Quantitative Evolution. XVII.
The Shape and Pattern of Evolution.

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(With 1 Figure in the Text)

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This is not a theoretical discussion of hypothetical methods of evolution. It is a factual analysis of the details of patterns which together have historically resulted in certain common and generally recognised "shapes" for total numbers of kinds of organisms within "groups" in relation to time. Time, on a million-year (m. y.) scale, has been one of the major factors in the development of diversity within groups of related organisms.

The common "shape" of evolution is well known and has been presented in many readily recognisable forms by those who have considered the histories of groups of families or genera or even species. But the pattern details which have given rise to this shape are only beginning to be recognised and presented in specific details (SMALL 1945—1949).

The common "shape" of a group in time is usually given as total numbers of "kinds" in any one category graphed against some kind of time-scale. ZEUNER 1946 a and b, and RENSCH 1947 have brought together a number of such "shapes", and RENSCH 1947:fig. 22 has made a beginning to analysis of the inner pattern by distinguishing between (a) the new element in each period-quota and (b) the total older element which has continued from previous periods of time. But RENSCH does not go further into such details of pattern, and does not distinguish the durations of the long-lived elements in each geological period. He never considered that type of duration, as "short" or "long", could be an inherited characteristic of species and consequentially of genera and larger groups, as has been proved for diatoms in particular (SMALL 1945, 1948 a). Species-duration as an innate characteristic of species is of fundamental significance for the proper understanding of evolution in general and particularly for analysis of the patterns in time.

The Shape

The common "shape" of a genus in time is given in fig. 1, as "Totals" graphed against a uniform time scale and dissected into four parts or phases, A, B, C, and D.

Phase-A is a meagre first stage during which increase was slow and total numbers were low (ZEUNER 1946: "lag phase").

Phase-B has attracted much attention because of the rapid increase in total numbers of diverse kinds of organisms; in the genus these "kinds" are species, but phase-B is well-known for higher categories also, such as genera within families and families within orders. Many still uncompleted "shapes" show only these first two phases, even after long periods of time, especially in the higher categories of still expanding families or orders.

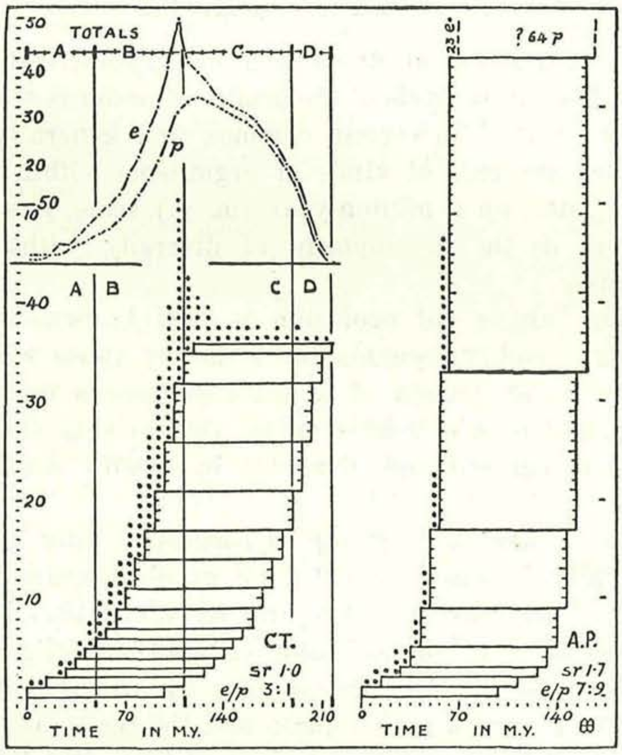

Fig. 1.
(For explanation see text.)

Phase-B has been rather enthusiastically described as "explosive" (see RENSCH 1947: 97; ZEUNER 1946 a and b; and others), also "eruptive" (CLOUD 1948:322), but on a purely objective view phase-B is the phase of increase in numbers of "kinds" and in diversity of "kinds" within the main category. In genera and larger groups of diatoms this increase has been a geometric progression in numbers of species (SMALL 1946, 1948 a and b).

These first two phases of increase (A—B) have, in many genera and in a small proportion of families and orders, been followed by two other phases, C and D.

During phase-C the group is maintained at a high level of diversity and of numbers of kinds (species in fig. 1) by the continued existence of kinds produced during earlier periods of time. This is quite obvious in all the diagrammatic histories given by RENSCH 1947:fig. 22 for orders, families, and genera of various groups of animals, and it becomes obvious when the fossil history of plants is graphed on a uniform time-scale either from the Tables of geological distributions by SEWARD 1933 or from the phylogenetic diagrams given by ZIMMERMANN 1930: fig. p. 28 and LAM 1936:160, fig. 6; also 1948. Some groups of plants show only phases A—B as a whole, but contain within this general expansion some elements (genera or families) which show phases C and D. The phase-C has been described for evolution in general as the stage of "dominance", or "crystallisation" (SCHILLINGER 1948), but RENSCH considers that this phase is one of "specialisation". From a purely objective point of view, phase-C is one in which the number of diversified kinds is maintained by forms which in themselves are not undergoing specific changes and which, in this sense, may be said to have "crystallised" or biologically attained a fixed distribution in all their available and appropriate ecological niches. Phase-C may be described objectively as the phase or stage of "maintenance".

Phase-D is the stage of abrupt decrease with a high rate of extinction. This phase-D has attracted much attention and has for long been regarded as somewhat mysterious. SCHILLINGER 1948 points out that "disintegration" follows "crystallisation", and so connects phase-D with phase-C. RENSCH 1947:228—240 considers this phase-D under the heading of over-specialisation, degeneration, and extinction. So far as the genus, or other main category, is concerned phase-D is objectively "disintegration" of the group; historically this is brought about by extinctions of units of the group within a period which is usually shorter than the period of increase (phase-B). It should be noted that the occurrence of phase-D is a logical consequence of the origins, during phases A—B, of long-lived species which are of more or less equal duration and arise in a geometric progression of quotas for equal periods of time. The subsequent geometric progression in extinctions is in this case inevitable, and is in itself no mystery. This is not theory: it is part of the known generic history of diatoms (SMALL 1945—1949). How it happens that long-lived species have had somewhat similar durations of about 100 m. y. in both diatoms and foraminifera (SMALL 1946—1948) is still unexplained, but that particular duration does seem to be usual within the limits of 100 ± 20 m. y.

The Pattern

The pattern within the general shape has, as yet, been worked out in specific detail only for diatoms, but many other groups show enough of the same kind of detail to indicate that the pattern for diatoms has a basic significance, and a basic similarity to what has happened elsewhere in both plants and animals. The modifications and variations in detail for land organisms do not seem have affected the numerical end-products very much, as is explained below.

The construction of the diagrams in fig. 1 is based upon the regularities of generic patterns which have been measured in diatom fossil history. Imperfections in the fossil record cannot now be pleaded as an excuse for disregarding the mass of complex regularities disclosed as "rules-within-limits" among the numerical data for numbers and durations of species and genera of diatoms. On the contrary these "rules-within-limits" can be used for extended work in other groups.

The main phenomena used in the diagrams of fig. 1 are as follows:

1. Species-durations have been of two types, "short" (**e**) or "long" (**p**): in diatom history "short" has been mainly not more than 7 m. y. down to less than 1 m. y. (m. y. = million-years); while "long" has been mainly from origin to Recent.
2. The proportion of "shorts" to "longs", or the **e**/**p** ratio, has been 3/1 for *Centrales* diatoms (CT.) and 7/9 for allogamous *Pennales* (A.P.).
3. The history of diatom species has been monopodial in that parental **p**-species have continued in living existence after having produced new species from one or more of their individual organisms (macromutation in unicells). Therefore the rate of speciation has been measured as **sr** = A/O, where **sr** = speciation-rate per subperiod of about 7 m. y., A = number of new species arising in any given subperiod, and O = number of old **p**-species present as possible parents. The speciation-rates, determined in this way for the subperiod quotas of each genus and for the two groups of diatoms in total subperiod quotas, have been about 1.0 for *Centrales* and about 1.7 for allogamous *Pennales*. These **sr** values give the basic rates for increase per subperiod, but the new species arising in each subperiod must be divided into **e**-species which have not continued beyond their subperiod of origins (dots ... in fig. 1), and **p**-species which have continued for about 100 m. y. or 14 of the 7 m. y. units on the uniform basal time-scale, (rectangles in fig. 1, with uncompleted rectangles in blocks where the height of the rectangular block indicates the number of new **p**-species in each subperiod quota). This division of each quota into short-lived and long-lived species is determined by the **e**/**p** ratio.

Following these three "rules-within-limits" the pattern for phases A—B develops as a numerical filling-up for the first part of the graph for "Totals" above "CT". in fig. 1. Then, in accordance with what has happened historically in some old genera of centric diatoms, the production of **p**-species stops, either abruptly or gradually, relatively soon after the extinction of the first **p**-species in the genus. Thus the series of origins for **p**-species in *Centrales* runs 1-1-1-1-1-1-1-2-2-3-3-4-5-6-0 or the end may be gradual -4-5-6-3-1. The series for **e**-species is determined by the total number of **p**-species available as parents during phases A—B, but as a matter of observed history very few new **e**-species are produced after the production of **p**-species has stopped, and this has occurred just after the extinction of the first one or two **p**-species in the genus.

Meanwhile, the early **p**-species become extinct, one at a time over a period of 6 or 7 subperiods, as in *Aulacodiscus* (SMALL 1945 b: 31—40, Table I, 3). This slow rate of extinction means that the generic size is maintained for a long time. Then in the later part of phase-C the **p**-species extinctions begin to occur as 2-2-3-3; and the phase-D of rapid disintegration to total or subtotal extinction develops with extinctions of -4-5-6-3 — in only four subperiods. The last -1 **p**-species, continuing for seven million-years after the rest of a once large genus has become extinct, is another phenomenon which has received much attention. *Latimeria chalumnae* and *Metasequoia glyptostroboides* are only two recently found examples of a large class of monotypic relict genera.

These specific details, as worked out for CT. on the basis of **sr** = 1.0 and **e**/**p** ratio of 3/1, are added up for each subperiod unit; and the "Totals" for **p**-species yield the lower graph, while the "Totals" for **p** + **e** species yield the upper graph directly above the CT. diagram and on the same horizontal timescale. These graphs for the "Totals" present the common "shape" of evolution for a genus or some larger very old categories. The specific details given below present the new analysis of that shape in terms of a "pattern" of long-lived species of defined durations, combined with short-lived species of durations which do not go beyond their subperiod of origin.

The A. P. diagram is built up along the same lines, with **sr** = 1.7 and the **e**/**p** ratio 7/9, in accordance with the values found for allogamous *Pennales*. These values yield an $x2^n$ increase per subperiod for **p**-species, thus 1-1-1-2-4-8-16-32-64, which has already given not a few large genera in this relatively young group. An observed increase from 3 A. P. in Paleocene to 3500 A. P. in Recent follows very closely this geometric progression (SMALL 1949 b), and the basal genus *Navicula* has a known history very like the first half of the A. P. diagram of fig. 1 (SMALL 1948 c). The A. P. diagram is historically factual in its first two phases A—B, but beyond the 77 m. y. vertical it is merely a possible future extension similar to the facts of the CT. diagram for which history is available in younger genera for phases A—B, in some genera for phases B—C, and in a few genera for phases C—D; so that the complete pattern for a genus can be built up, by combining the available parts into one whole "pattern" for the complete generic history of the well known "shape".

The few genera showing the phases C—D include *Hemiaulus, Trinacria, Aulacodiscus,* and probably *Asterolampra.* The "youth" of allogamous *Pennales* is shown, not only by its Paleocene beginning with only 3 species (*Navicula* spp.), but also by its history, since there are only 5 extinct genera out of 49 with fossil-and-Recent records, as compared with 61 extinct genera out of 114 with fossil-and-Recent records in *Centrales.*

The combination of a comparatively high speciation-rate with a high proportion (9 out of 16) of long-lived species has made allogamous *Pennales* an exceptional group, while the end-products of the arithmetical history of *Centrales* compare closely with other groups of plants and animals.

The Significance of Shape and Pattern

The facts concerning the quantitative history of the diatoms, including a mass of demonstrated regularities as rules-within-limits, emerged from a completely objective collection and tabulation of the fossil records which are particularly abundant for this group of organisms. This long piece of work was undertaken because of the many theoretical possibilities for explaining previous quantitative results (SMALL 1937—1938). The kinds of regularities which have been found were completely unexpected, and in some cases are incompatible with current theoretical dogmas, some of which are now undergoing changes. In particular, the once dominant neo-Darwinian dogma of universal sympodial evolution is now being abandoned by at least some neo-Darwinians. It is no longer positively asserted that the origin of a new species necessarily involves the extinction of the parent species, and it is now widely recognised that there have been and are species of very long duration. Indeed it is not now necessary to demonstrate monopodial evolution involving both fixity and mutability for these long-lived species, (see SMALL 1948 b).

RENSCH 1948: 86—88 gives 3 species of mastodons with durations of 5—8 m. y., and quotes a few of the many species of marine molluscs with durations of 6—25 m. y. MAYR 1942:224 noted both short and very long species-durations for insects and other groups. Long and short species-durations have long been known for marine organisms, and have been recorded by many diatomists, and for *Foraminifera* (CUSHMAN 1948; GLAESSNER 1945; etc.). The same phenomenon for genera and families has been widely recognised, and long durations are noted by RENSCH 1947:84—85 in terms of 25—540 m. y.

All these long durations and monopodial evolutionary developments show that it is a mistake to assume, as SIMPSON 1944 did, that there has been in any one period a 1:1 correlation of origins and extinctions.

HUXLEY 1943, in his tabulation of (a) modes of speciation and (b) separation of new species, gives first the sympodial succession in time with gradual separation, which has dominated evolutionary thought since 1858; but most of his Table (1943:386) is occupied by other modes, many of which involve abrupt, instead of gradual, separation of new species. These abrupt modes of speciation are regarded sceptically by neo-Darwinians, but LÖVE and LÖVE 1943, 1948 have demonstrated the occurrence of polyploidy in 74 per cent of the monocotyledons and in 50 per cent of the dicotyledons of their whole northern area. Polyploidy is definitely an abrupt mode of speciation and so also are various other methods classed as genetic by HUXLEY 1943. The history of diatoms does not prove that the gradual successional modes have never occurred in other groups, but the various regularities demonstrated for diatoms definitely prove that it has been possible for a large group, of mainly marine unicellular plants, to develop without natural selection acting at the specific or generic levels either in the regular origins or in the regular extinctions of species. Species-durations in diatoms have very definitely been genetically fixed within certain limits, as short or long, and there is no place here for natural selection, except in so far as some types have been limited in their distribution to particular kinds of ecological "niches", such as large ocean currents, estuarine muds, epiphytic substrata, freshwater lakes of varying mineral content, etc. As HENDEY 1937:207 (seee also SMALL 1948a:309) has shown, diatom species have variants within the specific orbit, and there are phases under given sets of environmental conditions and also according to the stage of vegetative multiplication, but the specific pattern is fixed and has a fixed duration in time, short or long (SMALL 1945—49).

It is fairly obvious that the genetic development of diatoms has taken place in the absence of some disturbing factors; this development has occurred in organisms which are unicellular and autotrophic, living bathed in solutions of inorganic food, mainly in the oceans which have not varied in composition during Tertiary time beyond the range of present-day local differences, (see CONWAY 1942). In these circumstances, and with the large degree of completeness of our knowledge of the Tertiary records for diatoms, it has been possible to obtain convincing numerical data which demonstrate arithmetically the working of fundamental rules-within-limits.

When relatively large numbers show regular relations, and when these numbers can be analysed out as series of smaller numbers which still show something like the same regular relations, there must be some significance in the relations of the numbers. With very small numbers, the principle of a "nearest approach" with a given small quota must be used : a simple example is the 3:1 ratio which is exactly possible only with 4 or multiples of 4; with only 7 units available the proportions of

6/1 = 6 and 5/2 = 2.5 are the two nearest approaches to the ratio 3:1, and so on (see SMALL 1948 a:264). Using this principle, many regularities have been disclosed during a close study of the known geological history of diatoms, and parts of the phenomena found among diatoms have been seen in many other groups.

When the dogma of compulsory and universal sympodial development for species is removed, as unjustified by the facts, a certain degree of freedom is attained in the understanding of numerical developments. For example, it becomes possible and obvious that one can measure production rates for species, genera, or other categories by the ratio A/O, where A is the number of new members of any one category, and O is the number of old but still living members of the same category. When this value A/O is referred to a uniform length of time which is short in relation to the speed of production, such as 10 million-years, then $A/O \times 10/T$ yields values which are comparable for all periods of time and for all categories of groups. This has been done for diatoms, foraminifera, and bivalve molluscs (SMALL 1948 b).

Variations and modifications of these rules-within-limits, such as the **e/p** ratios and the speciation-rates, are to be expected, but the extent to which such variations and modifications, of basic essentially numerical rules-within-limits, have altered the end-products (the answer to all these additions, subtractions, and multiplications) can be measured. The answer to the sum, the result of these arithmetical processes acting for the duration of the group up to the present time, is the frequency distribution of present generic sizes, or FDGS for Recent. This distribution can be made comparable for all groups by reducing the known distribution to a percentage basis and grouping the generic size-classes so that there is a minimum of dispute about which genera are to be put into a particular size-class. Such disputes often refer to large genera, so a size-class of over-40 puts all these genera into the same size-class. Similarly, with very small genera there is sometimes a difference of opinion as to whether there are 2 or 3 species in the genus, and this dubiety is avoided by having one 2—3 size-class. When the other sizes of genera, as measured by their numbers of species, are grouped as 4—8, 9—20, 21—40; and the number of genera in each size-class is reduced to a percentage of the total genera in the group, this percentage FDGS for Recent becomes comparable with similar frequency distributions for other groups. This is just one more application of WILLIS's "Hollow Curve" (WILLIS 1922 and 1940, and YULE 1924), and some of the results are as follows (Table I).

An examination of Table I will show that the allogamous *Pennales* FDGS differs more from that of the *Centrales* than any of the other three groups given, although these three include families from the highest group of plants and one family from the highest group of animals. The allogamous *Pennales* is known to have had an arithmetical history which has differed in the values of its constants from that of *Centrales*, therefore a different end-product is to be expected. Conversely the fact that the *Muridae* is almost the same as *Centrales* for the size-classes —1, 4—8, and 9—20 — must be considered as strong evidence in favour of the *Muridae* having had an arithmetical history very similar to that found for *Centrales*. The same argument applies more or less forcibly for *Compositae*, *Gramineae*, and any other group for which the percentage FDGS for Recent comes within the Key given at the top of Table I. This Key, with its ± ranges for diminishing percentages as the size-classes increase in value, is based upon the Tertiary history of fluctuations in the FDGS for *Centrales* (SMALL 1948 c), which was found to have varied historically since Oligocene within the limits specified.

Table I.

Percentage Frequency Distributions of Present Generic Sizes.

Present Size-groups	1	1—3	2—3	4—8	9—20	21—40	over 40
KEY %	—	58	—	22	10	6	4.5
range ±%	—	7	—	6	5	3	2.5
Diatoms							
Centrales	34	54	20	19	11	5	11
Allog. *Pennales*	15	32	17	22	20	7	19
Compositae	32.5	53.5	21.0	20.3	14.7	5.5	5.6
Gramineae	32.6	53.6	21.0	20.9	12.5	5.9	6.8
Muridae	33.9	60.5	26.6	18.2	10.9	6.3	4.1

Long durations for species are particularly well known among the micropaleontological records and among marine organisms, but they are known also among fossil higher plants as given for some species within genera in the Tables of geological distributions by SEWARD 1933. When SEWARDs Tables for various parts of the geological record are re-set to read continuously, it becomes obvious that the historical development of the plant kingdom has been more or less monopodial, for species within genera, for genera within families or orders, and for phyla none of which are yet extinct. Even with LAMs 1948 phyla there is no phylum which is yet extinct. The extinct plant groups are mainly some early branches of still living main branches of the whole "tree". Among animals there are some extinct phyla, but there are living representatives of most animal phyla. This degree of monopodiality in larger groups and even among genera has long been recognised, but it is only recently, as a result of cytogenetic studies, that neo-Darwinians have admitted that evolution could be monopodial so far as species are concerned.

Given these possibilities the well known "shape" of evolution can be analysed into the specific details of the "pattern" which can be re-synthesised into a general "shape". Then the form of the general "shape" is seen to depend largely upon the width or duration of phase-C which in its turn depends upon the durations of long-lived species (fig. 1, CT.), or upon the duration of constituent units when families or other higher categories are being graphed.

This form of curve, with an exponential rise followed by an exponential decrease, is the mirror-image of one of the curves for output voltage when a rectangular pulse is given to a basic **RC** network with both resistance (R) and capacitance (C) across the output, in some oscillograms. When the pulse width is large compared with the time constant of the network; that is when, with R + r constant, r/R is greater than one for the rectangular pulse of a duration T which is greater than (R + r) C[1]); the mirror image of the "Totals" curve, for **p**-species in fig. 1, appears; so this type of curve is not altogether unknown in the physical world (see FRANK 1945:figs. 17 and 41). The relative duration of a "pulse" is a factor in both curves; the biological pulse being the aromorphic appearance of a new generic or familial form.

This biological "pulse" involves all systemic changes in categories higher than species, which in comparison merely diversify within the generic limits. The passage from one genus to the next (nearest) may be only of specific rank in some disputed cases, but most genera are separated by gaps of more than specific width. The changes which produce most genera, most families and most orders, are qualitative rather than quantitative. These changes have been distinguished as "aromorphic (SEWERTZOFF, see ZEUNER 1946 a) and as "Anagenese" by RENSCH 1947 who contrasts this with "Kladogenese" or the working out of the potentialities of a given pattern at the specific or generic level, which is the subject of the present contribution.

Since the length of **p**-species duration governs the rate of generic decay in phases C—D, and therefore the 'shape' of these phases (fig. 1, CT. and graphs of Totals), it becomes possible to deduce from the graph of "Totals in time" for any given genus the extent to which the genus has been maintained in time by the continued existence of species with long durations. This gives an added interest to comparisons of generic graphs with high narrow peaks, such as that of *Salenia* (ZEUNER 1946 a:fig. 98) and similar graphs for species or genera with broad tops, such as those for *Lingula* and *Poiretia* (ZEUNER 1946:figs. 5 and

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[1]) R = resistance parameter, C = capacitance parameter, $RC = \frac{Vt}{q} \times \frac{q}{V} = t \rightarrow$ time; r = internal generator resistance, V = voltage, t = time, q = instantaneous charge.

13) and for various genera, families, and orders (RENSCH 1948:113, fig. 22). As a rule, the higher categories have relatively wider maxima in relation to time, but there have been some short-lived families in which monopodial evolution can be detected even when generic durations have not been longer than their period of origin, such as parts of the *Fusulinidae* among *Foraminifera* (see CUSHMAN 1948; and GLAESSNER 1945:199).

This brings out an obscure but important point, namely, that the clarity of the "diatom diagram" as expounded by SMALL 1945—49 depends largely upon the low speed of speciation in relation to the length of the available subperiod units of time. If speciation in diatoms had been so rapid that the time concerned could not be divided into a readily recognisable sequence for deposits, then the regularities would not have emerged as known facts. Similar work in other groups, therefore, requires a knowledge of the chronological sequence of deposits, which is close enough to permit the division of the total time into subperiods short enough to show whether the speciation has been sympodially successional or monopodially genetic. Much of the so-called successional evidence depends upon rather long intervals of time between the so-called successive stages in lineages with relatively high production-rates. In marine micropaleontological data, changes have usually been slower and, therefore, the monopodiality of speciation in such groups is more clearly demonstrable.

Summary

1. The common numerical geological history of a genus, or larger group of related species, has taken the form of an optimum curve with (a) some "skewness" on the right or later half of the curve, and (b) some hollowness in the left or earlier half of the curve, when the total numbers existing are graphed upon a basal uniform time-scale. This is the most usual "shape" of evolution for an extinct or almost extinct group or genus, but many living groups and genera show only the first parts of the complete shape.
2. This "shape" is here analysed into a "pattern" of species (or genera) with either short or long durations measured on a time-scale with one million years (m. y.) as the unit.
3. It is demonstrated that these two types of durations, when combined with a geometric progression of origins, fully account for the details of the common shape of the curve for numerical histories.

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