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FRIDAY, MAY 20, 1898.

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New Books

A PRECISE CRITERION OF SPECIES. *

A. The General Method. By C. B. DAVEN-PORT, Harvard University.

THE aim of this paper is to propose a definite method of judging whether two closely allied and intergrading groups of organisms belong to distinct species or only to subspecies or varieties.

I. The Present Criteria of Species. The practical criteria employed at the present time to distinguish a species from a variety are either one of the two following: 1. A certain considerable degree of dissimilarity in characters-of divergence between the types. 2. A sharp demarcation between the types, their mutual isolation, or, in other words, the absence of intergrading forms. Of these two criteria, that of divergence is most generally employed; yet one influential body-The American Ornithologists' Union-adopts the second in a strict form. Its remarkable rule reads : "Forms known to intergrade, no matter how different, must be treated as subspecies; forms not known to intergrade, no matter how closely related, must be treated as full species." This clear cut rule does not seem however to have been worked in practice.⁺ Nearly all naturalists, indeed, recognize a

*Read before the Boston Society of Natural History, April 6, 1898.

[†]See, for example, the discussion by Merriam, Allen and Roosevelt in SCIENCE, Vol. V., pp. 753, 877 and 879.

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certain amount of intergrading between species. What is needed is a method of precisely defining the degree of isolation and the degree of divergence necessary for distinct species.

II. Method of attaining a Precise Criterion of Species. We shall accept in what follows the general opinion that the distinction between species and varieties is one of degree of divergence and degree of segregation. The question is always where to draw the line.

In drawing the line between species and varieties we must act somewhat arbitrarily, just because there is no natural division between species and varieties—one shades over into the other. We must, however, have regard to usage—recent usage, on the whole—because species have never before been studied so critically and so extensively as to-day. We must seek to define the position of the line with precision, *i. e.*, quantitatively.

1. The General Method. Any adequate quantitative method of studying species must start with the individual. It must recognize that a species is composed of individuals, each differing more or less in any quality from every other individual of the species. The species exist not because all of its component individuals are alike in all respects, but because in certain qualities, such as size, color or form, they tend to group themselves about a certain typical condition, which is at the same time the most frequent condition. We may call it the mode.*

Normally, this tendency for measurements of qualities to group themselves about the mode follows a very definite law. This law is the same as that followed by the deviations of a large number of rifle bullets from the center of the target at which they were aimed. It is known as the Law of Error, and is described in text-books on Least Squares. According to this law the smallest errors are the commonest; the larger ones are rarer, and the errors on one side of the mode are counterbalanced by an equal number of errors of the same size on the other side of the mode. If we lay off at equal intervals on a horizontal line a series of points corresponding to the successive classes of magnitude of an organ, and erect at each one of these points vertical lines proportional in length to the number of cases falling in that class, the curve made by joining their tops will be a normal variability curve (Fig.1). This curve is a definite one capable of being expressed by a mathematical formula* and of being subjected to further analysis.



The curve will, however, vary in certain respects with each species measured. Especially will the curve vary in steepness. In some cases 50 per cent. or even more of the individuals will occur in the middle class at the mode. In other cases 10 per cent. or even less will lie here. In the former case the curve will be very steep—the horizontal distance between the two ends of the curve, the *range*, will be small—the character is somewhat invariable or conservative. In the latter case the range of variation will be very great—the character is, we may say,

^{*} As Professor Minot has suggested to me, 'center of variation' would be a more suggestive term. Mode has the convenience of brevity.

x The formula is $y = k.e^{-h^2x^2}$, in which k and h are constant for any curve.

very variable. Thus the variability of any curve will be roughly defined by the range, or when the curve is symmetrical, as is usually the case, by the half-range.*

When the relative frequency of the different magnitude-classes gives us the normal curve we may be sure that we are dealing with a single homogeneous group of individuals—a species showing no tendency to break up into varieties, or a pure race. But individual measurements do not



* The half-range is suggested as the measure of variability on account of the fact that its determination requires no calculation. In all cases in which the curve does not end normally, but, on the contrary, includes a few highly abnormal individuals, or in cases of groups lying near the line between species and varieties, it would be best to measure divergence in terms of the 'standard deviation.' This quantity is obtained by first finding the mean of all the measurements, next getting the deviation of each class from the mean, squaring it, and multiplying it by the number of individuals in the class. Add these products, divide by the number of individuals measalways fall into the normal curve. We may get any one of a variety of curves such as are shown in Figures 2, 3, 4, 5 and 6. Figure 2 is an asymmetrical curve. Figures



ured, and take the square root of the quotient. These operations are briefly indicated in the formula: standard deviation $= \sqrt{\frac{\sum d^2}{n}}$, where $\sum d^2$ is the sum of the squares of the deviations from the mean and n is the number of individuals. When only half of the

the squares of the deviations from the mean and n is the number of individuals. When only half of the curve can be used, find the $\sum d^2$ and n for that half. The standard deviation is normally about one-third of the half range. 4 to 6 are bimaximal curves. All such curves indicate that the material is not homogeneous; that there is a tendency to break up into two races or species with different modes and different indices of variation.

The relationship of the two groups indicated in these curves is not equally close in all. Thus in curve Fig. 2 the two races are hardly separable. In Fig. 6 they appear as distinct, almost completely segregated species. These cases differ both in the degree of isolation and the degree of divergence of the constituent races. We need quantitative expressions for these two qualities.

The degree of isolation may be measured by the depth of the depression between the maxima. By depth of depression we mean the distance of the deepest part of the depression below the level of the lower maximum. This depth may be expressed in per cents. of the length of the shorter mode. It is clear that in Figures 2 and 3 there is no real depression, in Figure 4 one is just appearing; Figures 5 and 6 represent cases of successive increase in the depth of the depression reaching 82% in Figure 6. This ratio of the depression to the length of the shorter mode may be called the Index of Isolation.

The degree of divergence between two groups may be measured by the distance between their modes. This distance must, however, be expressed in a unit independent of the particular units employed in measuring the characters of the species. The unit must be some quality of the curve. The variability of the curve is expressed, as we have seen, by the half-range. * We may use as our unit the average of the two half-ranges of the broader curve when they are both approximately known, otherwise to its outer half-range. The divergence between the races will then be ex-

* Or thrice the standard deviation.

pressed as the ratio of the distance between the modes to the half-range,* or thrice the standard deviation, of the broader curve. This may be called the Index of Divergence.

These two indices, however, are not independent but are curiously bound together. Thus if two equal, symmetrical curves with the same variation overlap so that the inner end of each curve just touches the mode of the other—in other words, when the Index or Divergence, is 100, the Index of Isolation will be found to be about 56. If the curves are of very different area or form, the Index of Isolation may be, with the Index of Divergence still at 100, diminished, but where large numbers are used it will rarely, in practice (provided the curves are symmetrical) be less than 50.

The question arises whether it would not be necessary to draw curves for many characters. Practically it will not be necessary, for confluent species are usually separated chiefly by one most distinctive character. This character may be termed the *chief differential*. It may be used alone to measure the isolation and divergence of the groups, to test their specific value.

Again, how are the individuals which are measured for the differential to be selected? They must be taken methodically at random. This sounds paradoxical, perhaps, but it is not. One takes methodically at random when one lays a yard stick on a grass plot and plucks those blades which lie nearest the inch divisions, or gathers field mice from traps set in a straight line at distances of one mile apart, or at the angles of hundred-mile rectangles, and so The individuals measured are rigidly on. taken on some other basis than their own characters. It will not, of course, always be possible to have individuals gathered so rigidly at random. This is only the ideal which can rarely be realized.

In plotting results the actual and not the percentage frequency of each class should be given. One of the two groups indicated may have many fewer individuals than the other. Very good; this is an important fact which the curve should be left to show.

To sum up: The general method of attaining a precise criterion of species, as opposed to varieties, is to measure the chief differential of the groups, plot the curve of measurements showing the relative number of cases in each class of measurements and determine the index of isolation, or, if more convenient, the index of divergence. If either of these indices is less than a certain number we have varieties; if above that number, species.

2. Determination of the Line between Species and Varieties. The question now remains: What is this number below which we have varieties, above which species? To determine it we must, as we have said, have recourse to the usage of systematists.

Let us consider first a clear case: Fig. 7 is formed from measurements of two species of jumping mouse, Zapus hudsonius and Zapus 80 individuals of each species, insignis. from New Brunswick, New Hampshire, Massachusetts and New York, were measured by Mr. G.S. Miller,* from whose work the data are taken. The two species occur in the same localities. Zapus insignis differs from Z. hudsonius (1) in having longer ears, (2) in being paler and more fulvous, and (3) in being larger. Numerical data are given on characters (1) and (3) only. These show the length of ears to be the chief differential. Plotting the length of ears, disregarding the very slight sexual differences, we see that there is an absence of inter-The index of divergence is 200; grades. that is, the distance between the modes is twice the average distance of the ends of the broader curve from the mode.

Secondly, we have in Figure 8 a curve of

*G. S. Miller, Jr. A Jumping Mouse, Zapus insignis, Miller, new to the United States. Proc. Biol. Soc. Washington., VIII., 1-8, 1893. three undoubted varieties. The curve is based on measurements of 130 individuals of *Scalops aquaticus*, the Eastern mole, from data furnished by True.* The moles were



collected from (1) the Atlantic and Gulf Slope, (2) the Mississippi Valley as far south as Louisiana, (3) Texas and Oklahoma. In different parts of its range the species shows differences in length of skull and in the form of the coronoid-process of

*F. W. True, A Revision of the American Moles. Proc. U. S. Nat. Mus., XIX., 1-112. the lower jaw. Data are given on length of skull, which we assume to be the chief differential. Plotting these data (Fig. 8) we find that they form one curve with, however, three maxima. The index of isolation between the first and second modes is 8%; between the second and third 18%. The curves from each locality overlap the adjacent modes. The index of divergence is less than 100.

Again we have a case of three alleged species of the mole Scaphanus from the extreme northwestern part of the United The differentiæ are size of body, States. color and length of face. Numerical data are given by True on skull length which is closely correlated with the size of the body. The curve (Fig. 9) gives three maxima. The index of isolation between the first and second maxima is 66; between the second and third, 100. The end of the constituent curves do not overlap the adjacent modes. The indices of divergence are about 170 and 130 respectively. We may admit these as distinct species.

Again the hare, Lepus palustris, varies in different localities chiefly in the breadth of Miller and Bangs * from a study the face. of eight individuals concluded that there were two species which they called L. palustris and L. paludicola. Later Chapman † concluded from a study of nineteen individuals from the same localities as those of Miller and Bangs that the two forms are only varieties. Which view is correct? Plotting (Fig. 10) the ratio greatest nasal width, basilar length of skull, we find that the index of isolation is 33, the index of 70. These forms are no divergence is doubt varieties.

A case from fishes: Two species, Leuciscus balteatus and L. hydrophlox, from the Columbia River basin differ in the number of rays in the anal fin. The mode of these two groups is different, but an overlapping occurs. Are not these groups perhaps varieties? (Fig. 11.) The index of isolation is 50%; that of divergence is 100%. The case is a doubtful one. We are near the limit between species and varieties.

Additional examples from mammals, birds and fishes might be given, but those already considered may suffice to illustrate the method by which a conclusion as to where the line should be drawn has been reached for animals. The conclusion is that when the chief differential of any two groups shows an index of isolation of 50%or more, or when their index of divergence is 100% or more, the two groups are species; otherwise they are varieties.

B. The Chief Differential and Specific vs. Individual Characters. By J. W. BLANKIN-SHIP, Harvard University.

In the previous part of this paper a method was shown for the determination of the value of species by means of the isolation and divergence indicated by the chief-differential. In this will be considered the determination of the chief-differential itself as the most marked of the specific characters, and also the mathematical discrimination of specific and individual characters.

I. Determination of the Chief-differential.

Necessarily all the specific characters are considered in the determination of species, but these characters are of different values and their variation from one species into the other is never strictly correlative, hence systematists in the case of critical intergrades are compelled to separate the species by a single character in order to ensure uniformity in their determinations. That character is taken which is most distinct in the two species and exhibits correlative variation with the other, minor, specific characters. That most distinctive character is

^{*} Proc. Biol. Soc. Wash., IX., 1894.

[†] Bull. Amer. Mus. Nat. Hist., VI., 341, 1894.

here called the chief-differential. Now it is frequently the case that different systematists working in the same groups select different characters as the most distinctive, and consequently, as the characters are not perfectly correlative, the specific line is drawn at different points. For instance, one botanist may separate Thalictrum purpurascens, L. from T. polygamum, Muhl., by the characters of the leaf, another by the form of the stamens; one distinguish Calli. triche verna, L. from C. heterophylla, Pursh by the persistence of the stigmas; another by the shape of the fruit. It is necessary then to have a method for determining the chiefdifferential in order that the specific lines be uniformly drawn and that the value of the species be justly estimated. The method for obtaining the chief-differential may be shown by taking a particular case.

Two species of the marsh plant *Typha* are found in the eastern United States and are often confluent at the point where the brackish marshes pass into fresh-water swamps. Seven characters regarded as probably specific were measured in about 250 specimens taken mainly from eastern Massachusetts and selected one meter apart, as nearly as possible, across the swamps were found. These seven characters were each arranged separately by classes, according to size and the relative frequency of each class enumerated, as shown in the following table :

(Fig. 12.)	(Fig. 12.) I. STEM-HEIGHT, measured from the ground or water to base of Pistillate Spike.								
Decimeters.	7 8 9 10 11 12 13 14 15 16 17 18 19 20 21								
No. of Individuals.	2 2 6 8 18 30 33 38 38 27 18 16 7 2 2								
	(Fig. 13.) II. BASE DIAMETER OF STEM, including leaf-sheaths.								
Millimeters.	6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36								
No. of Individuals.	2 20 45 21 19 4 10 13 17 19 16 13 5 5 2 1								
	(Fig. 14.) III. MID-STEM DIAMETER, taken at half the height.								
Millimeters.	2 3 4 5 6 7 8 9 10 11 12								
No. of Individuals	5 10 68 43 29 31 25 23 11 2 1								
	(Fig. 15.) IV. LEAF-WIDTH, largest leaf in widest part.								
Millimeters.	4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23								
No. of Individuals.	12 26 39 25 15 6 5 14 11 16 15 20 15 12 7 8 1 1 0 2								
	(Fig. 16.) V. PISTILLATE SPIKE-LENGTH.								
Centimeters.	3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26								
No. of Individuals.	1 0 5 7 9 17 23 22 37 37 26 23 12 11 6 3 7 1 0 0 1 0 0 1								
	(Fig. 17.) VI. FISTILLATE SPIKE-DIAMETER.								
Millimeters.	9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35								
No. of Individuals.	1 7 3 6 6 12 13 30 29 19 3 5 2 10 6 6 16 8 17 15 5 10 6 3 1 1 1								
(Fig. 18) VII INTERVAT between Staminate and Pictillate Spiker									
(Fig. 10.) VII. INTERVAL DEUWCEII Staininate and Fistinate Spikes,									
Centimeters.	0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15								
No. of Individuals.	110 15 7 16 37 40 9 4 2 0 1 1 0 0 0 1								

TABLE OF RELATIVE FREQUENCY.

From the table above we may collect the following data:

tively with that of the chief-differential. Any variable character in the two species

	Total Va- riation.	Modes at	MINIMUM OF SINUS.	H'GHT OF Lower Mode.	Index of Isolation	DIVERG- ENCE OF MODES.	GREATER HALF- RANGE.	INDEX OF DIVERG- ENCE.
Stem Height. Base Diam. Mid-Diam. Leaf-Width. Spike Length. Spike Diam. Interval.	7-21 dm. 6-36 mm. 2-12 '' 4-23 '' 3-26 cm. 9-35 mm. 0-15 cm.	14–15 dm. 10 & 24mm. 4 & 7 '' 6 & 15 '' 11–12 cm. 16 & 27mm. 0 & 5 cm.	 29 5 2 7	19 31 20 17 40	79 7 75 89 83	14 mm. 3 "' 9 " 11 " 5 cm.	12 mm. 5 " 8 " 8 " 10 cm.	116 60 112 137 50

Of these seven characters the stem-height and the spike-length show no apparent differentiation for the two species; the differentiation is slight in the mid-stem diameter, but is marked in the other characters. Both isolation and divergence are greatest in the spike-diameter, which therefore should be taken for the chief-differential. The isolation being above 50 per cent. (89) and the divergence above 100 per cent. (137), both are undoubtedly good species.

Taking those characters showing marked differentiation, the modes indicate the most frequent form of the species, the smaller size being angustifolia and the larger latifolia, and hence represent the specific types of those species as they occur in this region. This specific type must not be confused with the historical type, which is the form of the species first described and may occur at any point within the normal limits of the variation of the species.

II. Specific and Individual Characters.

In order to make the enumeration of differentiæ accurate it may be necessary in the discrimination of species to determine which characters can be regarded as specific and which as individual. Those characters are called specific which differ in some respect in the two species and whose difference increases or diminishes correlanot exhibiting such correlation is regarded as individual.

In order to determine this fact of correlation, these same characters of Typha were compared with the spike-diameter as subject. The average stem-height, base-diameter, leaf-width, etc., was found of all specimens having a spike-diameter of 8 mm., the same of 9 mm., 10 mm., and so on up to 36 mm. Correlation is then shown by the character having a proportional increment or reduction in size in comparison with the chief-differential, the spike-diameter. The result is given in the table below.

From this it appears that the correlation with the spike-diameter is well-marked in the case of the base-diameter, the mid-stem diameter and the leaf-width. It is apparent in the stem-height and spike-length, yet is not so close as to give rise to two modes in the table of frequency. The case of the interval is peculiar. In the table of frequency it exhibits a combined normal and half Galton-curve, while in the table of correlation above, there is little increase or decrease in the first ten numbers (good angustifolia) and the subsequent decrease is probably due to intergrading. This character then exhibits individual variation for this species.*

* Of the other characters of Typha not here considered, the pollen-grains might possibly prove a better

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No. Measured.	Spike Diam. mm.	Stem Height cm.	Base Diam. mm.	Mid-Stem. Diam. mm.	Leaf Width mm.	Spike Length cm.	Interval mm.
			_				
1	8	115	9	2	4	7	50
3-5	9	100	8	2	3	8	43
7-10	10	100	8	2.	4		69
5-6	11	105	10	3	5	8	57
11–15	12	110	9	3	4	7	58
11-12	13	124	11	4	5	7	44
23-34	14	117	11	3	5	11	53
29 - 36	15	130	11	4	6	10	49
46-57	16	140	11	4	6	11	50
37–41	17	141	12	4.	7	12	43
30-35	18	173	15	4	8	12	37
15-16	19	153	16	5	10	12	15
18-20	20	169	19	6	11	13	8
7-10	21	153	17	6	10	11	13
36-38	22	168	18	6	11	13	7
22-28	23	163	17	6	10	14	5
24 - 27	24	158	19	6	11	13	6
33-34	25	155	21	7	13	13	3
17-18	26	159	22	7	13	11	2
33-37	27	168	23	7	14	13	1
23-27	28	170	23	7	15	13	1
9–12	29	175	22	9	15	13	0
15 - 21	30	172	24	8	15	13	1
11-12	31	162	24	7	14	13	0
6	32	167	24	8	15	13	0
1–4	33	184	23	8	17	11	4
2-3	34	205	25	8	19	18	0
1	35	167	27	9	15	13	0
1	36	142	26	7	13	10	Ō
							-

TABLE OF CORRELATION.

A normal curve of variation extends an equal distance on each side of its mode, and hence in a dimorphic curve composed of two such normals the continued extension of the interior curves below the point of confluence may be determined approximately by reference to the exterior halves. In the curve of the spike-diameter (Fig. 17) this overlapping portion of the curves of *latifolia* and *angustifolia* (19–23 mm.) represents the region of intergrades between

differential than any of those measured, but their extremely short duration (about two weeks in the year) and their microscopic size do not render them generally available for systematic work. From my observation of Typha in this region, I do not think the color of the spike or shape of the stigmas are reliable as differentials between these two species, and the floral bracts are doubtfully absent in *latifolia*, becoming gradually larger through the intergrades to typical angustifolia.

those two species. Also, the minimum of the sinus (21 mm.), where occur the fewest intergrades between the two species, is the point where systematists would naturally separate them.

It has now been shown that confluent species can be separated by a fixed amount of isolation and divergence, as indicated by their most distinctive character—the chiefdifferential, which can be determined mathematically by the measurement of all the specific characters; and finally, a method has been indicated whereby specific and individual characters may be distinguished by correlation.

It should be remembered that the measurement of individuals of a species, selected impartially after a fixed method throughout a given region, gives the characteristics of that species—its type and variation, the



relative abundance of its forms and its confluence with allied species—only for that region. For the complete determination of its true characteristics the species must be studied throughout its entire range. This can often be done approximately by the study of a large collection representing the various parts of that range, as is now done in ordinary systematic work. However, two groups found to be so isolated and divergent as to constitute distinct species in any one region where their ranges or specific factors overlap will doubtless be found to continue distinct in all parts of their ranges, as the greatest confluence of such groups is necessarily at points where they occur together.

This method attempts only to express in mathematical terms the facts already recognized by systematists in the discrimination of species; it attempts to determine, by impartial quantitative enumeration of individuals, the specific type and the limits of specific variation, as well as the relative

value of the species or variety, and this more accurately than can be done by the ordinary descriptive terms. The discrimination of species has hitherto been dependent upon the experience and judgment of each systematist, and consequently the results have often been most conflicting and confusing. By the use of a precise mathematical criterion of species 'splitting' and 'lumping' is no longer possible and any hybrid or intergrade, which may have been described as a species or a variety, is clearly shown by its intermediate position and by the absence of isolation, while a sport is indicated by its relative fewness of individuals and its place at the extreme of variation.

The possibilities of statistical methods in the study of individual variation extends far beyond the applications here proposed. The gradual change of the specific type and of the variability of a species, the distinguishing of stable from plastic groups, the influence of environment upon specific form, and many other matters of importance to the philosophical naturalist and systematist, are in the future to be investigated quantitatively.*

JULIUS SACHS (II).

IT was at Würzburg that Sachs first found fit opportunity to develop his talent for teaching. Too often it happens in lecture-rooms that 'man Viele sieht, die nicht da sind,' but this did not apply to him. His fascinating, lucid expositions stimulated the students, whilst he knew well how to practically illustrate his subject. He worked incessantly at the materials for demonstrating, drew and painted a number

*Those who desire further information on the quantitative study of species are referred to the excellent paper of Dr. F. Ludwig: 'Die Pflanzlichen Variationscurven und die Gauss'sche Wahrscheinlichkeitscurve,' in the Botanisches Centralblatt, 73: 241, 1898.

of diagrams, and was constantly adding to his stock of dried plants, alcohol preparations, models and cultures. He considered that all should be in due relation to the subject-matter in a scientific lecture as in the acting of a play. In the winter he lectured on general botany (anatomy and physiology), and in the summer on the 'Natural History of the Plant World.' Besides this he often gave experimental demonstrations in the summer and this necessitated a great deal of work; occasionally he lectured on the history of botany and on the physiological basis of morphology. After 1874 he had a class every term for microscope work.

A great number of botanists worked at one time or another in his laboratory. The first were Dr. Kraus and Millardet (both formerly at Bonn and Freiburg). Among others attracted by him to Würzburg were Baranetzky, Brefeld, Francis Darwin, Detlefsen, Elfving, W. Gardiner, Godlewski, Goebel, Hansen, Hauptfleisch, Klebs, H. Müller-Thurgau, Moll, Noll, Pedersen, Pfeffer, Prantl, Reinke, D. H. Scott, Stahl, Vines, De Vries, Marshall Ward, Weber, Wortmann and Zimmermann. He insisted upon his pupils being in earnest about science, and he brooked no laziness. Weak natures naturally felt his influence most strongly, but he set a higher value on those from whom he could gain something.

With failing health he withdrew more and more into himself. "I am beginning to take private pupils again," he writes, "but there is little pleasure in it. When a professor reaches the age of sixty he ought *eo ipso* to be pensioned off with his full salary; it might be possible to arrange a university that would serve as an almshouse, but I would not go into it."

He urged his pupils to make comprehensive studies even as he was constantly striving after wide generalizations. He was a master in the art. We have only to