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MECHANICAL SOLUTION OF FORMULAS FOR GROWTH RATES

BY

ROBERT V. KESLING

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CONTENTS

INTRODUCTION

IN recent years paleontological and zoological literature has contained an increasing number of articles in which quantitative methods are used for the study and description of species. Such mathematical and statistical methods are termed biometry. The trend to biometry is the result of a new concept of a species as having the ranges, limitations, association of characters, and variations of the individuals which compose the population, rather than one comprising the characteristics of a single specimen.

Many workers have avoided using statistical treatment of specimens, because of the involved procedures required in many of the formulas. In some instances, however, it is possible to devise easier methods for the solution of a problem and still obtain results with a degree of precision commensurate with the data. This is true of the growth-rate formulas proposed by Huxley and by Schmalhausen.

HUXLEY'S GROWTH-RATE FORMULA

Julian S. Huxley proposed (1924, p. 895; 1932, pp. 6–8) a formula for comparison of relative growth rates. This formula has been subsequently used in many studies of growth. It is based on the assumption that the ratio of the relative growth rate of an organ (or part) to the relative growth rate of the body remains constant for a given species and sex over the period of time being considered.

Any organ whose growth is related to that of the remainder of the body is said to be heterogonic. An organ whose growth is more rapid than that of the body has positive heterogony; an organ whose growth is slower than that of the body has negative heterogony; and, any organ growing at exactly the same rate as the rest of the body is said to be in an isogonic condition.

Certain basic concepts are involved in the formula. If y is the volume of an organ and x is the volume of the rest of the body, then

$$\frac{dx}{dt} = mxG \qquad \text{and} \qquad \frac{dy}{dt} = nyG,$$

where dt is a time interval, G is derived from conditions of growth, m is the specific constant of the body, and n is the specific constant of the organ. Because the organ and the rest of the body are growing under the same conditions and over the same time interval, the values of G and dt are the same in both equations. Therefore

$$\frac{dy}{dx} = \frac{ny}{mx}.$$

Integration reduces this equation to

$$y = bx^{n/m},$$

which can be written as

$$y = bx^{k},$$

where k is the constant differential growth ratio, equal to n/m, the ratio of the relative growth rate of the organ to the relative growth rate of the body. This is the formula as stated by Huxley. It can also be written

$$\log y = k \log x + \log b.$$

Because the formula holds true from the beginning of the growth interval (t_1) to the end (t_2), then at time t_1

$$\log y_1 = k \log x_1 + \log b$$

and at time t_2

$$\log y_2 = k \log x_2 + \log b.$$

If the first equation is substracted from the second, the following formula is derived for the value of k,

$$k = \frac{\log y_2 - \log y_1}{\log x_2 - \log x_1}.$$

When the values of y_2 and y_1 are plotted as the abscissas and the values of x_2 and x_1 as the ordinates on double logarithm paper, the logarithms of these four terms are graphically portrayed. If a line is drawn through the points (y_2, x_2) and (y_1, x_1) on the logarithm paper, the value of k will be the cotangent of the angle formed by this line and the horizontal.

The formula

$$\log y = k \log x + \log b$$

now gives a graphic method for solving b. At the line $x=1$, $\log x=0$ and the above formula becomes

$$\log y = \log b.$$

This means that if the line through (y_2, x_2) and (y_1, x_1) is extended to the line $x=1$ on the double logarithm paper, the intersection of the two will have identical values of y and b.

Figure 1 illustrates double logarithm paper appropriately numbered for use in the graphic solution of Huxley's formula. Figure 2 is a diagram of a special protractor designed to measure the cotangent of angles. This special protractor is made on transparent film, and gives direct reading of k, when values of y and x are plotted according to the procedure outlined above. If greater accuracy in the reading is desired, a vernier may be used with a large protractor. This vernier should be set on the same number as that number on the special protractor which is nearest to the value of the line being measured, and is read as any other vernier.

The accuracy which can be obtained with this system of solution depends upon (1) the size of the scale on the double logarithm paper, and (2) the size and accuracy of the special protractor. The rapidity of this method permits solution of the growth coefficients for numerous readings in an ontogenetic series in a matter of seconds.

The general application of Huxley's formula has been to specific organs as compared to the rest of the body, but it is equally useful for comparison of any two measurable variables in a growth series. Burma used this formula (1948, pp. 750–52) for the study of *Pentremites,* comparing seven other measurements in turn with the length of the standard radial. The length of the standard radial was chosen for x, the independent variable of the formula; height, thickness, base of radial, deltoid, azygous basal, ambulacrum, and the number of side plates were then used in turn for y, the dependent variable.

The double logarithm paper (Fig. 1) can also be used to compare the "scatter" or distribution of the two factors x and y within size ranges. This is particularly applicable to crustaceans or other arthropods which have fixed stages and increase in size only by molting and secreting new carapaces. Each instar or stage forms a certain size range. For each instar the value of the standard deviation of length (σ_l) may be plotted as a line from (h, l) to $(h, l + \sigma_l)$. The actual lengths of such lines plotted for the different instars of a species can be compared to show whether the standard deviation is increasing or decreasing from one instar to the next. Similarly, the standard deviation of height can be compared for different instars by plotting σ_h as a line from (h, l) to $(h + \sigma_h, l)$ for each instar and measuring actual lengths of these lines.

TABLE I

STUDY OF *Ctenoloculina cicatricosa* (WARTHIN)

Instar	Number of Specimens	Mean Length (μ)	Mean Height (μ)	k	$\sigma_l(\mu)$	$\sigma_h(\mu)$
Adult	38	874.2	473.9		79.3	41.1
				1.03		
8	89	685.5	368.9		59.5	34.5
				1.04		
7	49	540.6	287.6		33.6	21.5
				1.00		
6	18	441.1	235.0		36.1	17.4
				0.86		
5	11	338.	187.			

Examples: The growth ratios given in Table I are for specimens of *Ctenoloculina cicatricosa* (Warthin) from the Norway Point formation of the Middle Devonian Traverse group of Michigan. All specimens were collected at the same locality. The k is computed as the growth ratio of the average height compared to the average length. The values of k show that the height and length increase from one instar to another at very nearly the same rate. The standard deviations of length and height are found by measurement on double logarithm paper to be comparably the same for the eighth and adult instars, but are appreciably less for the seventh instar. This means that the increase in variation is coincident with the entrance into the eighth instar, which in living ostracods marks the beginning of sexual development.

TABLE II

STUDY OF *Cypridopsis vidua* (O. F. MÜLLER)

Instar	Number of Specimens	Mean Length (μ)	Mean Height (μ)	*k*
Adult	15	617.0	372.6	
				1.054
8	60	528.0	316.2	
				0.998
7	77	418.0	250.5	
				0.912
6	72	333.4	203.8	
				0.865
5	49	269.8	169.7	
				0.886
4	53	226.8	145.6	
				0.886
3	65	188.2	123.8	
				0.814
2	68	155.5	106.0	
				0.878
1	41	132.2	92.0	

The growth ratios in Table II are for living members of *Cypridopsis vidua* (O. F. Müller), a parthenogenetic ostracod. All specimens were collected from an aquarium culture started from one ostracod taken from Crystal Lake, Champaign County, Illinois. In general, the growth ratio of height compared to length gradually increases throughout the ontogeny of this ostracod.

Any set of similar measurements taken at different stages of development can be compared against length by Huxley's formula.

SCHMALHAUSEN'S GROWTH-RATE FORMULA

Schmalhausen (1927, p. 294) proposed a formula for expressing the rate at which an organ is growing. This rate expresses increase in size with time, and is an absolute figure, not a ratio. The formula is

$$C_v = \frac{\log_{10} v_1 - \log_{10} v}{0.4343\ (T_1 - T)},$$

where C_v is the growth rate, v_1 is the volume of the organ at time T_1, and v is the volume of the organ at time T. $(T_1 - T)$ is the time interval over which C_v is computed. The factor 0.4343 is introduced in the formula as the divisor necessary to convert logarithms from the base 10 to the base e. Thus, Schmalhausen's formula may be rewritten

$$C_v = \frac{\log_e v_1 - \log_e v}{T_1 - T}.$$

It will be seen that the units chosen for measurement of T and for v will affect the value of C_v; therefore the same units should be used throughout a study if values of C_v are to be compared.

The transparent overlay described for use in solution of Huxley's formula can also be used to read directly the values of C_v in Schmalhausen's formula. The diagram on which the points are plotted is shown in Figure 3. It has numerical values as the ordinates (T) and values of logarithms to the base e as the abscissas (v). Powers of 10 may be used as multipliers to adapt the diagram to the ranges of observed readings, and the answer adjusted accordingly.

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CONSTANT DIFFERENTIAL GROWTH–RATIO SCALE

FOR RAPID SOLUTION OF JULIAN S. HUXLEY'S FORMULA

$Y = BX^K$, *WHERE*

Y = MAGNITUDE OF HETEROGONIC ORGAN
X = MAGNITUDE OF REMAINDER OF ANIMAL
B = CONSTANT
K = GROWTH-COEFFICIENT

ALSO, WHEN THE GROWTH-COEFFICIENT HAS BEEN ESTABLISHED, THE GROWTH INCREMENTS OF EITHER THE ANIMAL OR THE HETEROGONIC ORGAN CAN BE QUICKLY DETERMINED, SINCE —

$$K = \frac{dY/dT}{Y} \Big/ \frac{dX/dT}{X}$$

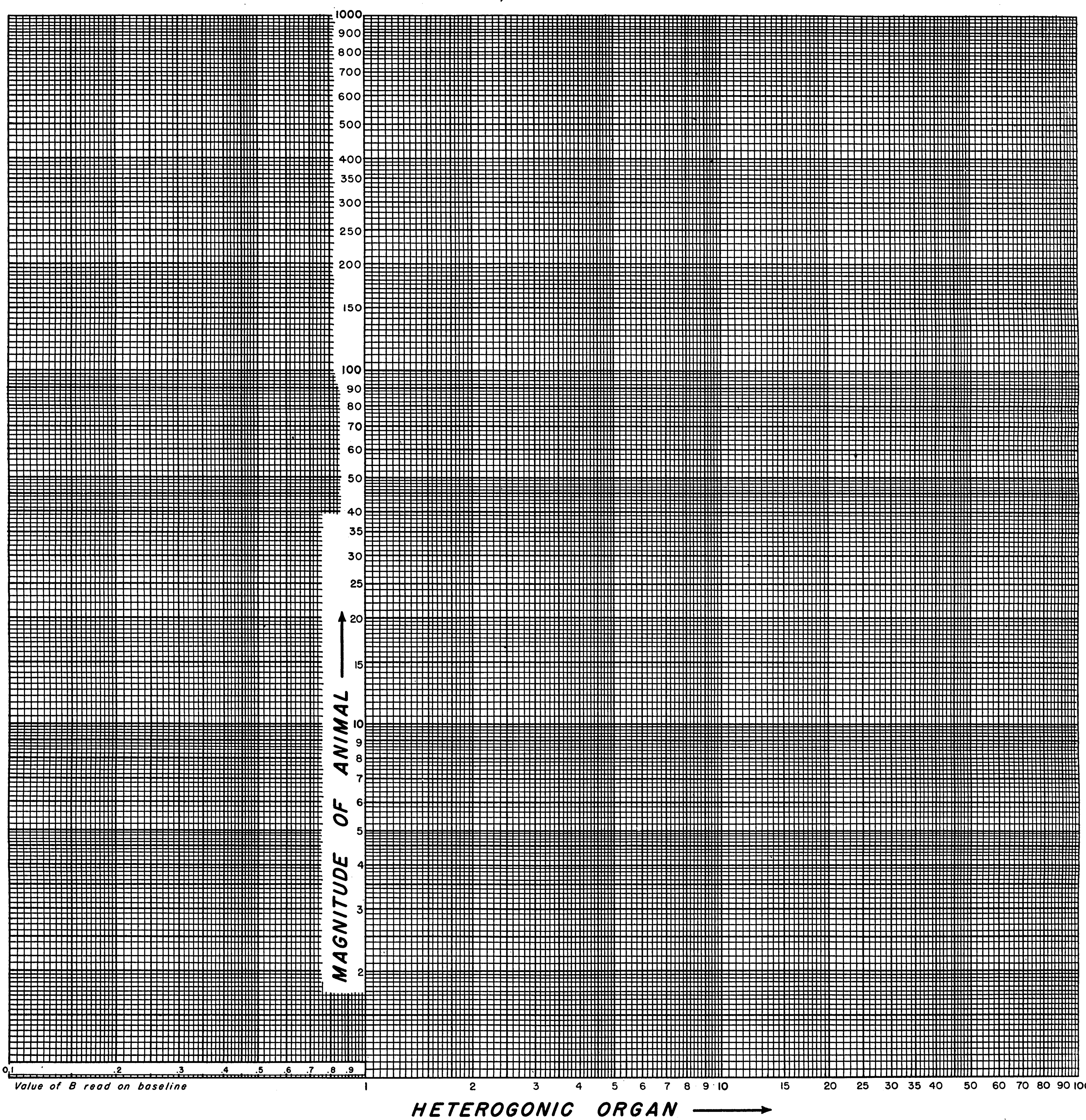

FIGURE 1

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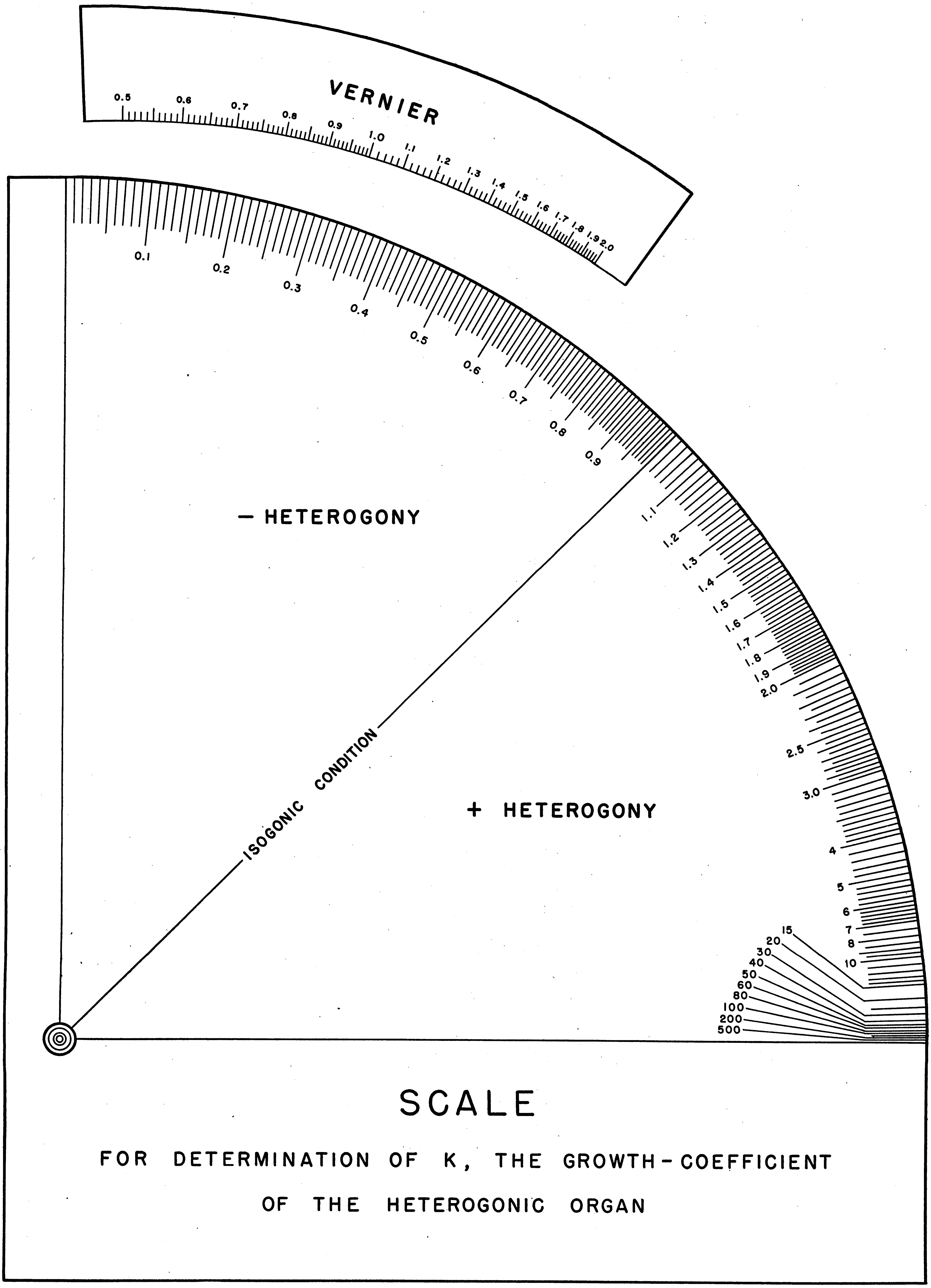
VERNIER
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
1.4
1.5
1.6
1.7
1.8
1.9
2.0
0.1
0.2
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1.9
2.0
2.5
3.0
4
5
6
7
8
10
15
20
30
40
50
60
80
100
200
500
— HETEROGONY
ISOGONIC CONDITION
+ HETEROGONY
SCALE
FOR DETERMINATION OF K, THE GROWTH-COEFFICIENT
OF THE HETEROGONIC ORGAN

FIGURE 2

TRUE GROWTH RATE GRAPH

USED IN SOLUTION OF SCHMALHAUSEN'S FORMULA

$$C_v = \frac{\log_{10} V_1 - \log_{10} V}{0.4343\ (T_1 - T)}$$

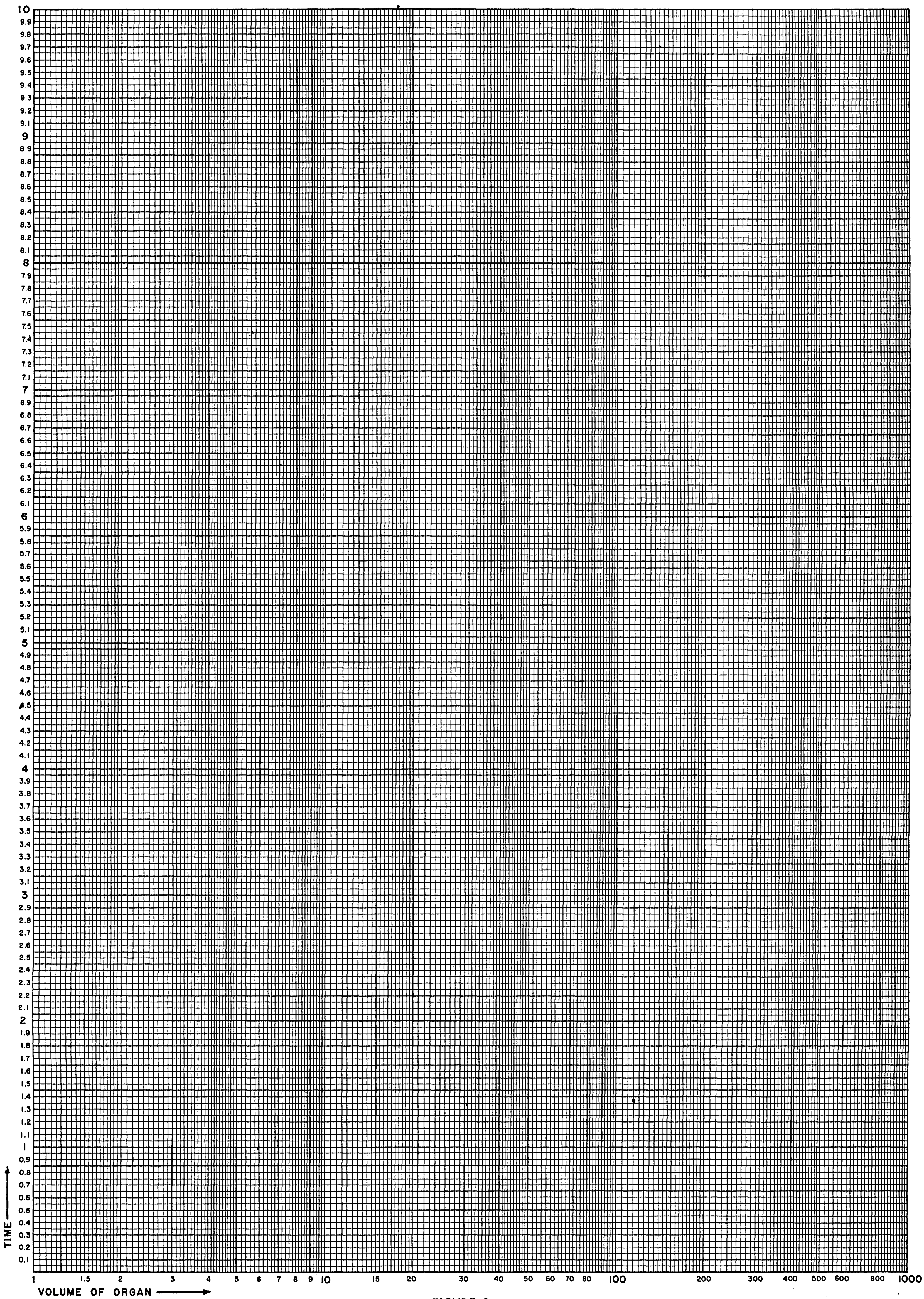

FIGURE 3

Volume VIII