XIII. — ON THE NATURE OF SYSTEMATICS AND BIOGEOGRAPHY. — I. THE WILLIS-CURVE

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Since the appearance of „Age and Area" by Dr. J. C. Willis in 1922 the progress in this matter has not been so great as before. From the contribution of a few chapters by some well-known biologists, and from many approving remarks by others quoted throughout the book one might derive that the theory of origin and evolution of species, etc., presented in it, had already a remarkable success. But there is also a whole chapter in the book, containing the diversified objections, to which Dr. Willis makes head. The „very strong evidence based upon definite facts, not upon *a priori* reasoning", however, required by Willis (p. 233), has turned out to be more of a repetition of the same statements with more or less different materials than of the discovery of conclusive facts. The situation seems to us best characterized by quoting Dr. Ph. P. Calvert's (1923) statement: „..., I fail to find the key to the origin and evolution of species with the ease which Dr. Willis's commendation of Age and Area would lead me to expect, and which I would welcome if the key but turned in the lock".

It is of no use trying to entangle all the controverses to which the theory gives cause: they are almost without exception of the nature of putting one probable explanation against the other. Dr. Willis could easily refute them, because the objections were so fragmentary. Therefore the only way promising results in finding the real meaning of Willis's statements must consist in the analytical examination of them.

The most striking result and attribute of Willis's considerations, of course, is the „hollow curve", which we propose to term the „Willis-curve". It is a representation of the frequency-distribution of systematic units (of species, genera, or families) when arranged to their geographic range of dispersal or to their size (number of species per genus, or genera per family), which always has the same shape, called the J-shaped frequency-distribution by Yule (1927). The lowest class appears invariably with the highest frequency, the curve firstly very steeply sloping down but gradually slackening, thus tapering away. „The hollow curve is apparently a universal principle of distribution, whether it be distribution in space — geographical distribution — or distribution in time — evolution" (Willis, 1922, p. 199). In the last quotation the size of a genus or a family is already mentioned in the terms of the explanation given by the theory of „age and area", in which the number of species of a genus, etc., should be proportional to its age. This is based upon the implication that species should give rise to new species, and also genera to new genera at a considerably constant rate, the monotypic genera thus being the youngest. We must add, of course, that this can only be true in the main, as in the theory is most strongly laid stress on. Furthermore it is held that this principle should be accounted for in general, so that it is wrong to apply the theory to individual cases.

The frequency-distribution according to size of genera or families forms the special subject of the present paper. Its explanation, just mentioned above, has been chiefly based upon two main factors: 1. the coincidence of small sizes of genera or families with small areas occupied, and of large sizes with large areas, on the assumption that the younger a species is the less time it will have had to spread and 2. the peculiar regularity of the curve, so as to suggest a continual accumulation of new species and genera according to a compound-interest law. Thus time being the master-factor, although it can do nothing in itself.

It is obvious that such a statement involves largely hypothetic assumptions on the nature and occurrence of mutations, on the influence of ecological factors, and on the responses to them by the orgamisms. Here we only want to mention that in genetics it has been the general experience that the most regular frequency-distributions have always proven to be the result of the coöperation of just a number of factors (cf. Johannsen, 1926). This, however, is a statement concerning the probable truth of the theory with which nothing decisive can be reached. It would be a criticism of a similar insufficiency as those already existing. The only way out is to trace the limitations of the principles implied, because in these principles are contained the characteristics of the theory which cannot be found elsewhere.

Now we must bear in mind that in studying systematic units of organisms, we are dealing with units of things capable of mutation, living in a certain environment, etc.; all sorts of peculiarities occurring nowhere else. The systematics of organisms is quite another thing than that of crystals, but we may apply a method similar to the systematics of organisms to anything else. An excellent description of this method is given by Tschulok (1922) in his „Deszendenzlehre" in which he describes the nature of natural systematics. In contrast with any artificial systematization of objects varying at some rate or other and in any direction, by grouping them according to a certain set of principles determined beforehand, the natural systematization is carried out with no other aim than of taking together those objects which in regard of the variability of the whole group are more similar to each other than to the rest. Supposing that all objects are in a way different but all must be regarded in a sense as belonging together, we may have within this group a varying similarity and dissimilarity, which after systematization will become apparent in the different groups obtained. If then these groups are arranged in regard to their size, a frequency-curve must be the result. If now the Willis-curve is an expression of the ability of organisms to mutate at a certain rate, to spread in the course of time, etc., we may expect a different curve to result from a group of different objects systematized in a similar way as is now generally done with organisms.

In our opinion gravel is a kind of material excellently suitable for our purpose; all the pebbles are of the same origin (if taken from the same locality, e. g., from a newly graveled pathway, which did not contain it before, as we took it from). In this case all the objects may be considered as belonging to the same family and lastly all pebbles are varying sufficiently that they may be sampled into different groups of varying size, and not a single pebble can be considered as being as similar to another that the two must be judged as being identical. Thus we may consider each pebble as a species, each group of pebbles as a genus, and the whole group as of the rank of a family.

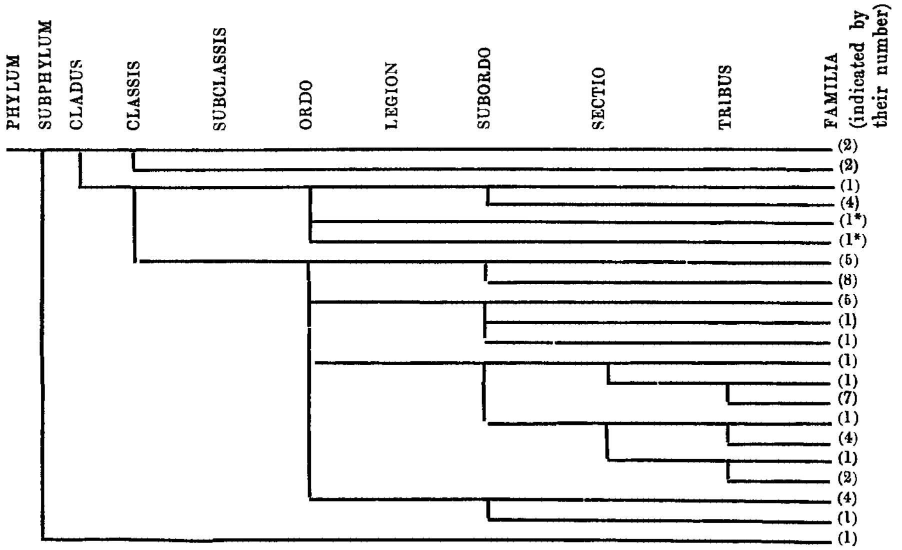
So we took some handfuls (1944 g) of gravel, and both of us started to work simultaneously at the same table, putting together similar pebbles into groups, consulting with each other in dubious cases. In this way we could eliminate our personal opinion as far as possible, and thus we obtained a fairly objective result.

After a considerable time we became convinced that we could put an end to our work. Then we counted the groups and listed. The result is the following: 110/1 (i. e., 110 groups of one pebble); 33/2; 21/3; 13/4; 9/5; 5/6; 6/7; 2/8; 0/9; 0/10; 1/11; 1/12; 2/13; 0/14; 1/15; 2/16; 0/17; 1/18;... 1/23;.... 1/37.

Comparing this result with those obtained by Willis and others on the grouping of species in genera, this represents a regular Willis-curve with a similar degree of irregularity at the tail. This, of course, can have no other meaning than that the phenomenon indicated by the Willis-curve exists very much more generally than may be expected by Willis's theory of „age and area". This phenomenon indeed may be more likely the result of measuring a group of objects with continual variation from nearly similarity to extreme dissimilarity by degrees of similarity. Here we had two degrees: 1. from the individual pebbles to the groups and 2. from these groups to the entire material. In biological systematics we use about a dozen degrees (genus, family, etc.). Tschulok has pointed out that from the lowest to the highest degree the same method of classification is used, therefore we may conclude that the checking of groups in regard to every second higher degree must produce such a Willis-curve.

To demonstrate this we constructed a diagram of ramifications, based upon the systematic representation of the grouping in zoology as it is used by Claus-Grobben (1917) in the „Lehrbuch der Zoologie". Of course this system is somewhat simplified for pedagogical reasons, but this does not throw over the system. In this textbook the families are the lowest degree represented.

Our diagram was made in columns, each column representing a degree of systematic subdivision, from left to right being: divisions; phyla; subphyla; cladus; classes; subclasses; orders; legions; suborders; tribus; families (see the figure).



* Extinct groups, counted as one family each.

Part of the diagram of ramifications of systematic units in zoology.

In this way all systematic divisions of the same degree are found below each other, and those belonging to the same next higher group are connected horizontally. So a family may originate from a tribe but also from a higher degree, even from a class. Now we can count as a corresponding tribe, subclass, legion, etc., each passing of a vertical column by such a horizontal, and the points connected vertically we may regard as a group. At the ends of the horizontals were put the figures indicating the number of families. Of 16 ends in the Protozoans and 10 ends representing extinct groups the number of families was not stated; they were counted as one family each. The following results were obtained:

Families per next following higher subdivision: 152/1; 96/2; 55/3; 38/4; 17/5; 13/6; 13/7; 4/8; 0/9; 3/10; 1/11; 2/12; 1/13;... 2/17; 2/18;... 1/20; 1/21.

Tribus per next following higher subdivision: 299/1; 11/2; 9/3; 3/4; 3/5; 1/6; 1/7.

Sections per next following higher subdivision: 265/1; 18/2; 2/3; 2/4; 1/5; 1/6.

Suborders per next following higher subdivision: 120/1; 36/2; 10/3; 7/4; 4/5; 1/6;... 1/13.

Orders per next following higher subdivision: 22/1; 13/2; 7/3; 6/4; 1/5; 3/6;... 1/9; 1/10;.... 1/17;.... 1/24.

Subclasses per next following higher subdivision: 38/1; 4/2; 2/3; 1/4.

Classes per next following higher subdivision: 6/1; 3/2; 4/3; 1/4; 1/5; 2/6.

A glance at these numbers shows that there is always the same regularity! Even in the case of classes with such a small number of instances (17) the thing comes out: all appear to be of the type of regular Willis-curves. The steepness, however, is of a different degree; the families, orders and classes present the least degree of steepness, while the tribes, sections, suborders and subclasses present the highest. According to the explanation given by Willis this is due to a different degree of age and rate of evolution. The latter is true, but only when we consider it as the evolution of science, because tribes, sections, suborders and subclasses are made use of in a much later state of development of systematics (cf. Tschulok, 1922).

To consider this point in some more detail we made an enumeration of the genera found in Fabricius's „Systema Rhyngotorum" to detect the frequency-distribution of the species in the genera proposed in this work. The result was the following: 1/1; 3/2; 1/3; 1/4; 0/5; 2/6; 0/7; 3/8; 2/9; 2/10; 1/11; 0/12; 0/13; 0/14; 1/15; 1/16; 3/17; 1/18; 1/19; 0/20; 1/21;... 1/23;... 1/29;... 1/34; 1/35;... 1/38; 1/39;... 1/43;... 2/50;... 1/56;... 1/58;... 1/63;... 1/70;.. 1/77;... 1/90;... 1/112;... 1/122.

As we see the aspect is quite different from that found in publications of recent years. When a diagram is made from these data it is in a sense no curve at all. Such an effect may be produced just as well when the criteria of classification are taken too small in comparison to the size of variability and the frequency to be measured. Bearing in mind that Fabricius's genera are almost of the order of a present-time family, and his next-higher division almost of that of a superorder, we produced from our system-graph (see page 300) the enumeration of: 1. families per suborder, 2. families per order and 3. families per subclass. We obtained the following lists:

1. Families per suborder: 114/1; 55/2; 28/3; 28/4; 7/5; 12/6; 8/7; 6/8; 3/9; 5/10; 4/11; 3/12; 3/13; 2/14; 0/15; 1/16; 3/17; 2/18;.... 1/21; 1/22;... 1/24; 1/25;... 1/28;... 1/32.

2. Families per order: 56/1; 30/2; 11/3; 11/4; 9/5; 7/6; 3/7; 2/8; 4/9; 5/10; 3/11; 4/12; 2/13; 3/14; 3/15; 3/16; 3/17; 0/18; 1/19; 2/20; 1/21;... 1/24;... 1/26;... 2/28; 1/29;... 1/31;... 1/53;.. 1/65;... 1/76.

3. Families per subclass: 9/1; 7/2; 3/3; 3/4; 1/5; 2/6; 1/7; 1/8; 2/9; 1/10; 1/11; 2/12; 2/13; 1/14; 3/15;... 2/22;... 1/27;.. 1/31;... 1/36; 1/37;.... 1/42; 1/43;.... 1/50;.... 1/60;.... 1/85; 1/86;.... 1/106;... 1/122;... 1/148.

In comparing these results with that obtained from Fabricius's system, we notice that the last enumeration (3) shows the closest resemblance to the scattered frequency-distribution derived from the „Systema Rhyngotorum". Of course the system of Fabricius does not show the highest frequency-class at the monotypes. There does exist, however, a remarkable skewness in this distribution, both in the case of Fabricius's „Systema Rhyngotorum" and in that of families per subclass in Claus-Grobben's treatise. It becomes more apparent when we take the frequency-classes in allies of ten:

	Fabricius Syst. Rhyng.	families per subclass		Fabricius Syst. Rhyng.	families per subclass
1—10	15	30	81— 90	1	2
11—20	8	9	91—100	0	0
21—30	3	3	101—110	0	1
31—40	4	3	111—120	1	0
41—50	1	3	121—130	1	1
51—60	4	1	131—140	—	0
61—70	1	0	141—150	—	1
71—80	2	0			

The comparison of the two columns may be liable to critisism, because species per genus are compared with families per subclass. Our reply to this is contained in the consideration of the Willis-curves of the families, tribes, suborders, orders, subclasses and classes. No doubt a modern and fully developed system produces curves of a more equal slope, if compared among each other, but all these curves are the result of principally the same method of comparing a continually varying material, varying in a way that it does not show a hiatus in its gradation from the very large till the very minute differences such as subspecies may present. This continual grading is dealt with in steps of approximately equal degree. By reason of this, resemblances exceeding a certain maximum produce a throwing together of types, while little resemblance produces a setting apart of types. Thus the regular form of the Willis-curve must be considered as a statistical expression of the graded resemblance of the living world, a gradation which is also found in the curve of our pebbles.

Of these pebbles we may be able to imagine the origin from the rock, and their varied but in general the same destiny, which is the cause of their resemblances of different degree. The organisms present us many difficulties in this regard. We owe to Tschulok (1922) the understanding of the real problem to be solved with the theory of evolution by means of slight variations of the descendents. Just the graded resemblance as it is expressed in the natural system, together with the absence of spontaneous generation, the „like produces like" but also the slight variations formed the enigma which was to be solved by the idea of evolution.

Tschulok showed that also the idea of history (that of a continual change of the world's aspect in form of a process) which idea certainly is alive at the times of Lessing, is a necessary attribute, which lacked Linnaeus. Even Linnaeus tried to explain this enigma by a theory of crossings certainly in contradiction with his more generally known principles; so strong was the impression! (cf. Tschulok). Willis's attempt certainly bears a strong resemblance to that of Linnaeus. If it were true we had also to expect, that in the same way as species are produced by other species, genera may be thrown off by other genera, families by other families, etc. But what is the exact meaning of, e. g., Chordates to be thrown off by, say Protozoans? That is the same as throwing over the whole idea of evolution!

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