesis. He goes on to say that adaptive zones are part of the environment and exist independently of the taxons to exploit them (the 'empty niche' concept failed to the trans-specific level) and that the way of life must be fitted to some adaptive zone but may occupy only a small part of a larger, relatively undivided zone. He then becomes completely ambiguous: "The part of the resource space in-

cluded in an adaptive zone may be called a resource zone; resource use then corresponds to 'way of life' with respect to resources." (Underlined words italicized in the original.)

Van Valen can not mean that part of the resource space is not in the adaptive zone; but that is what he is saying. However he does specifically state that the extinction of higher taxa (he uses the Multituberculata as an example) has probably often occurred by "gradual infiltration of their adaptive zone by one or more other taxa." Thus, competition can occur in the adaptive zone after all, and it can occur between taxa higher than species.

According to Mayr, Linsley and Usinger (1953, page 49 and following) the genus is more than a group of species descended from a common ancestor and possessing certain morphological characters in common. Upon close examination it is usually found that all species in a genus occupy a more or less well-defined ecological niche. "The genus is thus a group of species adapted for a particular mode of life. The 'genus niche' is obviously broader than the 'species niche', but both exist." Further (page 115), just as no two species with identical ecological requirements can coexist in the same place, likewise for genera and still higher categories; each occupy a separate adaptive plateau (citing Dobzhansky, 1951) or adaptive zone (citing Simpson, 1944).

Mayr et al. (1953) instance Lack's (1947) study of Darwin's finches in the Galapagos where each genus is restricted to a separate zone: Geospiza - ground finches, Camarhynchus - tree finches, Certhidae - warbler finches.

Both Van Valen and Mayr (1963) accept the concept of the 'empty niche' or 'empty adaptive zone'. This concept is somewhat peripheral to this thesis but does merit some consideration.

Mayr (1963, page 87) begs the question then proceeds to give instances. He asks: "Why are so many empty niches unfilled?" He notes that there are twenty-eight species of woodpeckers in Borneo and Sumatra and none in the similar forests of New Guinea. According to Mayr, the woodpecker niches seem to be almost vacant east of Weber's Line. [Weber's Line is an imaginary line separating those islands of the East Indies with a preponderant Malayan fauna from those with a preponderant Papuan fauna.]

Another example he gives is the opening of the Suez Canal which permitted more than a dozen Red Sea species to invade the Mediterranean without apparently displacing any native species. The invaders must have found partly unoccupied niches. Mayr claims that an invading species only rarely displaces a native species from its niche. He gives the European Starling, Sturnus vulgaris, in North America as an example. He has chosen a particularly bad example here. The starling and the Eastern Bluebird, Sialis sialis



compete for nesting sites. Since the Starling nests earlier, Bluebirds find most nesting sites already occupied. The Bluebird is now scarce where it is sympatric with the Starling (Pough, 1949). Mayr also cites a study that shows that desert ants occupy different niches in the Old and New Worlds (Kusnezov, 1956) - presumably if the two ant faunas were mixed they would not compete.

Mayr admits that the concept of a vacant niche is not popular with ecologists. Ecologists would hold that the New Guinean insect larvae not eaten by woodpeckers are otherwise disposed of. But Mayr says that this is not the same as filling the woodpecker niche. If a local biota can be enriched by a new species, it proves [sic] that a vacant niche had existed. He seems to have ignored the possibility that a species can invade by subdividing a previously occupied niche and thus, in a sense, creating a new niche. Nor need there be any diminuation in the biomass of the other species since some factor, not shared, may be the limiting factor.

Bats versus Birds: A possible example of trans-specific competition.

If taxa higher than species do not occupy adaptive zones by competitive exclusion, then even more serious ecological problems are raised. For instance, consider the bats and the birds.

All the data for the following section is from the articles in Grzimek (1972) on swallows by Peters; swifts by Sick, Meise, de Roo and Smythies; owls by König; oilbirds by Dorst; Podargues and owlet nightjars by Severtzy; potoos by Sick; nightjars by Lehonten; falcons by Mebs and bats by Eisentraut. Further information on bats is from Wimsatt (1970), Allen (1939) and Walker (1964). Further information on birds is from the articles in Thomson (1964), on oilbirds by Snow; swallows by Thomson; swifts by Lack; potoos by Hamerstrom; nightjars by Junge and frogmouths by Severtzy.

As far as is known there are no diurnal bats. Within the bats, there are two general modes of life. The megachiroptera are nocturnal fruit and flower eaters, locating their food by scent - and by sight on bright nights - and using echolocation only to avoid obstacles. The microchiroptera are generally nocturnal insect-eaters. They hunt flying insects by echolocation and capture and eat them on the wing. Bats never hunt like avian flycatchers, sortieing from perches to capture passing insects, nor do they forage for insects on vegetation or on the ground. A very few microchiropteran species have taken-up other modes of life: one is a vampire, two or three capture and eat small fish from surface waters and there is circumstantial evidence that a few species may be crepuscular and nocturnal raptors preying on late-flying birds and noctur-

nal insectivorous bats. There are about 120 species of frugivorous bats and about 700 species of insectivorous bats.

Insectivorous bats possess two prime adaptations to their way of life. First, insect flight is highly dependent on weather and temperature; bats can go into torpor to wait-out unfavourable times. Second, most night-flying insects are invisible; bats have a superb echolocating ability.

As far as is known there are no nocturnal birds which 'hawk' after insects in the manner of bats. There are three major taxa of birds which hawk after insects: the swallows, Hirundinidae, 74 species; the swifts, Apodiformes in part, 74 species; and some of the 97 species of Caprimulgiformes. Two owls, Otus trichopsis and Micrathene whitneyi, have also been observed to hawk after flying insects.

Swifts and swallows are strictly diurnal. The nightjars, Caprimulgidae, 72 species, are mainly nocturnal foragers, those that hawk are crepuscular and feed only during the relatively brief twilight hours of dusk and dawn. Caprimulgus may hunt on nights when there is a bright moon, apparently flying low and silhouetting insects against the brighter sky. The Night-Hawk, Cordeiles minor, actually hunts while the sun is up.

There are no apparent barriers to the invasion of

the bats' nocturnal adaptive zone by birds. Birds possess the main adaptive features of bats - torpor and echolocation and some species of swiftlets (Collocalis) possess both. Some swifts and some nightjars can go into torpor during periods of unfavourable insect hunting weather. Echolocation is well developed in some species of swiftlets, but is used exclusively to guide flight in the lightless caves in which they nest. Otherwise, swiftlets hunt by day. Those swiftlet species that cannot echolocate nest in the twilight zone of caves. Some swifts apparently fly all night. Both Lack and Sick (in Grzimek (1972) and Thomson (1964)) accept as true that non-nesting and juvenile individuals of some species of swifts spend the night aloft at considerable altitude, certainly over 2000 meters. There do not seem to be any reports of these birds feeding at night, in any case the number of flying insects at this height must be very small compared to the number near the ground.

There is one very interesting exception to the rule that birds do not behave like bats and vice versa. The Oilbird, Steatornis caripensis (Caprimulgiformes), is strictly nocturnal, nests in caves, can echolocate and does so to avoid obstacles while flying and feeds on fruit which it finds by smell and sight. This is exactly the habit of a fruit-eating bat. This species is apparently the only night-flying, fruit-eating bird. The unique Oilbird

has thus not been excluded from the fruit-bat adaptive zone. I suggest that this is because there are no fruit-bats sympatric with the Oilbird. The range of the Oilbird is generally in northern South America and the adjacent islands. There are no fruit-bats in the New World and hence an 'empty niche' or empty adaptive zone exists to be filled by any species seizing the opportunity.

[The bat family Emballonuridae which is ~~sympatric~~ with the Oilbird is reputed to be mainly insectivorous but occasionally frugivorous. I can not find any reference to fruit eating in this family except for a statement, repeated in all references, of some "nibbled épave beans" on the floor of a cave inhabited by a species of this family. Genus entries in Walker (1975) indicate that the species are insectivorous, fish-eaters or so rare and local that nothing is known about their feeding habits.]

If bats as a taxon do not exclude birds as a taxon, then we must suppose that either some morphological or physiological barrier permanently excludes bats from catching day-flying insects, birds from catching night-flying insects, bats from daytime fruit-eating, birds from nighttime fruit eating; or there has been a one-on-one, bat-on-bird competitive interaction in which the bats always won the night and the birds always won the day. In view of the bird adaptations noted, and in view of the long time involved for interactions to occur (both bats and swifts were

present in the Eocene for instance (Romer, 1966, 1968)), both a barrier hypothesis and a species-species interaction hypothesis seem highly unlikely. Therefore one is left with a taxon-taxon interaction at a level higher than the species by default, however hard it may be to visualize a mechanism.

#### The longevity of species

In addition to the assumption of competitive exclusion at the trans-specific level, we must also assume that sufficient time is available for the genus-abundance curve to come to equilibrium. If species and higher taxa are too ephemeral, then the genus-abundance curve would be the result of pure random processes; if sufficient time is available, random processes might still be operative but biological processes might also come into play.

Rensch (1960) has published some data on the longevity of various taxa and one can also extract additional data from Romer's (1966, 1968) taxonomic lists. It must be realized that all such data are truncated. Taxa are aged by first and last appearance in the fossil record, Recent taxa from first appearance to present. In all lists Recent species have an apparent shorter life span but this is an artifact since Recent species are not yet extinct. We are also living close to the Pleistocene-Recent boundary and boundaries are usually defined by the extinction of older

species and the radiation of newer taxa. This also distorts the data.

A more serious problem is the highly selected nature of the fossil record with hard-bodied marine forms favoured. But there is no reason to think that such species are intrinsically either shorter-lived or longer-lived than soft-bodied species. See, for instance, Berrill's (1955, page 159) reinterpretation of the Burgess Shale fauna.

Rensch lists the longevity of classes as ranging from 600 to 170 million years with an average for terrestrial classes of 380 million years, marine classes average about 150 million years more. Orders range from 410 million years according to Rensch (but some Brachiopod orders are 600 million years according to Rudwick (1970)), down to 65 million years for birds and mammals. Families are equally ancient although some mammal families are as young as 10 million years. Mammal families average about 25 million years.

Genera range from the stupendous 220 million years for Limulus down to a bare million for many living mammals such as Alces (moose). Nevertheless, many common genera of mammals are more than 20 million years old, such as Sus (pigs), Tapirus (tapirs), Canis (dogs), Putorius (pole-cats), Lutra (otters) and Geomys (wood-chucks) - and many very common genera of birds are 50 to 60 million years old, among them Aquila (eagles).

The longevity of species presents a problem. It is impossible to decide how close the genome of a fossil species is to a later fossil or to a living species although there may be a close phenotypic resemblance. For instance, Hyman (1959, page 577) states: "Although the genus Lingula is known since the Ordovician, reckoned at 350,000,000 years ago, no existing species of Lingula goes very far back, contrary to current belief." (Underlining in italics in original.) She gives no evidence for this flat statement, while admitting that the difference between extinct and present species appear minor. Indeed, the 'Red Queen' hypothesis (Van Valen, 1973, 1974; Smith, 1976a) asserts that each evolutionary advance made by one species in an ecosystem is experienced as a deterioration of the environment by other species. If evolution is to be a zero-sum game (I prefer the term 'existential game'), then all species' genomes must change rapidly and steadily if they are to survive (in existential terms, the prize is to stay in the game).

There have been some studies on species longevity and rates of evolution. Smith (1976b) has a mathematical model with unquantifiable variables and which tells how rapidly a species is evolving when it is at the point of extinction. Webb (1969) asks the interesting questions whether extinction-origination is owing to some feedback mechanism involving competition between higher taxa



and whether the rate of extinction controls origination. He does not answer these questions.

We are forced to accept the conclusions of classical morphologists regarding the time limits within which a 'species' can be considered as a species in the orthodox sense. Björn Kurtén has done very careful work in this field. References are contained in Kurtén (1958). I refer to Kurtén (1959a, 1959b) in what follows. Lerman (1964) has a complete summary of the problem.

Kurtén has concentrated on the longevity of mammalian species in the Tertiary. He estimates the mean species longevity in years for the Palaeocene, Neogene and Pleistocene. As might be expected, the mean age for all mammalian species is lower in the Palaeocene (1,500,000 years) owing to radiation and the Pleistocene (620,000 years) owing to extinction, than in the Neogene. In the Neogene, for all orders, it is a surprisingly high 5,200,000 years. Mean Neogene ages range from a high of 7,500,000 years for insectivores to a low of 3,800,000 years for primates.

It would be legitimate to conclude, especially if Kurtén's data are indicative of other taxa, that species last through many generations - of the order of several hundreds of thousands to millions - which should be time enough for equilibrium to be reached in any ecosystem imaginable.

## HYPOTHESES OF ARTIFICIALITY

Before considering possible biological mechanisms which might generate the genus-abundance curve it is necessary to examine hypotheses which ascribe the curve to non-biological mechanisms. These hypotheses have in common the premise that it is the taxonomic process itself which generates the curve, either the choice of taxonomic criteria or the taxonomic philosophy. To test these hypotheses it is therefore necessary to consider a taxon as if it were an empty construct made according to certain rules, the particular organisms being irrelevant.

I have chosen amphibian taxonomy and amphibian taxonomists to test the hypotheses that it is the taxonomic process itself that generates the genus abundance curve.

There are two reasons for choosing amphibians. First, Gorham's (1974) checklist of the world's amphibians is complete, up-to-date, authoritative and contains extensive synonymities. Synonymities are lists of scientific names of taxa which have been rejected for one reason or another by later revisors of the taxa. Since each synonym is listed with the currently valid name, and has attached its author's name and date, it is possible to trace the historical process of lumping and splitting in any taxa for the last two hundred years.

The second reason for choosing the amphibians is

that Schmidt (1955), Duellman (1977) and successive issues of the 'Herpetological Review' are rich sources of anecdotal information about taxonomists, taxonomic schools and their influence on each other.

It is, of course, first necessary that amphibians present no peculiarities of taxonomy or taxonomic criteria not generally present in other taxa, and secondly necessary that amphibian taxonomists are neither less or more peculiar than taxonomists of other major taxa. On these two points one can only use the argument of silence; no one has suggested that amphibians or amphibian taxonomists are in any way peculiar.

The data to test the hypotheses of artificiality were assembled as follows. The pages of Gorham (1974) were photocopied. The species and genus entries - each with the species or genus name, author (and co-author if any) and date of description - were cut from the photocopied pages into narrow strips about half a centimeter wide. There were 3384 species slips and 350 genus slips. The slips were then sorted by author and tabulated by author and date and cross-referenced by co-author(s). The number of species described each decade and the 'describing life' of each author recorded. The describing life is from the date of the first description (species or genus) to the date of the last description for any one author. Part scores for numbers of species and genera described were prorated for

multiple authorship.

The proportionate criteria hypothesis

Koch (1966) suggested that taxonomic processes themselves could generate a lognormal genus-abundance curve by introducing multiplication of factors with proportionate variations. He states: "There is one further mechanism that introduces the multiplication of factors with proportionate variations and hence tends towards the lognormal distribution. This mechanism arises logically in the process of classification. It may be of great significance because it does not require a historical sequence. Thus, the number of Linnaean species in families may be lognormal, because each family may be divided into species in which constant proportions have one or other characteristics. If the proportion does not depend on which family is under consideration and if there are enough characteristics used in the classification, the conditions will be met [for a lognormal genus-abundance distribution]... For example, if all organisms are classified on the basis of eye color, number of digits, mating behavior, number of young, diurnal behavior pattern, etc., then the maximum number of species in a family would be the product of the number of distinguishable eye colors, the number of different digit numbers, the number of recognizably different types of mating behavior, etc."

Koch is not saying that if, for instance, within a taxon there are two eye colours, three different numbers of digits, four different mating patterns and five different numbers of young, and if these were the basis of classification, then there would be  $2 \times 3 \times 4 \times 5 = 120$  species. He recognizes the near universal occurrence of character correlation which will reduce the number of species. What he is saying is that the tendency in classification is multiplicative rather than additive and that the resulting pattern is lognormal rather than normal.

The artificial generation of a genus-abundance pattern within one taxon requires that most taxonomists working within that taxon apply the same criteria in the same way to most of the species. Consistent application requires a set of agreed-upon criteria which are applied over most of the taxon by one taxonomist or a school of like-minded taxonomists.

The amphibian data were used to investigate:  
(1) whether one taxonomist was responsible for most amphibian classification or (2) a particular school was responsible and (3) whether there was an agreed-upon set of taxonomic criteria.

Table 1: The number of amphibian species described by the top five-percent of describers.

<u>Name of Describer</u>	<u>Number of Species</u>	<u>Percent of All Species</u>	<u>School</u>
Boulenger	453	13.4	British Museum
Taylor	222	6.6	Kansas
Cope	145	4.3	U.S. National Museum
Ahl	104	3.0	British Museum
Günther	103	3.0	British Museum
Peters	99	2.9	Paris
Dunn	59	1.7	Eastern Establish.
Bokermann	58	1.7	Kansas
Laurent	56	1.7	British Museum
Parker	54	1.6	Eastern Establish.
Boettger	48	1.4	British Museum
Smith, H.E.	46	1.4	Kansas
Lutz	44	1.3	Kansas
Loveridge	40	1.2	Eastern Establish.
Rivero	39	1.2	-
Schmidt, K.P.	34	1.0	Eastern Establish.
		47.4	

The taxonomists: Table 1 (above) lists the top five percent of amphibian species describers, all of whom have described at least one percent or more of the currently recognized living species of amphibians. The last column - 'school' - will be discussed later. It is interesting to note that the number of species per describer also forms a hollow curve.

Only Boulenger, and perhaps Taylor and Cope, have described a large proportion of the world's amphibian fauna. But thirteen percent is not 'most species', one can not support a hypothesis that any one taxonomist has applied a consistent set of taxonomic criteria over most of the species of amphibia.

The schools: In addition to the sixteen taxonomists listed in table 1, 302 authors have each described or co-described less than one percent of the amphibian species. A surprisingly large number appear to have worked or are working independently or at least their affiliation is not obvious. Nevertheless, most of the more productive workers can be grouped into schools.

It is difficult to define a school of taxonomy. It is an affiliation and not a place. Ultimately it must be a group of taxonomists working within one taxon and who have common assumptions as to what constitute critical taxonomic characters. Since these assumptions seem to be nowhere written down, except scattered through the descriptive literature, a reasonable operational definition of a school would be first, a dependence on an agreed taxonomic catalogue or taxonomic journal and second, an affiliation between taxonomists which could take the relation of teacher and pupil, author and coauthor or even an institutional affiliation contemporary with acknowledged members of a school.

Schmidt (1955) has much to say about several schools and Duellman (1977) has a short essay on the Kansas school with a list of members. Some very active schools of herpetology do not form taxonomic schools since their members' interests lie elsewhere, such as ecological or ethological studies.

With these provisos, five schools are identifiable. They are listed below in table 2.

Table 2: The 'Schools' of amphibian taxonomy.

<u>Name of School</u>	<u>Number of Species Described</u>	<u>Percent of All Species</u>	<u>Number of Identifiable Members</u>	<u>Percent of All Amphibian Taxonomists</u>
British Museum	962	28.4	22	6.9
Kansas	468	13.8	24	7.5
Eastern Establish.	284	8.4	21	6.6
Paris	282	8.3	23	7.2
U.S. Nat. Museum	267	7.9	11	3.5
		<u>66.8</u>		<u>31.7</u>

The Paris school in a sense started the science of herpetology. It could also be called the school of Duméril and Bibron since all amphibian classification was based on these authors ten volume 'Erpétologie Général' published in 1854 until the advent of Boulenger's British Museum catalogues in 1882. The Erpétologie recognized 218 species of amphibians. Members of this school described an additional 223 species in the next century. One cannot see any very clear taxonomic philosophy associated with Duméril and Bibron. Although most of the work of this school was completed by the end of the nineteenth century, the tradition extended into the 1960's according to Schmidt (1955).



Also according to Schmidt, the guiding philosophy of the British Museum school was sheer carelessness. The British Museum was the recipient of enormous collections from all over the world during the late nineteenth century heyday of the British Empire. Under its succession of curators of ichthyology and herpetology - Gray, Günther and Boulenger - a very great number of species were described.

Boulenger, whose working life extended from 1879 to 1920, is the central figure in the British Museum school of amphibian, reptile and fish taxonomy. He published 618 refereed papers on herpetology (and 257 on ichthyology) and these papers form the basis of modern amphibian taxonomy.

One would think that, with Boulenger's enormous personal output and that of his school, he would be the major guide in principles of amphibian taxonomy. But such does not appear to be the case. Admittedly most major figures in the humanities and sciences go through a period of 'debunking' after retirement or death before they are rehabilitated and find their rightful place in the pantheon. Boulenger's debunking started during his working life and has continued unabated ever since. This would not be important except that his major critics also have been the most influential workers in present day amphibian taxonomy: Leonard Stejneger of the United States National Museum, the central figure in that school, Karl Schmidt of the Chicago Natural History Museum, (Field Museum), an

important figure in the Eastern Establishment school and Edward Taylor, the founder of the Kansas school.

Schmidt (1955) has summarized the criticisms of Boulenger's work; the criticisms are mainly those of inconsistency and carelessness and the "...unthinking multiplication of morphological species." Boulenger's indifference to the new rules and codes of the International Commission for Zoological Nomenclature are not particularly relevant since this only affected nomenclatorial priorities. But Boulenger's equal indifference to ecological and zoogeographical relations was more serious, as was his disinterest in subspecies and, astonishingly, evolutionary theory. Boulenger was strictly a museum taxonomist. He never undertook field studies. He frequently identified species 'through the bottle' and was disinclined to remove the specimen and check his identification. He was also disinclined to revise his criteria and frequently described new species instead of making the necessary revisions of his concepts.

Schmidt points out that neither Boulenger nor his catalogues ever gained much respect in North America. This, coupled with the fact that the three most active schools of herpetology are in North America (but describing on a world-wide basis) and the leaders of these schools repudiated Boulenger, makes it very unlikely that any 'Boulengerian' criteria are being consistently applied.

throughout the amphibia.

It is also doubtful if Boulenger himself consistently applied criteria - proportionate or otherwise. Many of his papers are becoming easily available through the republishing programme of the Society for the Study of Amphibians and Reptiles. Although difficult to quantify, the qualitative impression on seeing these papers together is that, where proportional or non-linear criteria are applied within one genus, the same criteria are not applied in the same way to other genera. Thus, the effect of such criteria is not consistent from genus to genus.

The American schools differ mainly in emphasis. The 'Eastern Establishment' - Museum of Comparative Zoology, American Museum of Natural History, Chicago Natural History Museum and many (but not all) eastern universities - is the same school which has given rise to the modern evolutionary synthesis as epitomized in Mayr (1963). The Kansas school is centered on the University of Kansas (Duellman, 1977) and includes most western universities and museums. The United States National Museum is not now very active and the British Museum and Paris schools are no longer important except for their magnificent study collections.

Do the two main American schools differ? This is a hard question to answer because it is essentially a subjective judgement. As an outsider - that is, a non-

describer - I have been struck by the difference in emphasis between the classical and very painstaking anatomical work of the Kansas school as shown, for instance, by Wake (1966) and Sever (1972, 1976) and the electrophoretic allele determinations of the Eastern Establishment with a concomitant distrust of 'mere' morphological differences, see, for instance, the many contributed papers by Guttman and others abstracted in 'Herpetological Review', volume 7, number 2.

Examination of table 2 shows that no school has described a majority of the species of amphibia. Amphibian taxonomic practices do not appear to support Koch's (1966) hypothesis.

#### The splitters versus lumpers hypothesis

This hypothesis is reviewed by Mayr, Linsley and Usinger (1953) and Williams (1964). In essence it says that taxonomists come in two brands: 'splitters' who split large taxa into smaller taxa and 'lumpers' who lump small taxa into larger taxa. This process allegedly produces too many small and monotypic genera and hence artificially generates the genus-abundance curve.

The authors noted seem to assume that the splitters always win, as do Platnick (1976) and Schmidt (1955). The grounds for this assumption are nowhere stated. There does not seem to be any study of this putative conflict in the

literature. But, if true, it could be that there are more splitters than lumpers or that the probability of a large genus being split is greater than the probabilities of two or more smaller genera being lumped, perhaps because large genera are big targets for splitters who manage to split-off new genera faster than lumpers can combine them.

The process of lumping and splitting leaves a trail of invalid synonyms. Smith et al (1978) refer to the results as a "nomenclatural graveyard". They have studied the conditions under which synonyms accumulated in Mexican amphibians. Unexpectedly, only one factor is of much significance in the accumulation of synonyms and that is the length of time that the taxon has been known. "Time dependent error" is their term. Subjective rating of the complexity of the taxon has a slight positive correlation; subjective rating of ecological inconspicuousness has a slight negative correlation.

Williams (1964) holds that, providing splitting or lumping is consistent, the shape of the genus-abundance curve remains the same. He gives some artificially generated examples.

But does the phenomenon of excessive splitting really exist? If the splitting occurs at the species level it will multiply species. This will result in big genera. If the splitting occurs at the genus level it will multiply genera and not species. This will result in small genera.

If it occurs above the genus level or below the species level it will not affect the shape of the curve.

It is also possible that this is a pseudo-problem raised by biologists who are not taxonomists and are misled by the nature of the taxonomic literature. Lists of synonyms read like a telephone directory. The impression is one of wild splitting. A further difficulty is that the two experimentally popular groups - birds and game animals - have been the frequent target of semi-amateur taxonomists. The non-taxonomist biologist might be forgiven for thinking that all species have been subject to similar treatment. But because a genus or species name is included in a list of synonyms does not mean it has been accepted by anyone other than its author.

The fate of all genus names of salamanders has been traced for this thesis and the results are shown in table 3 (page 71). Salamanders were chosen because synonymity data are readily available in Gorham (1974), the taxon has not been subjected to amateurs' or sportsmen's enthusiasms and it has not been dominated by one taxonomist or taxonomic school.

It must be pointed out that some splitting is necessary as a taxon becomes better known. Linnaeus (1766) listed only Bufo and Rana as amphibians, salamanders were included in the catch-all lizard genus Lacerta

Table 3: Disposition of the 169 published genus names for salamanders to 1974.

Names currently accepted as valid		54
Names currently considered synonyms		115
Application of rules of priority	43	
Variant spellings	25	
Proposed as substitutes for valid names	15	
Nomen nudum and preoccupied	11	
Accidental simultaneous descriptions	10	
'Splitting'	11	

Regarding table 3, the following comments apply.

The laws of priority - now codified in the International Code of Zoological Nomenclature - were applied more or less at the whim of the individual taxonomists before the 1920's. Seventy-eight percent of the valid names of genera predate 1900, fifty percent predate 1851. The same proportions are roughly true for synonyms. As a result, and as a result of the post-1920 application of the rules, 104 of the 115 synonyms are 'legal quibbles', only 11 are splits.

1. Application of the rules of priority: A taxonomist has renamed or redescribed a genus for which a valid name already exists. Usually accidental.
2. Variant spellings: Usually an attempt by a classicist to improve etymology - e.g., Amblystoma for Ambystoma - the former is etymologically correct; the latter is valid.
3. Proposed substitutes for valid names: A very

common practice early in the nineteenth century.

A more descriptive name would be substituted, often by the same author of the original name.

Sometimes several names would be proposed in the same paper.

4. *Nomen nudem*: No museum specimen exists to validate the description.
5. *Preoccupied*: Another animal genus already bears the same name. Almost always accidental.
6. *Simultaneous description*: Now rare but of frequent accidental occurrence in the early nineteenth century owing to poor communications and the existence of many obscure journals.

Of the eleven 'splits', Megalobatrachus was proposed for a living genus before it was realized that the fossil Andreas was the same genus. Axolotus, Siredon and Bathysiredon were proposed for puzzling neotenic ambystomids before physiological studies showed that they were congeneric with Ambystoma. Manculus was proposed for an aberrant pygmy species now recognized as Eurycea. It was accepted for a century. Eladina was proposed for an aberrant Bolitoglossa. All these examples are understandable. There remain five genera in synonymy which can only be interpreted as attempts by splitters to split.

A total of five attempts to split out of 169 names cannot be described as a high proportion. In any case



these five were lumped back into existing genera. There may be further room for lumping within the remaining 54 valid genera, most of which have been recognized for more than a century. On the other hand, some of the larger Central American genera could be split. There is no evidence that in the salamander genera either splitters or lumpers are 'winning'. Salamander generic taxonomy does not support the splitters versus lumpers hypothesis.

The taxonomy of salamanders below the genus level also does not appear to support the splitters versus lumpers hypothesis. Table 4 (page 74) shows the number of species recognized in the genus Desmognathus from the first revision in 1926 to the latest in 1975. Underlined names are those recognized as full species by the reviser indicated. Subspecies which have never reached specific status and species proposed and synonymized between revisions are not indicated.

Desmognathus was chosen because the number of species is not likely to be changed by extralimital searches. It is apparently limited to eastern North America. Thus, the increase in the number of species owing to splits (if any) cannot be confounded with the discovery of new species. Also, the genus is subject to constant taxonomic review by many workers and is subject to periodic recensions.

It can be seen that after the initial increase in

Table 4: The disposition of the species of the salamander genus Desmognathus.

Author	Year	Number of Species	Disposition	Author	Year	Number of Species	Disposition
Dunn	1926	3 species	<u>quadra.</u>	Conant	1958	9 species	<u>quadra.</u>
Bishop	1947	4 species	<u>quadra.</u>	Brame	1967	7 species	<u>quadra.</u>
Schmidt	1953	9 species	<u>quadra.</u>	Gorham	1974	10 species	<u>quadra.</u>
Bishop	1947	4 species	<u>monticolae</u>	Conant	1958	9 species	<u>monticolae</u>
Schmidt	1953	9 species	<u>monticolae</u>	Brame	1967	7 species	<u>monticolae</u>
Bishop	1947	4 species	<u>fuscus</u>	Conant	1958	9 species	<u>fuscus</u>
Schmidt	1953	9 species	<u>fuscus</u>	Gorham	1974	10 species	<u>fuscus</u>
Bishop	1947	4 species	f. <u>auric.</u>	Conant	1958	9 species	f. <u>auric.</u>
Schmidt	1953	9 species	f. <u>auric.</u>	Brame	1967	7 species	f. <u>auric.</u>
Bishop	1947	4 species	f. <u>briml.</u>	Conant	1958	9 species	f. <u>briml.</u>
Schmidt	1953	9 species	f. <u>briml.</u>	Gorham	1974	10 species	f. <u>briml.</u>
Bishop	1947	4 species	f. <u>ochro.</u>	Conant	1958	9 species	f. <u>ochro.</u>
Schmidt	1953	9 species	f. <u>ochro.</u>	Brame	1967	7 species	f. <u>ochro.</u>
Bishop	1947	4 species	f. <u>welt.</u>	Conant	1958	9 species	f. <u>welt.</u>
Schmidt	1953	9 species	f. <u>welt.</u>	Gorham	1974	10 species	f. <u>welt.</u>
Bishop	1947	4 species	-	Conant	1958	9 species	f. <u>plani.</u>
Schmidt	1953	9 species	-	Brame	1967	7 species	f. <u>plani.</u>
Bishop	1947	4 species	<u>wrighti</u>	Conant	1958	9 species	<u>wrighti</u>
Schmidt	1953	9 species	<u>wrighti</u>	Gorham	1974	10 species	<u>wrighti</u>
Bishop	1947	4 species	-	Conant	1958	9 species	<u>aeneus</u>
Schmidt	1953	9 species	-	Brame	1967	7 species	<u>aeneus</u>
Bishop	1947	4 species	-	Conant	1958	9 species	<u>cherm.</u>
Schmidt	1953	9 species	-	Gorham	1974	10 species	<u>cherm.</u>
Bishop	1947	4 species	-	Conant	1958	9 species	<u>ochoe</u>
Schmidt	1953	9 species	-	Brame	1967	7 species	<u>ochoe</u>
Bishop	1947	4 species	-	Conant	1958	9 species	<u>perlapsus</u>
Schmidt	1953	9 species	-	Gorham	1974	10 species	<u>perlapsus</u>

Abbreviations: quadra. = quadramaculatus, auric. = auriculatus, briml. = brimleyorum  
welt. = welteri, ochro. = ochrophaeus, cherm = chermocki,  
plani. = planiceps, f. = fuscus, a. = aeneus.

Symbols: '-' = form not known to author, '\*' = form reduced below subspecies.

Nominate subspecies indicated as species.

the number of species - owing to more intensive collecting and ecological studies - the number of recognized species has stabilized at nine or ten depending upon the opinion of the reviser. Work on the genus since Conant's (1975) rescension indicates that welteri and monticola may be two ends of a ring species (Caldwell and Folerts, 1976).

Collins et al (1978) recognize imitator, a population of Müllerian mimics of Plethodon jordani. Imitator has been known since 1927 as a subspecies of ochrophaeus. These changes would leave the number of recognized species unchanged at nine.

Salamander taxonomy does not support the suggestion of Williams (1964) and Mayr et al (1953) and others that the genus-abundance curve may be the result of taxonomic splitting, either by splitting genera and thus producing many small genera or by splitting species and thus producing a few large genera.

The generality of this conclusion rests on the assumption that the processes involved in salamander taxonomy and in salamander evolution are, in general, those of most other taxa.

#### A workload hypothesis

During the preparation of tables 1, 2 and 3, it became obvious that the number of species being described each decade was in general increasing. The question natur-

ally arises: "Does this increase in the number of species being described produce the genus-abundance curve?" What is meant here is whether or not a tendency to split or lump arises because of workload or other non-taxonomic factors.

The idea is vague but one could, for instance, hypothesize that, with the increasing number of species to be described, a taxonomist might be tempted to fit new species into existing genera as the fastest way to publish rather than laboriously to revise existing generic limits and erect new genera. Or he might, as Schmidt (1955) accuses Boulenger, unnecessarily describe new species rather than to go to the trouble of revising concepts.

One could also hypothesize that describing many new species gives a taxonomist a better grasp of generic limits because of increased familiarity with intra- and inter-specific variations. He thus becomes more reluctant to split and also more reluctant to describe new species.

To investigate these possibilities it is necessary to know how 'busy' are taxonomists and who describes new genera.

Table 5 (page 77) shows the number of new species described per decade, the number of working describers and the mean number of species per describer. The data are from Gorham (1974). A working describer is one whose working life falls within or bridges a decade, whether or not a

Table 5: Number of species of amphibians described per decade and number of 'working' describers per decade.

<u>Decade</u>	<u>Number of Species Described</u>	<u>Number of Describers</u>	<u>'Workload' (Species per Descriptor)</u>
1750 - 1759	15	1	15.0
1760 - 1769	14	2	7.0
1770 - 1779	3	2	1.5
1780 - 1789	7	8	0.9
1790 - 1799	14	3	4.7
1800 - 1809	19	6	3.2
1810 - 1819	7	5	1.4
1820 - 1829	60	14	4.3
1830 - 1839	68	21	3.2
1840 - 1849	90	19	4.7
1850 - 1859	126	27	4.7
1860 - 1869	181	18	10.1
1870 - 1879	209	33	6.3
1880 - 1889	227	20	11.4
1890 - 1899	244	28	8.7
1900 - 1909	225	26	8.7
1910 - 1919	176	35	4.5
1920 - 1929	334	49	6.8
1930 - 1939	319	58	5.5
1940 - 1949	264	54	4.9
1950 - 1959	299	77	3.9
1960 - 1969	483*	99*	4.9

\* Probably incomplete

species is described in the decade. Working life is defined as from the date of the first species described to the date of the last species described, by decades inclusive. Thus Taylor is counted in each decade from 1920 to 1960 since he described his first species in 1920 and his last (according to Gorham's record) in 1969.

It is at once apparent from this table that modern

taxonomists are not overworked. The workload trends generally downwards from the late nineteenth century. Any hypothesis that depends upon taxonomic workload cannot be entertained.

Table 6: The number of amphibian genera described by the top 16 describers. This table is to be compared with the top 16 species describers in table 1.

<u>Name of Describer</u>	<u>Dates</u>	<u>Number of Genera Described</u>	<u>Percent of All Genera</u>	<u>Percent of All Species</u>
Boulenger	1879-1920	35	10.0	13.4
Tschudi	1838-1845	23	6.6	< 1
Taylor	1920-1969	20	5.7	6.6
Parker	1925-1940	19	5.4	1.6
Cope	1859-1899	18	5.1	4.3
Peters	1844-1883	17	4.9	2.9
Fitzinger	circa 1830	14	4.0	0.0
Günther	1858-1902	14	4.0	3.0
Duméril et al	1841-1856	10	2.9	< 1
Wagler	circa 1830	8	2.3	0.0
Carvalho	1945-1958	8	2.3	< 1
Mirando Ribeiro	1920-1937	7	2.0	< 1
Gray	1831-1868	6	1.7	< 1
Laurent	1940-1969	6	1.7	1.7
Stejneger	1891-1927	6	1.7	< 1
Laurenti	circa 1768	5	1.4	< 1

Table 6 (above) lists the top genus describers. The number sixteen was chosen to facilitate comparison with table 1. Only seven names occur on both tables. In general, species describers are not genus describers. Two

describers - Fitzinger and Wagler - described no species at all. Furthermore, eleven of the sixteen worked, or did most of their work, in the last century while six did most of their work before 1850. On the other hand, of the sixteen top species describers, eleven worked only in the twentieth century, the rest did their major work after 1850.

#### Summary and comments on the hypotheses of artificiality

It has been shown that, in the amphibians at least, taxonomy has not been dominated by the philosophy of one taxonomist or by one school of taxonomy. Thus any mechanism producing the genus-abundance curve cannot be generated by taxonomic philosophy. Nor can it be generated by excessive splitting since it has been shown that, in the salamanders as an example, the majority of 'split' genera are rapidly reduced to synonymy and, in the genus Desmognathus as an example, the number of species has remained relatively constant over the last fifty years despite many changes in the names of species in the genus.

It has also been shown that, in general, amphibian genus describers pre-date species describers. That is, the majority of the genera had already been described before the majority of species had been described. The increased number of species known has not caused a concomitant increase in the number of genera.

One could argue: "But this applies to the amphi-

bians only, other taxa are different." The answer to this is: "In what way?" Even a cursory examination of the mammals and birds shows that taxonomists and taxonomic schools are even more widely dispersed than in the amphibians.

There remains another possibility. Perhaps taxonomy does not correspond to reality. Perhaps it is a purely mental construct which follows its own rules and these rules automatically generate the genus-abundance curve. Willey (1935) has pointed out the almost insuperable difficulties of becoming critically conscious of one's own habitual assumptions; "doctrines held as facts" can only be seen to be doctrines and not facts after great efforts of thought, and usually only with the aid of a first-rate metaphysician. Until such a metaphysician comes along, it can only be assumed that taxonomy reflects reality.



BIOLOGICAL HYPOTHESES

## THEORETICAL CONSIDERATIONS

Species-abundance data are usually shown as the number of species,  $n_r$ , represented by  $r$  members in a collection of animals or plants ( $r = 1, 2, 3, \dots$ ), the  $n_r$  are thus frequencies of frequencies. The distribution is truncated. The zero-class,  $n_0$ , the number of species which are not represented in the collection, is usually unknown. Elaborate methods have been developed to estimate the size of the missing zero-class and the population mean and variance (Cohen, 1961; Pielou, 1975, chapters 2 and 3).

Data may also be presented by ranked-abundance. If the data concerns only a few species, the number of individuals in each can be listed and ranked from largest to smallest. MacArthur's (1957) broken-stick model generates a ranked-abundance list. A ranked-abundance list becomes a species-abundance list if the collection contains many species. Pielou (1975, page 21) makes much of the difference between species-abundance and ranked-abundance and takes issue with May's (1975) ignoring the difference. But, like her controversy with MacArthur (Pielou and Arnason, 1965; Pielou, 1966; Vandermeer and MacArthur, 1966; MacArthur, 1966), she is probably concerned about a distinction without a difference.

Genus-abundance and genus-ranked data used in this thesis are more easily handled. In some cases, such as bird species, we are dealing with a practically completely censused population. The elaborate estimating procedures can be dispensed with. Instead of sample variance and mean, we are dealing directly with population variance and mean. For the less complete classifications, where a zero-class proportionately larger than the zero-class for birds may be suspected, we can proceed as though the sample variance and mean were the population variance and mean since, as shown by Chamberlin (1924) and Williams (1964), a newer or 'improved' classification will not change the shape of the distribution.

The total number of species present,  $S_T$ , and the total number of individuals present,  $N_T$ , go a long way towards describing a community. The ratio of the number of individuals to the number of individuals in the least abundant species,  $m$ , is  $J$  (May, 1975).

$$J = N_T/m$$

Equ. 10.

For genera-abundance  $G_T \equiv S_T$ ,  $S_T \equiv N_T$  and  $S_T \equiv J$  since the least abundant genus almost always contains one species and thus  $m = 1$ . One may ask: "How are the species distributed among genera or, more precisely, what is  $S_i$ , the number of species in the  $i$ -th genus?" Where  $G(S)$  is the number of genera with  $S$ -species, the probability distri-

bution function may be expressed as (May, 1975):

$$G(S)dS = \left\{ \begin{array}{l} \text{Number of genera each of} \\ \text{which contains between} \\ \text{S and S-dS species} \end{array} \right\} \quad \text{Equ. 11.}$$

The quantities  $G_T$  and  $S_T$  follow immediately from this:

$$G_T = \int_0^{\infty} G(S) dS \quad \text{Equ. 12.}$$

$$S_T = \int_0^{\infty} SG(S) dS \quad \text{Equ. 13.}$$

with sums replacing the integrals for the biologically discrete case.

In the following discussion the notation for species-abundance rather than for genus-abundance is retained to facilitate comparison with the literature. The notation substitutions indicated above can always be made.

There is a spectrum of theoretical distributions.

#### Random niche boundary hypothesis

At one limit are the 'flat' distributions to be expected when an ecological homogeneous group apportions a fixed amount of some governing resource randomly among themselves. MacArthur's (1957, 1960) 'broken-stick' model is an archetype of this sort of distribution. More generally descriptive names are 'proportionality space model' (Webb, 1974) and 'random niche boundary hypothesis'.

(Whittaker, 1972).

The random niche boundary hypothesis assumes that the boundaries between species' niches hypervolumes in resource space are set at random. That is, there is no mechanism of species dominance whereby a species arbitrarily 'preempts some fraction of the resource space. The most interesting model is the broken-stick model in which species are limited by competition at randomly located boundaries. It is fitted by the series (MacArthur, 1957):

$$P_r = \frac{N_T}{S_T} \sum_{i=1}^r \frac{1}{S_T - i + 1} \quad \text{Equ. 14.}$$

where  $i$  is the sequence of species from least to most important and  $r$  is the position of a species with relative importance  $P_r$  in the sequence.

The observation of a broken-stick distribution does not validate MacArthur's specific model. All it does suggest is that some one major factor is being randomly apportioned as opposed to the lognormal distribution which suggests an interplay of many individual factors. MacArthur (1957) also proposed an overlapping niche model ('model b') which predicts an even greater evenness in distribution. It is fitted by the series (Vandermeer and MacArthur, 1966; but see Pielou, 1966, for an alternative more precise formulation):

$$P_r = \frac{N_T}{S_T} \sum_{i=1}^r [(S_T+1)^{\frac{1}{2}} - (S_T-i+1)^{\frac{1}{2}}] \quad \text{Equ. 15.}$$

A reasonable genus-abundance hypothesis can be based on the broken-stick model if one assumes that the 'area' of an adaptive plateau, in the sense of Mayr (1963), controls the abundance of a genus rather than the genus controlling the area of the plateau. Plateau 'area', like niche hypervolumes and broken-stick segments can be generated by MacArthur's algorithm.

MacArthur's 'model b.' would imply that genera and higher taxa do not compete. Instead any category would be allowed to take what it needed from some limiting resource. For those who would deny genus-genus competition this is the most realistic model for generating genus-abundance curves. Unfortunately the high diversity equitableness - the extreme 'flatness' of the resulting curve - bears no resemblance to any natural community.

The broken-stick model and other flat models are one parameter distributions,  $S_T$ , or in this thesis,  $G_T$ .

#### Niche preemption hypothesis

At the other limit are 'steep' distributions of relative abundance to be expected if the community ecology is dominated by some single factor, and if the division of this niche volume proceeds in a strongly hier-

archical fashion. This is the 'niche preemption hypothesis' (Whittaker, 1972). In this model the most successful species preempts a fraction of the resource space, the next species a fraction approximating 'k' of the resource space not already preempted by the first species, and so on. The species importance forms a geometric series in this model:

$$p_i = p_1 c^{i-1} \quad \text{Equ. 16.}$$

where  $p_i$  is the relative importance of the  $i$ -th species as a decimal fraction of the corresponding importance value for all species sampled,  $p_1$  is the relative importance of the first species,  $i$  is the position of the species in the sequence from most to least important (note that this is opposite ordering to the broken-stick algorithm) and  $c$  is the geometric series ratio and equals  $k-1$ .

The geometric series is obviously an ideal case. A more statistically realistic expression of the geometric series model is the logseries distribution of relative abundance. The fractions, and the ratio  $c$  for their complement, can be expected to show random fluctuations from one species-pair to another in the sequence. Whittaker (1972) notes that the distribution can also be interpreted as lograndom.

Both the geometric and logseries are two parameter distributions,  $S_T$  and  $k$  (or  $J$ ) for the geometric series

and  $S_T$  and  $\alpha$  for the logseries.

In the logseries:

$$S_T = \alpha \ln(1 - J/ ) \quad \text{Equ. 17.}$$

and

$$p_i = \frac{\alpha x^i}{i} \quad \text{for } i = 1, 2, 3, \dots \quad \text{Equ. 18.}$$

$x$  and  $\alpha$  are found by solving simultaneously (Pielou, 1975, page 45);

$$S_T = -\alpha \ln(1 - x) \quad \text{Equ. 19.}$$

$$N_T = \frac{\alpha x}{1-x} \quad \text{Equ. 20.}$$

The assumption underlying the logseries distribution implies that it is never fully 'unveiled' so that the least abundant species is (or are) represented by a single individual. That is, in practice  $m = 1$  and  $J = N_T$  which is also the real situation for genus-abundance calculations. A logseries transspecific-abundance distribution would imply strong preemption of resources. The example given of the possible bird-bat interaction should lead to this type of curve. One might speculate also that the near elimination of equids and tylopids from most of the world's steppe, now occupied by bovids, is another example of resource preemption.

Lognormal hypothesis

Between the flat broken-stick and the steep log-series, both resource apportioning models, lies the log-normal distribution. Theory (Koch, 1966; Aitchison and Brown, 1966) and observation (Preston, 1958, 1960, 1962, 1969) point to its ubiquity once the number of taxa and individuals becomes very large and when relative abundance is governed by many independent variables. In general, two parameters are needed to characterize a specific log-normal distribution, but Preston (1962), by making certain further assumptions, reduces it to a one parameter family of 'canonical' distributions: if  $S_T$  is given, then  $J$  follows and vice versa.

May (1975) states: "The lognormal distribution reflects the statistical central limit theorem; conversely in those special circumstances where broken-stick, geometric series or logseries distributions are observed, they reflect features of the community biology."

What May is saying is that we should expect biological data to take a lognormal form, other distributions indicate non-random processes at work.

The genesis of the lognormal distribution is as follows (Koch, 1966; Pielou, 1975). Suppose that the variate is the product rather than the sum of a large number of independent factors. This will be the case if we assume the variate to have undergone a series of changes in value



with the magnitude of each successive change being a random proportion of the variate's immediately preceding value. Thus, if  $y_j$  denotes the variate's magnitude after the  $j$ -th change we assume that (Pielou, 1975; page 47):

$$y_j = y_{j-1} + E_j y_{j-1} \quad \text{Equ. 21.}$$

where the  $E_j$ 's are random variates, mutually independent of the  $y$ 's, then:

$$y_n = (1+E_n)(1+E_{n-1}) \dots (1+E_1)y_0 \quad \text{Equ. 22.}$$

$$\ln y_n = \ln y_0 + \sum_{j=1}^n \ln(1+E_j) \quad \text{Equ. 23.}$$

Assuming  $E_j \ll 1$  so that  $\ln(1+E_j) \approx E_j$

$$\ln y_n = \sum_{j=1}^n E_j + \text{constant} \quad \text{Equ. 24.}$$

By the central limit theorem  $\lim_{n \rightarrow \infty} \sum_{j=1}^n E_j$  is normally distributed, therefore  $\lim_{n \rightarrow \infty} y_n = y$  is normally distributed.

The foregoing justifies the following testable hypothesis about the genus-abundance distribution: The sizes of separate and independent subtaxa of some one taxa will be random variates from a lognormal distribution. I define independent as separate and/or non-interacting ecosystems. Equation 22 supports this hypothesis. Thus, because a genus contains  $n$  species at time  $t_0$  does not

guarantee that it will contain either more or less species at time  $t_f$ . The equation does suggest that a genus will have a change in its size (number of species) at  $t_f$  in proportion to its size at  $t_0$ . This is reasonable since a larger genus will tend to be 'hit' by a larger number of evolutionary events than a smaller genus solely because the larger genus is a bigger target. If, as appears true, most species of a genus are in separate ecosystems, then the 'hits' per genus will be random and independent.

A second lognormal hypothesis may also be entertained. Called the 'resource apportioning model' by Pielou (1975, page 48), it is an elaboration of the 'broken-stick' model. The following abbreviated discussion follows Pielou. A more detailed argument is contained in Bulmer (1974).

Imagine a stick of length  $L_0$  marked at one end then broken at a randomly chosen point. Choose one of the two parts and break again; and so on. At each step, every part, regardless of its length, has an equal chance of being chosen for the next break, i.e., the probability that a part will be broken is independent of its length. After a very large number of breaks have been made, the part of the stick with the mark at one end has the length:

$$L_n = L_0 \prod_{j=1}^n r_j \quad \text{Equ. 25.}$$

where  $n$  is the number of breakages this part has undergone

and  $r_j$  is the length of the marked part as a fraction of its length before the  $j$ -th breakage. Clearly  $L_n$  is the product of a large number of independent positive variates and is thus a lognormal variate. Because all broken parts have identical probability distributions, the distributions of the lengths of the parts tends to lognormal. As long as the number of pieces into which the part is broken is independent of its length, the parts may be broken more than once and (according to Bulmer, 1974), the breaks need not even be random.

For this model to apply to this thesis, we must assume that a many-genus 'community' has divided up some limiting resource among themselves in this manner and that the number of species in each genus is proportional to that genus' share of the resources. This genus-abundance hypothesis differs from the broken-stick genus-abundance hypothesis in that it implies a post hoc sharing of resources rather than a propter hoc determination of the resources to be allocated. The difference is subtle but real. This model, which is here hypothesized, is, I believe, unrealistic, in that most genera cannot interact because they are not sympatric, except in a world-community sense.

The lognormal distribution has the form (Aitchison and Brown, 1966):

$$S_T = \int \frac{1}{x\sqrt{V2\pi}} \exp [-1/2V(\log x - \mu)^2] dx \quad \text{Equ. 26.}$$

where  $V$  and  $\mu$  are the logarithmic variance and mean respectively.

The poisson lognormal is an interesting variant of the lognormal distribution. The lognormal distribution is continuous by definition. Abundance data are discrete. Consider the observed abundances as compound poisson variate with the poisson parameter  $x$  being lognormally distributed. Then, (Bulmer, 1974; Hologate, 1969) the probability of a species containing  $n$  individuals is:

$$P_n = \int \frac{1}{x^n \sqrt{2\pi}} \exp [-x - n \log x - 1/2V(\log x - \mu)^2] dx$$

Equ. 27.

for  $n = 1, 2, 3, \dots$ . The distribution has been little used. For most work it is computationally troublesome and introduces a spurious precision according to Pielou (1975, page 49). The curve is very steep for communities with many species because  $x^n$  rapidly becomes very large.

### Queuing hypothesis

Queuing theory has been developed by systems engineers to handle problems of traffic flow. It was first developed and applied to telephone networks but is now used to handle very general problems, see for instance Goode and Machol (1957, page 328 and following). The theory is based (Morse, 1958) on a sequence of units which arrive at some facility which services each unit and eventually

discharges it. The underlined words are to be understood in the most general sense: the units might be telephone calls or automobiles, the facility an exchange or toll booth, the service making a connection or accepting a token, and so on.

In most situations there may be variations in the regularity of arrivals or lengths of time for servicing or both. Sometimes units will arrive faster than they can be serviced and queues will develop, sometimes service facilities will be idle. In fact, every part of the operation may vary in a more or less random way and every measurable quantity associated with the operation may be a stochastic variable, fluctuating with time above and below some average value.

It is not usually advisable or appropriate to try to calculate the exact behaviour of these stochastic variables with time. Usually a probabilistic picture will give sufficient insight for one to be able to calculate the system's overall behaviour. (It is the job of the systems engineer to 'balance' the system.) But according to Morse (1958, page 4), if the mean rate of arrival and the mean rate of service are constant (that is, the fluctuations in both are short-time fluctuations), the state probabilities and the derived averages will be independent of time. It is this relatively simple system that is used in this thesis. It is assumed that the facilities are never over-

loaded so that only arrival probabilities need be calculated. Simple biological examples are not easily found. However, there is one engineering example familiar to everybody.

Consider automobiles (units) arriving at a constant mean rate of two per minute,  $\bar{x}$ , at an autoroute tollbooth (facility). That is, the average rate of traffic arrival is neither increasing nor decreasing. Furthermore, the tollbooths are fast enough and sufficient in number so that there is no waiting to deposit tokens (service) and no queues form. Then the mean rate at which the automobiles leave the booths (discharge) equals the mean rate of arrival and it does not matter whether we calculate the mean rate before or after servicing. Under such conditions the probability that a given number of automobiles will arrive or leave in any given minute,  $P(n)$ , is:

$$P(n) = \begin{cases} \frac{e^{-\bar{x}} \cdot \bar{x}^0}{0!} \\ \frac{e^{-\bar{x}} \cdot \bar{x}^1}{1!} \\ \frac{e^{-\bar{x}} \cdot \bar{x}^2}{2!} \\ \dots\dots\dots \\ \frac{e^{-\bar{x}} \cdot \bar{x}^n}{n!} \end{cases} \quad \text{Equ. 28.}$$

which are the successive terms of a poisson distribution and have the values  $P(0) = 0.135$ ,  $P(1) = 0.271$ ,  $P(2) = 0.271$  for the first three terms of the example used.

The assumption made is that the arrival of units at a facility is poisson distributed and this is generally true. The mean and variance must be equal to be a pure poisson. Where the mean and variance are not equal, the assumption is usually made that some non-random factor is affecting the system. Nevertheless, a modified poisson distribution can often be fitted. There are a very large number of 'special application' poisson equations (Haight, 1967) and there is a real danger of 'shopping around' until an equation is found to match the data. The simplest poisson equation that allows for a difference between mean and variance without using any ad hoc assumptions is that of Moroney (1956).

Solving equations 29 and 30 where  $\bar{x}$  is the mean and  $V$  is the variance:

$$c = \bar{x}/V - \bar{x} \quad \text{Equ. 29.}$$

$$k = c\bar{x} \quad \text{Equ. 30.}$$

The probabilities then become as shown in equation 31 on page 96.

Koch (1966) hypothesized that the evolutionary time during which radiation of species takes place is normally distributed. He appears to be suggesting that the opportunity to speciate occurs only during certain time intervals and that the duration of these intervals is normally

$$P(n) = \left\{ \begin{array}{l} (c/c+1)^k \cdot \frac{1}{0!} \\ (c/c+1)^k \cdot \frac{k}{1!(c+1)^1} \\ (c/c+1)^k \cdot \frac{k(k+1)}{2!(c+1)^2} \\ (c/c+1)^k \cdot \frac{k(k+1)(k+2)}{3!(c+1)^3} \\ \dots\dots\dots \\ (c/c+1)^k \cdot \frac{k(k+1)\dots(k+n-1)}{n!(c+1)^n} \end{array} \right. \quad \text{Equ. 31.}$$

distributed. He also hypothesized that there is a logarithmically distributed lag time between the opening of an evolutionary opportunity and speciation. Given these two hypotheses, then the conditions for a lognormal genus-abundance curve will be met, as Koch proves.

But there is no evidence for the hypothesized speciation lag nor for the speciation 'time gates'. There is some evidence that 'biological times' are lognormally or logarithmically distributed (Preston, 1966), but the evidence is not strong. Nevertheless, we can take the core of Koch's hypothesis and assume the arrival of incipient species (units) at the time gates (facilities) where they are processed into species (serviced) and become full species (discharged). As in our tollbooth example, we measure the rate after the fact. One or other of the parameters is logarithmic (it does not much matter which) and so we can take the logarithmic mean and variance of the



'resulting' genus-abundance distribution. Equation 31 will be used since the logmean and logvariance are not equal for any taxa used in this thesis.

The arithmetic mean and variance cannot be used in any case. There will always exist a  $P(0)$  class using an arithmetic poisson which implies that there is a probability of genera with no species. While such a concept might be entertained if one were searching for species and  $P(0)$  indicated the proportion of species not yet found, it is seen to be absurd for a taxon completely censused for 'all species' such as birds.

#### Proportion spaces and genus-abundance

Webb (1974) and Bhargava and Doyle (1974) recognized that there was an obvious relation between all measures of species-abundance. It can be seen that, in the context of ecological diversity and with a low individuals-to-species ratio, the broken-stick, logseries and lognormal are all 'hollow', that is, are more or less hyperbolic, and predict many rare species and few abundant species. As the individuals-to-species ratio increases all three curves take on a bell-shape but with different kurtoses and skewnesses. They differ mainly in the proportion of species allowed in each abundance interval.

Webb showed that these similar patterns arise because of the underlying mathematics of proportion.

Preston's lognormal curve and MacArthur's broken-stick model are only two examples. For instance, Webb notes that although MacArthur's broken-stick model is based on a biological premise - non-overlapping niches - it has been shown that other models give rise to the same series (Cohen, 1968). The relevance of the non-overlapping niche hypothesis to the observed distribution therefore becomes obscured.

Webb claims that the similarities between the broken-stick series and the natural populations arises from the initial choice to work with proportions. The mathematics of proportions and the mathematics of the broken-stick are just two of many ways of looking at the same thing.

Webb shows that over most of the biologically realistic hyperspace both diversity and the logarithmic standard deviation lie within narrow limits. If random elements are acting on a population the system has a reasonable chance of being found in, say, five percent of the total proportionality space. Thus measurements on the system will give results which are near the mean value for the space. Low diversities are found only at the very edge of the space. Webb re-examines many of Preston's examples and cites others, and these populations do indeed fall within the narrow limits predicted by his models. The few exceptions are the gregarious species which drive the system

into the outer regions of the proportionality space for obvious reasons. He says: "...as long as there is enough randomness in a biological system, one will obtain reasonable agreement with the results of the 'proportionality space' or 'broken-stick model'. ...the fact that the models of MacArthur and Cohen can give the broken-stick series arises not because of the biological principles they used, but because they include enough randomness." And Bhargava and Doyle show that whatever we may claim to be measuring when we measure diversity, it is just another way of looking at distance in hyperspace.

How does this apply to genus-abundance? Webb and Bhargava and Doyle have shown that any theory about the structure of natural communities must be formulated in terms of proportion spaces. This must also be true of genus-abundance if genus-abundance and species-abundance are homologous. Conversely, any statement about genus-abundance that is not formulated in terms of proportion spaces is not a statement about genus-abundance.

### Summary

Reasonable hypotheses have been made about the processes leading to the species-abundance distribution by various authors. These have been extended in this section to the genus-abundance distribution. Each hypothesis leads to a different distribution generating equation. Table 7

lists the hypotheses, the equations that follow from the hypotheses and the main references.

Table 7: Summary of the biological hypotheses used to explain the species-abundance and genus-abundance distributions, the resulting distributions and the main references.

<u>Biological Hypotheses</u>	<u>Resulting Distributions</u>	<u>Main References</u>
Random Niche Boundaries	Broken-Stick	MacArthur (1957) Cohen (1968)
Niche Preemption	Logseries	Williams (1964) Fisher et al. (1943)
Many Random Factors	Lognormal	Preston (1962) Aitchison and Brown (1966)
Processing Through Gates	Logpoisson	Koch (1966) Morse (1965)

## THE DATA

Criteria used in selecting data

Five criteria were used in selecting the taxa to be analysed. First the taxon must be well studied so that most species are known. Second, it must present no major difficulties or peculiarities of classification not generally present in other taxa. Third, there must be some consensus as to how many genera are included in the taxon and how the species are distributed between genera. Fourth, there must be enough different describers and revisors in consensus to avoid idiosyncratic or cranky classification. Fifth, there must be a generally accepted monograph of the taxon which states that genus X contains N species and names the species.

These criteria effectively eliminated the insects and nearly all arthropods. I know of no taxonomist who claims that any major group of insects is well known.

The bacteria highlight the problem of choosing taxa. The many successive editions of 'Bergey's Manual' seem to fulfil all the criteria. Bacteria have been well studied by many competent investigators for a long time and the manual is the epitome of a generally accepted monograph. Yet its latest revisors (Buchanan and Gibbons, 1974) have initiated many radical departures from past editions, in particular: "No attempt has been made to provide a com-

plete hierarchy, as in previous editions, because a complete and meaningful hierarchy is impossible." Their reliance on type cultures has relegated many formerly recognized species to a kind of incertis sedis limbo and the appalling list of synonyms, most being nomen nudum, in the 'Index Bergeyana' (Buchanan, Holt and Lessel, 1966) indicate some serious deficiencies in taxonomic practices. To what extent the bacteriologists' bias towards pathology has caused omission of free-living forms can only be surmised.

There is a further problem, as pointed out by Sneath (1974). We are ignorant of what selection pressures operate in the major habitats over enormous periods of time. What is the difference between a Devonian swamp and one of today, between the ocean now and in earlier epochs? If evolution depends on selection pressure and these have been the same for eons, then does this mean that non-pathogenic bacteria have not changed because they reached the limit of their adaptation eons ago?

For these reasons the bacteria were rejected.

The ferns are another well known group with excellent catalogues available. Unlike the bacteria, in which the species are in doubt; in the ferns the genera are in doubt. The traditional generic limits of Christensen (1905+) have been radically challenged by Copeland (1947) on the one hand and on the other hand by Ching (1940, cited by Copeland, 1947). The three classifications cannot be

reconciled.

Taxa accepted

Birds, mammals and amphibians were finally selected.

The taxonomy of birds is more or less 'closed', it being claimed that there are not more than three dozen undescribed species (Mayr, 1963). This may err on the generous side, new species are very seldom discovered and when one is it is a major event, for instance see Editors, New Scientist (1977). Bird taxonomy has been thoroughly revised recently (Mayr and Amadon, 1951), and Peters (1931+) catalogues keeps track of all changes. The results of the last twenty-five years have been brought up-to-date by Gruson (1976). Furthermore, most evolutionary processes are known to occur in birds, indeed most have been first noted in birds, and birds do not present any serious puzzles or anomalies in which unique evolutionary mechanisms are postulated. Thus if one can say anything about genus-abundance, it should be sayable about birds.

Mammal taxonomy has not reached the same degree of stability as has bird taxonomy. No doubt there are many more species to be described. Nevertheless, no one has suggested that the majority of species are not already known.

Mammalian supergeneric classification has reached a consensus (Simpson, 1945) and has been recently revised

(Ellerman and Morrison-Scott, 1951). There are presently three modern species lists: Morris (1965), Anderson and Jones (1967), and Walker (1964). This last has been revised by Paradiso (1968, 1975).

The first two lists are used in this thesis. They differ somewhat in detail: Morris admits 1018 genera and 4307 species, Anderson and Jones admit 984 genera and 3955 species. A chi-square test of their difference has an alpha between 0.950 and 0.975, while a two-tailed t-test has an alpha between 0.60 and 0.75. Thus they differ, but it cannot be said that they differ very significantly.

Walker (1964) is, in my opinion, badly edited. For instance, the editors of the rodents, which account for a large number of mammalian genera and species, follow Ellerman (1940) exactly, as a comparison of each genus entry will show. But the editors often confuse Ellerman's use of the terms 'form' and 'species' making it impossible to determine how many species are in many genera, for instance Rattus with 570 'named forms'. Furthermore, the expression "about a dozen species" and similar ambiguities occur too often to give one confidence in the editors' thoroughness. Therefore Walker is not used. The same ambiguities occur in the most recent revisions (Paradiso, 1968, 1975).

Of the two compilations used, Morris might be preferred to Anderson and Jones because it meets William's (1964) criterion of a single author. On the other hand,



each major taxon in Anderson and Jones is treated by a specialist in the taxon. There seems little reason to choose between the two.

Morris is quite blunt about the problems of compiling a taxonomic catalogue. He has tried to "...select the most erudite and up-to-date works. ...", but most seem to fall short of his standards. He actually produces an order of merit (pages 21 to 25) called an "order of priority" but which appears to me to be a descending list of believability. His comments on some authors are quite blunt: "[the] recent work is extremely detailed. It omits nothing - in fact it admits too much." "...unfortunate tendency to score many island forms as separate species." "...[the authors] are guilty of old-fashioned splitting... obviously valueless species...full of meaningless splittings" and so on.

The world's amphibian fauna is less well known than the mammals and amphibian taxonomy has not reached the same stability. We therefore have a descending order of completeness: birds, mammals and amphibians.

There are other important differences. The birds comprise 8736 species in 1986 genera, 168 families and 28 orders according to Gruson (1976); the mammals comprise (Morris, 1965) 4307 species in 1018 genera, 124 families and 19 orders; the amphibians comprise 3384 species in 350 genera, 27 families and 3 orders (Gorham, 1974). The

number of species of amphibians is eighty percent that of mammals and forty percent that of birds while the number of genera, families and orders is proportionately much lower. On the basis of the mammals one would expect the amphibians to have 849 genera, 97 families and 15 orders. The amphibians are therefore less taxonomically diverse than the birds and mammals.

Gorham (1974) has published a checklist of the world's amphibians. This has been followed exactly in this thesis with the following exceptions. The Madagascar species of Rhacophorus have been segregated-out as the genus Boophis at Gorham's own suggestion (page 9). Nine African subgenera of Rana have been segregated as full genera, also at Gorham's suggestion (page 139). I have used Poynton (1964) to sort-out the African ranids.

Method of collecting the data

The data were collected and treated as follows:

The number of species in each genus was counted and entered against the genus name. The species per genus from Morris (1965) and Anderson and Jones (1967) were compiled separately in order to facilitate comparisons between these two recensions.

The lists were then examined for the largest genus in each taxon which turned out to contain 404 species in the amphibians, 74 in the birds and 149 in the mammals according to Morris and 160 according to Anderson and Jones.

The numbers 1 to the number corresponding to the number of species in the largest genus in each taxon were written down consecutively in columns. These numbers, species per genus, are the independent variate 'X'. Then, starting from the first listed genus, a check mark was made against the appropriate x, one check mark per genus. For instance, since the frog genus Atelopus contains 36 species, a check mark was made against 36. After all the genera were tabulated, the check marks against each x were totalled. These are the dependent variate 'Y' or 'f', the frequency.

A total of 20,382 species were counted and used in this thesis. In addition, more than 22,000 ferns, bacteria, reptiles and mammals were counted and tabulated but later discarded because the sources did not meet the criteria.

### Mathematical methods

The arithmetic and logarithmic means and variances were then calculated for each set of data.

Logarithms to the base 2 were used. It makes no difference mathematically what base is chosen but it is of some practical importance. If data is grouped by integral logarithmic intervals, the logarithmic base must be small enough to allow several intervals, that is, it must allow a fine enough resolution of the data. Base 10 is too big, allowing only one interval for birds and two for mammals and amphibians. Preston (1962, and in many previous and subsequent papers) has chosen base 2, while suggesting that base 'e' would also be appropriate. But base 2 does have the added advantage that it allows sorting of integral data into logarithmic intervals by simple inspection. There are seven base 2 intervals for birds, nine for mammals and ten for amphibians.

The means and variances were then used to calculate the theoretical distributions.

The broken-stick distribution was calculated according to the method of MacArthur (1957), the logseries distribution according to the method of Pielou (1975, page 43), the lognormal distribution according to the method of Aitchison and Brown (1966) and the logpoisson according to the method of Moroney (1956) modified for logarithmic parameters.

The fitting of a lognormal curve to species-abundance data is usually quite a complicated procedure. It would be straightforward were it not for the fact that the observed distribution is zero-truncated, that is, 'empty' (unrepresented) species are unobservable. Pielou (1975, page 50) presents an elaborate estimating procedure which makes use of special tables prepared by Cohen (1961). Three chapters in Aitchison and Brown (1966) are given over to the same problem with non-biological data.

This problem does not arise in fitting lognormal curves to genus-abundance data since, for birds at least, if we are to believe Mayr, we are dealing with a population and not a sample, there being less than one percent of the species undescribed. Specifically, our statistics are  $\mu$  and  $\sigma$  and not sample mean and standard deviation. We can therefore 'plug-in' these values directly into the formula and generate the curve. In the case of the mammals and the amphibians we can assume that the 'sample' is the majority of the population and treat it as a population.

#### Tests of significance

It is a general feature of all distributions (Head-  
ing, 1970; page 592) that most individual observations satisfy the inequality:

$$|X - m| < 2s$$

while few, if any, satisfy the inequality:

$$|X - m| > 3s$$

If we have made an observation or calculated a theoretical datum point 'X', to what extent can we decide whether or not it is part of a distribution with mean 'm' and standard deviation 's'? If the observed distribution is known to be normal, poisson, binomial or one or other of the well-characterized distributions, a very precise answer can be given. But if the distribution function is not known, or if no other information is available, we can use the following tests:

First, we make a null hypothesis: "X is a member of a given distribution." Statistics can never prove such a hypothesis, but it can give evidence against it and the strength of the evidence can be given a number - a probability - whose size is directly proportional to the strength of the evidence against the hypothesis.

Second, we postulate as reasonable:

If  $|X - m| < 2s$ , no evidence exists against the hypothesis. The results of the tests are 'not significant'.

If  $2s < |X - m| < 3s$ , certain evidence exists against the hypothesis. The results of the test are 'significant'.

If  $|X - m| > 3s$ , almost complete evidence exists against the hypothesis. In this case we conclude,

almost certainly but still with a shadow of a doubt, that X is not a member of the given distribution. The results of the test are "very significant".

Where there are many datum points belonging to two collections of data we can still make the null hypothesis: "Distribution X is a member of distribution Y." Since it is unlikely that both distributions have the same mean and standard deviation, we decide by means of a t-test how many points from X fall within  $2s$  of Y and thus assess the probability that X and Y are in fact the same distribution and that the differences in means and standard deviations are owing to sampling. The t-test has the added advantage that it is directional. We can say that the datum points of one distribution are too large or too small in magnitude. With more than two distributions to test, where sampling error may, by chance, cause sufficient overlap to give a false "not significant", we can use more severe tests of significance (Winer, 1962) or use analysis of variance.

The t-test is probably the most used and the most sensitive test of significance. But it has one big disadvantage: it is not sensitive to ordering. As an example, consider the two distributions 1, 2, 3, ..., 10 and 10, 9, 8, ..., 1. They have the same mean and standard deviation. A t-test shows them to be identical, while simple visual inspection shows them to be unambiguously different.

9 What if, as in this thesis, all distributions have, by definition, the same mean and standard deviation? Then even though their shapes might differ radically, most X's of all distributions will satisfy the inequality:

$$|X - m| < 2s$$

and for the same reason will satisfy in the same way the null hypothesis and an analysis of variance.

Under such circumstances the chi-square test is the only test of significance available. When two ordered distributions are being tested against each other, the difference between the dependent variate  $y_i$  and the expected  $\hat{y}_i$  is taken for each  $x_i$ . Then if these differences are independent and normal (which can be assumed unless there is evidence to the contrary), the sum of the squares of the difference divided by  $\hat{y}_i$  is defined as the chi-square statistic. The test is relatively independent of the underlying means and variances being tested. In the example given above of the two series 1 to 10 and 10 to 1, the chi-square statistic lies far beyond three standard deviations.

Suppose that we know from past experience that most distributions will fall in the "no evidence against" range on the basis of a null hypothesis and using a chi-square test. That is, there is no evidence against the hypothesis that the observed distribution is not a member of the theoretical distributions A, B, C, and so on simultaneously.



And suppose further that these theoretical distributions are hypothesized to be mutually exclusive as are, for instance, the broken-stick and the logseries distributions. Then a non-null hypothesis must be used: "Distribution X is not a member of a given distribution." Then if, and only if, the alpha of the chi-square statistic falls below a probability of 0.05 can we say that the weight of the evidence is against the hypothesis - that is, distribution X is a member of a given distribution.

We know from past experience that the species-abundance theoretical curves show a 'good fit' in the "no evidence against" region for real natural communities. A priori, we can expect no better for genus-abundance curves. Some striking examples are Hairston (1959) where the broken-stick fit became better as the size of the sample of soil microarthropods was increased and mixed with samples drawn from different habitats - contrary to theory - and Whittaker (1969), who found that broken-stick, lognormal and logseries could all be demonstrated in one forest. The reasons for these discrepancies is not particularly relevant to this thesis (they are discussed by Slobodkin (1961) and Whittaker (1969)), except to illustrate the difficulties in using a null hypothesis.

It is easy to fit an ad hoc curve to genus-abundance data. As recognized by Chamberlin (1924) it is 'hyperbolic' but it is very much steeper than  $\hat{y}_i = k/x_i$  which he

suggested.  $\hat{y}_i = k/x_i^{\bar{n}}$  fits well, where  $k$  is the first term,  $y_1$ , and  $\bar{n}$  is the average of the  $n$ 's for all terms.

A much better fit can be made with  $\hat{y} = k/x_i^{\hat{n}_i}$ , where  $\hat{n}_i = ax_i + b$ . Such curves for birds and mammals fit with a chi-square alpha between 0.50 and 0.75. This is well within the "no evidence against" range for a null hypothesis.

An even better fit could be obtained by adjusting  $k$  and using a polynomial to calculate  $\hat{n}_i$ . But such a procedure would be futile; the equation has no biological meaning.

Log-log transforms of biological data to test hypotheses must be used with caution. Beauchamp and Olsen (1973) discuss some of the limitations and site relevant literature. A chi-square test of log-log transformed data may well give spurious significance levels because of the reduction of the magnitude of the 'y' variate by transformation. For instance, suppose  $y$  is found to be 256 but is expected ( $\hat{y}$ ) to be 128. Then the statistic  $(y - \hat{y})^2/\hat{y}$  is  $(256 - 128)^2/128 = 128$ . The logtransform statistic is very much smaller:  $(\log_2 256 - \log_2 128)^2/\log_2 128 = 1$ .

The following test was made using the x- and y-axis limits from the birds as a model. Twenty graphs were set up with the x-axis marked from 0 to 6 and the y-axis marked from  $\log_2 6$  to  $\log_2 882$  (2.5850 to 9.7846). Five-digit random numbers between these limits were chosen sequentially from the top of column 1, page 622 of the table of random numbers in Selby (1970). The seven numbers were then

ordered from largest to smallest and assigned in that order to the x values from 0 to 6. A least-squares straight regression line was drawn through the seven sets of ordered pairs of numbers and the chi-square statistic calculated. The procedure was repeated with new random numbers until twenty graphs were completed.

The mean of the chi-squares was 0.4699 with a standard error of the mean of 0.0982, the standard deviation was 0.4392 with a standard error of the standard deviation of 0.0694. With six degrees of freedom, we can expect, with a probability of 0.99, that 99 percent of such random sets will be 'significant' at the five percent level and 66 percent will be significant at the one percent level. If the y-numbers are non-random then even higher percentages at the one percent level can be obtained.

As will be shown, a straight or parabolic regression line drawn to log-log data yields a significant chi-square at better than the 0.005 level for birds, mammals and amphibians (except for a parabolic fit for birds which has an alpha of 0.05). On the other hand, the semilog retransforms of the log-log regression lines are not significant on the basis of a non-null hypothesis.

However, if the chi-square statistic cannot be used to test significance of log-log data, it can be used to test which of several lines is the best fit and it is so used in this thesis.

It is for this reason that I am unwilling to accept Anderson's (1974) statement that the genus-abundance curves are logarithmic.

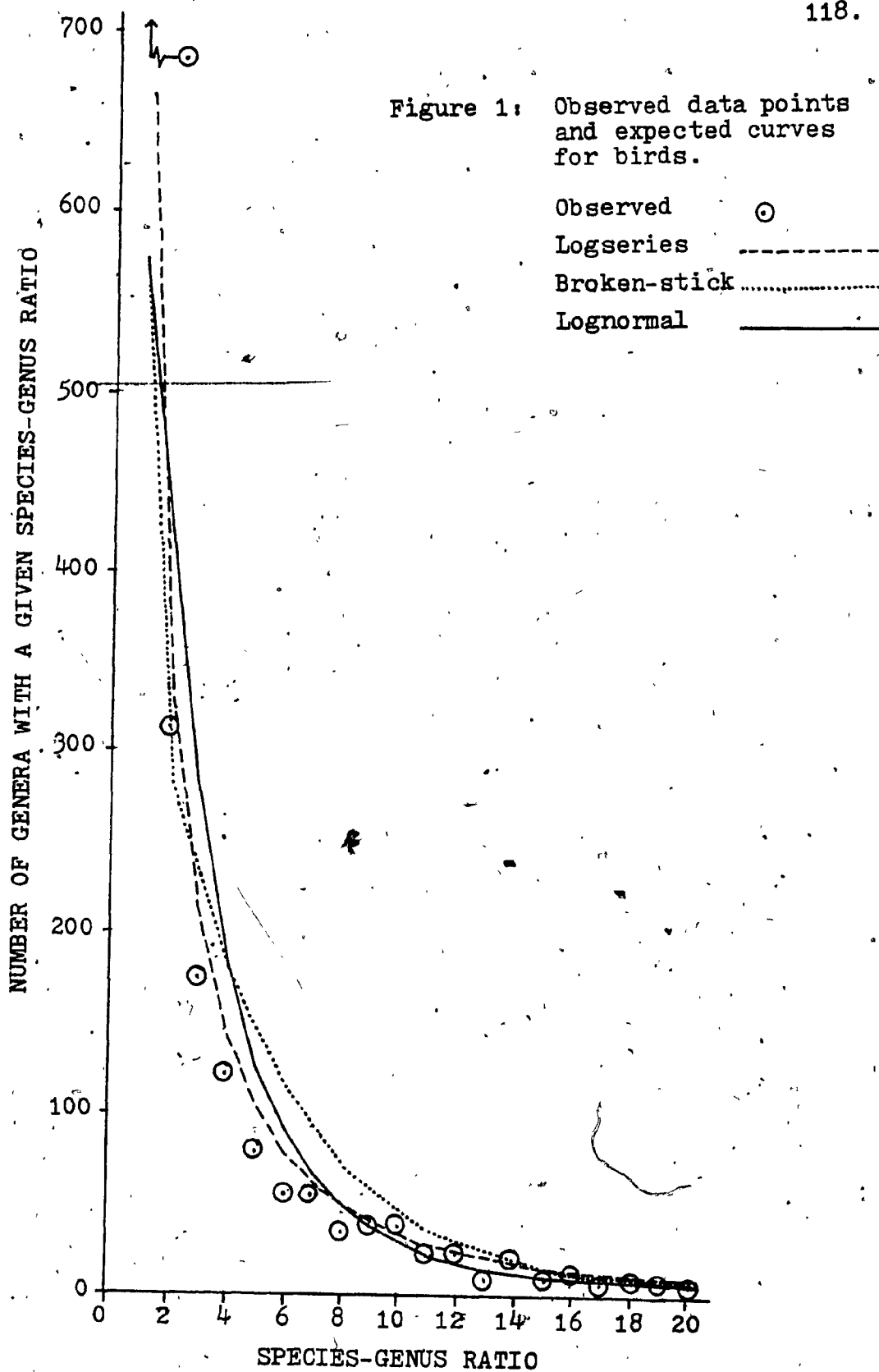
### Results

The results of the curve fittings are summarized in table 8. Figure 1 shows the curves for birds. The table is arranged as follows: First the number of degrees of freedom used (one less than the number of x intervals), second the sum of chi-squares and third, the alpha value of the chi-square with the degrees of freedom shown. The alpha values are from Selby (1970) and are as follows: 0.005, 0.010, 0.025, 0.050, 0.100, 0.250, 0.500, 0.750, 0.900, 0.975, 0.990, 0.995. The alpha for each fit is given as less than a certain value and is to be read as occurring in the interval. Thus,  $<0.990$  means an alpha value between 0.990 and 0.975. Alpha values greater than 0.995 are shown as  $>0.995$  or much greater  $\gg 0.995$ , similarly for less than 0.005.

A value above 0.050 is considered 'significant evidence against' a non-null hypothesis, between 0.050 and 0.010 'significant evidence for' a non-null hypothesis', below 0.010 'very significant evidence for' a non-null hypothesis. For a null hypothesis the limits are below 0.950 'no significant evidence against', 0.950 to 0.990 'significant evidence against', above 0.990, 'very significant evi-

Table 8: Chi-square statistics for fitted curves.

	Birds		Mammals: Morris		Mammals: Ander.		Amphibians.					
	df	Chi-S alpha	df	Chi-S alpha	df	Chi-S alpha	df	Chi-S alpha				
<u>Untransformed</u>												
Logseries	29	103.4	>>.995	21	456.5	>>.995	19	224.4	>>.995	18	32.50	<.990
Broken-Stick	22	598.7	>>.995	17	409.4	>>.995	17	263.2	>>.995	17	206.9	>>.995
Lognormal	29	393.4	>>.995	21	1487.	>>.995	19	354.4	>>.995	18	47.80	>.995
<u>Transformed</u>												
<u>Semilog</u>												
Logseries	5	80.61	>>.995	6	328.5	>>.995	6	462.9	>>.995	6	25.14	>>.995
Broken-Stick	4	355.4	>>.995	5	415.6	>>.995	4	248.1	>>.995	5	176.6	>>.995
Lognormal	5	354.0	>>.995	6	450.6	>>.995	6	339.9	>>.995	6	38.37	>>.995
Logpoisson	5	56.56	>>.995	6	17.40	>>.995	6	33.75	>>.995	6	3.67	<.500
<u>Log-log</u>												
Logseries	5	0.425	<.010	5	1.256	<.100	5	1.719	<.250	6	0.330	<<.005
Broken-Stick	4	0.326	<.025	5	10.88	<.950	4	4.520	<.750	5	1.006	<.050
Lognormal	5	1.223	<.100	5	5.603	<.750	5	9.045	<.900	6	1.698	<.100
Logpoisson	5	0.240	<.005	5	0.055	<.005	6	0.431	<.005	6	0.061	<<.005
<u>Regression</u>												
<u>Log-log</u>												
Straight line	5	0.004	<<.005	6	0.091	<<.005	6	0.047	<<.005	6	0.160	<<.005
Parabola	5	0.905	<.050	6	0.081	<<.005	6	0.109	<<.005	6	0.036	<<.005
<u>Semilog retransform</u>												
Straight line	5	32.02	>>.995	6	34.16	>.995	6	47.09	>>.995	6	11.80	<.950
Parabola	5	2623.	>>.995	6	56.18	>.995	6	238.2	>>.995	6	2.880	<.250



dence against'.

Transformed semilog has the x-axis, the number of species per genus, transformed to integral logarithmic intervals to base 2. Transformed log-log data has the y-axis, the number of genera in a loginterval, also transformed to logarithms to base 2. Semilog retransform is the transformation of a fitted log-log regression line to semilog.

#### Discussion

None of the results of the untransformed data are significant on the basis of either a non-null or a null hypothesis. For birds and mammals all the alphas are much greater than 0.995, for amphibians the logseries alpha lies between 0.975 and 0.990, still within the 'significant evidence against' range..

Generally the logseries is the best fit for the untransformed data. The exception is Morris' mammal data which best fits a broken-stick distribution. But the logseries best-fit merely reflects the fact that the logseries is the steepest of the three curves and therefore lies closest to the observed points which, nevertheless, are generally below it.

This should be all that one need say were it not for the statements of Yule (1925) and Williams (1964) that the logseries fitted genus-abundance data.

Yule has tested his own data and reports chi-square alphas for chrysomelids between 0.250 and 0.500, cerambycines between 0.500 and 0.750, snakes between 0.750 and 0.900 and lizards between 0.025 and 0.050. I have recalculated Yule's chi-squares. It is not entirely clear if he has fitted his curves for snakes and lizards at one or two points and thus should use  $n-1$  or  $n-2$  degrees of freedom. Assuming one point (as he seems to have used for the insects), the snake alpha should be between 0.500 and 0.750 and the lizards between 0.005 and 0.010. Thus lizards show either a significant or a highly significant fit depending upon the degrees of freedom used.

Yule uses a null hypothesis and, since he is in all cases below an alpha of 0.950, he reasons that the log-series fits the data. (The lizards were rejected for this thesis because they lack a recent world-wide recension.)

Williams (1964) makes no tests of significance for the logseries he calculates. I have calculated the chi-square alphas for his data with the following results: mantids of the world between 0.750 and 0.900, butterflies of Australia between 0.900 and 0.950, and world fleas, world crabronids and British fishes all greater than 0.995. Thus, three of his five sets of data are non-significant even on the basis of a null hypothesis.

Therefore, with the exception of Yule's lizard data, the logseries does not fit the genus-abundance data on the



basis of a non-null hypothesis.

There are no records in the literature of previous attempts to fit the broken-stick and lognormal curves to genus-abundance data. Since these curves are, in general, flatter than the logseries they are usually poorer fits. The sole exception, as noted, being a slightly better broken-stick fit for Morris's mammal data. But both the broken-stick and lognormal curves are far beyond an alpha of 0.995 in any case.

The data transformed to semilog gives a no better fit with the exception of a logpoisson fit to the amphibian data which has an alpha between 0.250 and 0.500. In all cases the logpoisson gives a better fit than do the other curves for the semilog data. This can be attributed to the steepness of a poisson curve with a numerically small mean. But the fit is everywhere so poor that one cannot ascribe a logarithmic poisson process to the generation of the data.

The log-log transformed data presents a very interesting situation and, I believe, a decisive test of the non-null hypothesis that the data is a member of the curves tested. On the basis of the tests with random numbers already described, one would expect almost all alphas to be less than 0.050. This is precisely what we do not find. Eight, or half, of the alphas are more than 0.050.

Paradoxically, if all the log-log transforms had been 'significant' in a chi-square sense, it would be 'not

significant' since we expect this result by pure chance, having discovered that even random numbers give this result. But, since half the numbers are 'not significant' in a chi-square sense, this becomes a 'significant' result. It indicates that the logseries, broken-stick and lognormal fits are very much worse than we would expect by chance; in fact, worse than if we had used ordered random numbers for our data. In the same way, the very good logpoisson fit is no better than chance.

The 'very significant' fit of the straight and parabolic regression lines to the log-log transformed data is, again, to be expected. The retransformations of these lines is straight forward. I have not used the methods of Beauchamp and Olsen (1973) because I consider these data as populations and not samples. The retransforms are not significant.

## CONCLUSIONS

The logseries, lognormal and broken-stick distributions do not fit genus-abundance data for birds, mammals or amphibians, whether the data be untransformed or semilog transformed. The logpoisson distribution does not fit semilog transformed data. Most logseries, lognormal and broken-stick fits to the log-log transformed data is much worse than can be expected from a fit to random numbers.

Therefore, whatever process or processes generates the genus-abundance curve, it is not a random niche-boundary process (broken-stick), a niche preemption process (logseries), or a purely random process (lognormal or logpoisson).

Whether the genus-abundance and species-abundance curves are homologous and whether processes operating in ecological time also operate in evolutionary time is still moot. There is no unambiguous evidence that the mechanisms postulated to generate the logseries, lognormal or broken-stick curves are actually operating over any real natural community. If one of these mechanisms can be shown to operate universally, then the curves are not homologous. But it is still an open question whether some, as yet undescribed mechanism, may generate both distributions.

## LITERATURE CITED

- Aitchison, J., and J.A.C. Brown. 1966. The lognormal distribution. Cambridge Univ. Press, Cambridge. 176 p.
- Allen, G.M. 1939. Bats. Harvard Univ. Press, Cambridge, Mass. 369 p.
- Anderson, S. 1974. Patterns of faunal evolution. Quart. Rev. Biol. 49: 311-332.
- Anderson, S., and J.K. Jones, Jr. 1967. Recent mammals of the world: A synopsis of families. Ronald Press Co., New York. 453 p.
- Ayala, F.J., J.W. Valentine, D. Hedgecock and L.G. Barr. 1975. Deep-sea asteroids: High genetic variability in a stable environment. Ecology 29: 203-212.
- Batson, W. 1923. Area of distribution as a measure of evolutionary age. Nature 111: 39-43.
- Beauchamp, J.J., and J.S. Olsen. 1973. Correction for bias in regression estimates after logarithmic transformation. Ecology 54: 1403-1407.
- Berril, N.J. 1955. The origin of vertebrates. Oxford Univ. Press, London. 257 p.
- Bhargava, T.N., and P.H. Doyle. 1974. A geometric study of diversity. J. Theoret. Biol. 43: 241-251.
- Bishop, S.C. 1947. Handbook of salamanders. Comstock Publishing Company, Inc., Ithaca, New York. 555 p.
- Boulenger, G.A. 1882. Catalogue of the Batrachia Gradienta s. Caudata and Batrachia Apoda, in the collection of the British Museum, 127 p., Catalogue of the Batrachia Salienta s. Ecaudata in the collection of the British Museum, 503 p. British Museum, London.
- Brame, A.H., Jr. 1957. A list of the world's recent Caudata. Privately published. c/o Biol. Dept., Univ. Southern Calif., Los Angeles. 21 p.
- Brame, A.H., Jr. 1967. A list of the world's recent and fossil salamanders. Herpeton, J. Southwestern Herpetologists' Soc. 2: 1-26.

- Buchanan, R.E., and N.E. Gibbons (Editors): 1974. Bergey's manual of determinative bacteriology. Eighth edition. The Williams and Wilkins Company, Baltimore. 1246 p.
- Buchanan, R.E., J.G. Holt and E.F. Lessel Jr. (Editors) 1966. Index Bergeyana. The Williams and Wilkins Company, Baltimore. 1472 p.
- Bulmer, M.G. 1974. On fitting the poisson lognormal distribution to species-abundance data. Biometrics 30: 101-110.
- Cain, A.J. 1956. The genus in evolutionary taxonomy. Syst. Zool. 5: 97-109.
- Caldwell, R.S., and G.W. Folkerts. 1976. Variations and systematics of the Desmognathus monticola complex. Herpetological Rev. 7: 76.
- Chamberlin, J.C. 1924. The hollow curve of distribution. Amer. Natur. 58: 350-374.
- Ching, R.C. 1940. On the natural classification of the family Polypodiaceae. Sunyatsenia 5: 201-268.
- Christensen, C. 1905+. Index Filicum. Copenhagen.
- Cody, M.L., and J.M. Diamond (Editors). 1975. Ecology and evolution of communities. Belknap Press, Harvard Univ., Cambridge, Mass. 545 p.
- Cohen, A.C. 1961. Tables for maximum likelihood estimates: Singly truncated and singly censored samples. Technometrics 3: 535-541.
- Cohen, J.E. 1968. Alternate derivations of a species-abundance relation. Amer. Natur. 102: 165-172.
- Collins, J.T., J.E. Huheey, J.L. Knight and H.M. Smith. 1978. Standard common and current scientific names for North American amphibians and reptiles. Soc. for Study of Amphibians and Reptiles, Misc. Publ., Herpetol. Circular 7. 36 p.
- Conant, R. 1958. A field guide to reptiles and amphibians of the United States and Canada east of the 100th meridian. Houghton Mifflin Company, The Riverside Press, Cambridge, Mass. 366 p.
- Conant, R. 1975. A field guide to reptiles and amphibians of eastern and central North America. Second edition. Houghton Mifflin Company, Boston. 429 p.

- Copeland, E.B. 1947. *Genera Filicum. Annales Cryptogamici et Phytopathologici*, Vol. 5. Ronald Press, New York. 247 p.
- Dobzhansky, T. 1951. *Genetics and the origin of species*. Third edition. Columbia Univ. Press, New York. 364 p.
- Duellman, W. 1977. *Herpetology at the University of Kansas*. *Herpetological Rev.* 8: 30-32.
- Duméril, A.M.C., G. Bibron and A. Duméril. 1854. *Erpétologie générale*. Ten volumes. Librairie Encyclopédique de Roret, Paris.
- Dunn, E.R. 1926. The salamanders of the family Plethodontidae. *Smith College Fiftieth Anniv. Publ.*, Vol. 7., Smith Coll., Northampton Mass. 441 p.
- Editors, *New Scientist*. 1977. New owl in the Andes. *New Scientist* 76: 284.
- Ellerman, J.R. 1940. The families and genera of living rodents. Vol. 1: Rodents other than murids. Vol. 2: Murids (1941). *Publ. British Mus. (Nat. Hist.)*, London.
- Ellerman, J.R., and T.C.S. Morrison-Scott. 1951. *Checklist of Palaearctic and Indian mammals, 1758 to 1946*. *British Mus. Nat. Hist.*, London. 810 p.
- Fernald, M.L. 1924. Isolation and endemism in northeastern America and their relation to the age-and-area hypothesis. *Amer. J. Bot.* 11: 558-572.
- Fisher, R.A., A.S. Corbet and C.B. Williams. 1974. The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Animal Ecol.* 12: 42-58.
- Gleason, H.A. 1925. Species and area. *Ecology* 6: 66-74.
- Goode, H.H., and R.E. Machol. 1957. *Systems engineering: An introduction to the design of large-scale systems*. McGraw-Hill Book Company, Inc., New York. 551 p.
- Gruson, E.S. 1976. *Checklist of the world's birds*. Quadrangle/The New York Times Book Company, New York. 211 p.
- Gorham, S.W. 1974. *Checklist of world amphibians. Liste des amphibiens du monde*. New Brunswick Mus., St. John, New Brunswick. 173 p.

- Grzimek, B. (Editor). 1972. Animal life encyclopedia. Birds, Vols. 1, 2 and 3. Mammals, Vol. 2. Van Nostrand Reinhold Co., New York.
- Guppy, H.B. 1903. Observations of a naturalist in the Pacific between 1896 and 1899. Two vols. (Second vol. 1906.) The MacMillan and Co., Ltd., New York.
- Haight, F.A. 1967. Handbook of poisson distributions. Publ. in operations research, 11. John Wiley and Sons, Inc., New York. 168 p.
- Hairston, N.G. 1959. Species abundance and community organization. Ecology 40: 404-416.
- Hairston, N.G. 1969. On the relative abundance of species. Ecology 50: 1091-1094.
- Heading, J. 1970. Mathematical methods in science and engineering. Second edition. Edward Arnold (Publishers) Ltd., London. 692 p.
- Hennig, W. 1966. Phylogenetic systematics. Univ. Illinois Press, Urbana, Ill. 263 p.
- Holgate, P. 1966. Species frequency distributions. Biometrika 56: 651-660.
- Hyman, L.H. 1951. The invertebrates. Vol. 5: Smaller coelomate groups. McGraw-Hill Book Company, Inc., New York. 783 p.
- Kendal, D.G. 1948a. On some modes of population growth leading to R.A. Fisher's logarithmic series distribution. Biometrika 35: 6-15.
- Kendal, D.G. 1948b. On the generalized 'birth-and-death' process. Ann. Math. Stat. 19: 1-15.
- Kissinger, D.G. 1963. The frequency of genera of a particular size in three families of phytophagous beetles. Syst. Zool. 12: 15-19.
- Koch, A.L. 1966. The logarithm in biology I. Mechanisms generating the log-normal distribution exactly. J. Theoret. Biol. 12: 276-290.
- Koch, A.L. 1969. The logarithm in biology II. Distributions simulating the log-normal. J. Theoret. Biol. 23: 251-268.

- Kurtén, B. 1958. A differentiation index, and a new measure of evolutionary rates. *Evolution* 12: 146-157.
- Kurtén, B. 1959a. Rates of evolution in fossil mammals. Cold Springs Harbor Symp. Quant. Biol. 24: 205-215.
- Kurtén, B. 1959b. On the longevity of mammalian species in the Tertiary. *Soc. Sci. Fennica, Comm. Biol.* 21: 1-13.
- Kusnezov, N.N. 1956. A comparative study of ants in desert regions of central Asia and South America. *Amer. Natur.* 90: 349-360.
- Lack, d. 1947. Darwin's finches. Cambridge Univ. Press, Cambridge: 204 p.
- Lawrence, G.H.M. 1951. Taxonomy of vascular plants. The Macmillan Company, New York. 823 p.
- Lerman, A. 1965. On the rates of evolution of unit characters and character complexes. *Evolution* 19: 16-25.
- Linnaeus, C. 1766. *Systema Naturae*. Twelfth edition: p. 347-393. Facsimile reprint 1963. The Ohio Herpetological Soc. Published by Cushing-Malloy, Inc., Ann Arbor, Mich.
- Lynch, J.D. 1971. Evolutionary relationships, osteology and zoogeography of leptodactylid frogs. *Univ. Kansas Mus. Nat. Hist., Misc. Publ.* 5: 1-238.
- MacArthur, R.H. 1957. On the relative abundance of bird species. *Proc. Nat. Acad. Sci.* 43: 293-295.
- MacArthur, R.H. 1960. On the relative abundance of species. *Amer. Natur.* 94: 25-36.
- MacArthur, R.H. 1966. Note on Mrs. Pielou's comments. *Ecology* 47: 1074.
- MacArthur, R.H.; and E.O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, New Jersey. 203 p.
- May, R.M. 1975. Patterns of species abundance and diversity. p. 81-119. In: Cody, M.L., and J.M. Diamond (Editors). *Ecology and evolution of communities*. Belknap Press, Harvard Univ., Cambridge, Mass.



- Mayr, E. 1963. Animal species and evolution. Belknap Press, Harvard Univ., Cambridge, Mass. 797 p.
- Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill Book Company, Inc., New York. 428 p.
- Mayr, E., and D. Amadon. 1951. A classification of recent birds. Amer. Mus. Novitates 1496: 1-42.
- Mayr, E., E.G. Linsley and R.L. Usinger. 1953. Methods and principles of systematic zoology. McGraw-Hill Book Company, Inc., New York. 336 p.
- Michener, C.D., and R.R. Sokal. 1967. A quantitative approach to a problem in classification. Evolution 11: 130-162.
- Moroney, M.J. 1956. Facts from figures. Third edition. Penguin Books Ltd., Harmondsworth, Middlesex. 472 p.
- Morris, D. 1965. The mammals: A guide to living species. Harper and Row, New York. 448 p.
- Morse, P.M. 1965. Queues, inventories and maintenance. The analysis of operational systems with variable demand and supply. Publ. in operations research, 1. John Wiley and Sons, Inc., New York. 202 p.
- Paradiso, J.L. 1968. Mammals of the world. Second edition [of Walker 1964] of Vols. 1 and 2. The Johns Hopkins Press, Baltimore.
- Paradiso, J.L. 1975. Mammals of the world. Third edition [of Walker 1964] of Vols. 1 and 2. The Johns Hopkins Univ. Press, Baltimore.
- Peters, J.L. 1931+. Checklist of the birds of the world. Mus. Comp. Zool., Harvard Univ., Cambridge, Mass.
- Pielou, E.C. 1966. Comment on a report by J.H. Vandermeer and R.H. MacArthur concerning the broken stick model of species abundance. Ecology 47: 1073-1074.
- Pielou, E.C. 1975. Ecological Diversity. Wiley Interscience Publ. John Wiley and Sons, Inc., New York. 312 p.
- Pielou, E.C., and A.N. Arnason. 1965. Correction to one of MacArthur's species-abundance formulas. Science 151: 592.

- Platnick, N.I. 1976. Are monotypic genera possible? *Syst. Zool.* 25: 198-199.
- Pough, R.H. 1949. Audubon bird guide. Small land birds of eastern and central North America from southern Texas to central Greenland. Nat. Audubon Soc. Doubleday and Company, Inc., Garden City, New York. 312 p.
- Poynton, J.C. 1964. The Amphibia of southern Africa: A faunal study. *Ann. Natal Mus.* 17: 1-334.
- Preston, F.W. 1958. Analysis of the Audubon Christmas counts in terms of the lognormal curve. *Ecology* 39: 620-624.
- Preston, F.W. 1960. Time and space and the variation of species. *Ecology* 41: 611-627.
- Preston, F.W. 1962. The canonical distribution of commonness and rarity. *Ecology* 43: Part 1: 185-215. Part 2: 410-432.
- Preston, F.W. 1969. Diversity and stability in the biological world. Brookhaven Symp. in Biol. 22: 1-12.
- Raup, D.M., S.J. Gould, T.J.M. Schopf and D.S. Simberloff. 1973. Stochastic models of phylogeny and the evolution of diversity. *J. Geol.* 81: 525-542.
- Rensch, B. 1960. Evolution above the species level. Columbia Univ. Press, New York. 419 p.
- Romer, A.S. 1966. Vertebrate paleontology. Third edition. Univ. Chicago Press, Chicago. 468 p.
- Romer, A.S. 1968. Notes and comments on vertebrate paleontology. Univ. Chicago Press, Chicago. 304 p.
- Rudwick, M.J.S. 1970. Living and fossil brachiopods. Hutchinson Univ. Library. Hutchinson and Co. (Publishers) Ltd., London. 199 p.
- Salthe, S.N., and N.O. Kaplan. 1966. Immunology and the rates of enzyme evolution in Amphibia in relation to the origin of certain taxa. *Evolution* 20: 603-616.
- Schmidt, K.P. 1953. A checklist of North American amphibians and reptiles. Sixth edition. Amer. Soc. Ichthyologists and Herpetologists. Univ. Chicago Press, Chicago. 280 p.

- Schmidt, K.P. 1955. Herpetology. p. 591-627. In Babcock, E.B., J.W. Durham and G.S. Myers (Editors). A century of progress in the natural sciences, 1853-1953. Calif. Acad. Sci., San Francisco.
- Selander, R.K., S.Y. Yang, R.C. Lewontin and W.E. Johnson. 1970. Genetic variation in the horse-shoe crab (Limulus polyphemus), a phylogenetic relict. *Evolution* 24: 402-414.
- Selby, S.M. (Editor). 1970. Standard mathematical tables. Eighteenth edition. The Chemical Rubber Co., Cleveland, Ohio. 724 p.
- Sever, D.M. 1972. Geographic variation and taxonomy of Eurycea bislineata (Caudata, Plethodontidae) in the upper Ohio valley. *Herpetologica* 28: 314-324.
- Sever, D.M., H.A. Dundee and C.D. Sullivan. 1976. A new Eurycea (Amphibia: Plethodontidae) from southwestern North Carolina. *Herpetologica* 32: 26-29.
- Simberloff, D.S. 1970. Taxonomic diversity of island biotas. *Evolution* 24: 23-47.
- Simberloff, D.S. 1972. Models in biogeography. p. 160-191. In Schopf T.G.M. (Editor). Models in paleobiology. Freeman, Cooper and Company, San Francisco.
- Simpson, G.G. 1944. Tempo and mode in evolution. Columbia Univ. Press, New York. 237 p.
- Simpson, G.G. 1945. The principles of classification and the classification of mammals. *Bull. Amer. Mus. Natur. Hist.* 85: 1-350.
- Simpson, G.G. 1953. The major features of evolution. Columbia Univ. Press, New York. 434 p.
- Simpson, G.G. 1961. Principles of animal taxonomy. Columbia Univ. Press, New York. 247 p.
- Simpson, G.G. 1969. The first three billion years of community evolution. *Brookhaven Symp. Biol.* 22: 162-177.
- Sinnot, E.W. 1924. Age and area and the history of species. *J. Bot.* 11: 673-578.
- Slobodkin, L.B. 1961. Growth and regulation of animal populations. Holt, Rinehart and Winston, Inc., New York. 184 p.

- Slobodkin, L.B. 1968. Toward a predictive theory of evolution. P. 187-205. In: Lewontin, R.C. (Editor). Population biology and evolution. Syracuse Univ. Press, Syracuse, New York.
- Smith, H.M., D. Chiszar and R.B. Smith. 1978. Rate of accretion of taxonomic nomenclatural errors in the postlinnaean literature on Mexican amphibians. J. Herpetol. 12: 337-341.
- Smith, J.M. 1976a. A comment on the red queen. Amer. Natur. 110: 325-330.
- Smith, J.M. 1976b. What determines the rate of evolution. Amer. Natur. 110: 331-338.
- Sneath, P.H.A. 1974. Phylogeny of micro-organisms. p. 1-36. In: Carlile, M.J., and J.J. Skehel. (Editors). Evolution of micro-organisms. Twenty-fourth symposium of the Soc. for Gen. Microbiology. Cambridge Univ. Press, Cambridge.
- Sokal, R.R., and P.H.A. Sneath. 1963. Principles of numerical taxonomy. W.H. Freeman and Company, San Francisco. 359 p.
- Thomson, Sir A.L. 1964. A new dictionary of birds. British Ornithologists Union. Nelson and Sons, London. 928 p.
- Van Valen, L. 1963. The origin and status of the mammalian order Tillodontia. J. Mammal. 44: 364-373.
- Van Valen, L. 1971. Adaptive zones and the orders of mammals. Evolution 25: 420-428.
- Van Valen, L. 1973. A new evolutionary law. Evolutionary Theory 1: 1-30
- Van Valen, L. 1974. Predation and species diversity. J. Theoret. Biol. 44: 19-21.
- Vandermeer, J.H., and R.H. MacArthur. 1966. A reformulation of alternate (a) of the broken stick model of species abundance. Ecology 47: 139-140.
- Walker, E.P. (Editor). 1964. Mammals of the world. Three volumes. The Johns Hopkins Press, Baltimore.
- Walters, S.M. 1961. The shaping of angiosperm taxonomy. New Phytol. 60: 74-84.

- Wake, D.B. 1966. Comparative osteology and evolution of the lungless salamanders, Family Plethodontidae. Mem. Southern California Acad. Sci. 4 1:1-111.
- Webb, D.J. 1974. The statistics of relative abundance and diversity. J. Theoret. Biol. 43: 277-291.
- Webb, S.D. 1969. Extinction-origination equilibria in late Cenozoic land mammals of North America. Evolution 23: 688-702.
- Whittaker, R.H. 1969. Evolution and diversity in plant communities. Bookhaven Symp. Biol. 22: 178-195.
- Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21: 213-251.
- Willey, B. 1934. The seventeenth century background: Studies in the thought of the age in relation to poetry and religion. Doubleday Anchor Books reprint 1953. Doubleday and Company, Inc., Garden City, New York. 316 p.
- Williams, C.B. 1964. Patterns in the balance of nature. Academic Press, New York. 324 p.
- Willis, J.C. 1922. Age and Area. Cambridge Univ. Press. Cambridge. Reprinted 1970 by A. Ascher and Vaals, Amsterdam. 259 p.
- Willis, J.C. 1940. The course of evolution by differentiation or divergent mutation rather than selection. Cambridge Univ. Press, Cambridge. 207 p.
- Wimsatt, W.A. 1970. Biology of bats. Three volumes. Academic Press, New York.
- Winer, B.J. 1962. Statistical principles in experimental design. McGraw-Hill Book Company, New York. 672 p.
- Wright, S. 1932. The role of mutation, inbreeding, cross-breeding and selection in evolution. Proc. Sixth Internat. Congr. Genetics 1: 356-366.
- Wright, S. 1941. The 'Age and Area' concept extended. Ecology 22: 345-347.
- Yule, G.U. 1925. A mathematical theory of evolution based on the conclusions of Dr. J.C. Willis. Roy. Soc. (London), Phil. Trans., B, 213: 21-87.