

# Growth and Division of *Escherichia coli*

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Two assumptions frequently have been made in studies on the growth of individual bacteria. The increase in volume of rod-shaped bacteria has been assumed to consist of an increase only in length; thus, measurements of length have been used to estimate the volume of a cell (A. L. Koch et al., *J. Gen. Microbiol.* **29**:421, 1962; J. F. Collins and M. H. Richmond, *J. Gen. Microbiol.* **28**:15, 1962). Secondly, it has been assumed that the cytoplasm of the mother cell is equally divided between the two daughter cells (A. L. Koch and M. Schaechter, *J. Gen. Microbiol.* **29**:435, 1962). We present evidence that these assumptions are substantially correct.

*Escherichia coli* ML30 was grown for five generations in glucose minimal medium at 30 C. Cells were harvested by centrifugation, washed, and suspended in distilled water. A sample of the suspension was sprayed on Formvar-coated grids and air-dried. Electron micrographs were made with a final magnification of 20,000 ×. The outlines of the cells were regular and showed no appreciable alteration of shape. Lengths and diameters of 214 cells were measured from the micrographs.

If growth consists of an increase only in length, regression of diameter as a function of length should show a slope of zero. Linear regression of the data gave a slope of  $0.0032 \pm 0.0099$  micron per micron, which is not significantly different from zero at the 10% level of probability as measured by the *t* test. Confidence limits (95%) for the slope were  $\pm 0.019$  micron per micron. Thus, the assumption that the increase in volume during growth of *E. coli* consists of an increase only in length is proven.

Fifty-six cells had an obvious constriction; the length of each half was measured. It was assumed that constricted cells would eventually divide at the plane of constriction and that each half would increase in volume in the same proportion before division. The ratio of the length of one half formed by constriction to the length of the entire cell would then be equal to the ratio (E. O. Powell, *J. Gen. Microbiol.* **37**:231, 1965):

$$p = \frac{\text{volume of daughter cell at division}}{\text{volume of parent cell at division}}$$

TABLE 1. *Distribution of daughter-parent ratio*

Parameter	Estimate
Mean.....	0.500 ± 0.002
Standard deviation.....	0.0192 ± 0.0024
Coefficient of variation.....	0.0383
$g_1$ †.....	0.0000 ± 0.257*
$g_2$ †.....	-0.1228 ± 0.508*

\* Not significantly different from zero at the 5% level of probability.

† Values  $g_1$  and  $g_2$  are statistics calculated from the third and fourth moments about the mean, respectively. Both are zero for a Gaussian distribution.

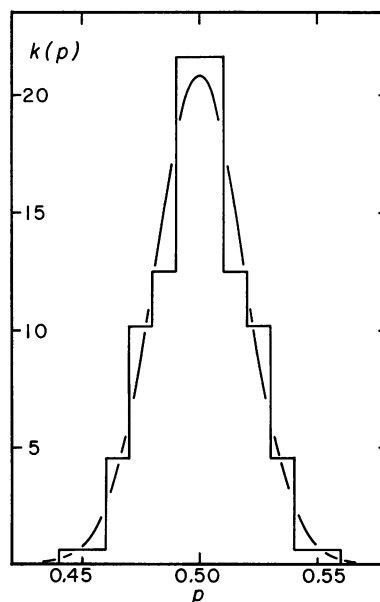


FIG. 1. Frequency function,  $k(p)$ , of daughter-parent ratio,  $p$ , for *Escherichia coli* ML30. Histogram: measured distribution; curve: Gaussian distribution with the same mean and variance. Sum of chi-square of the difference between the two distributions is 1.579 for 5 degrees of freedom. The probability that the value of chi-square is due to chance is 0.90.

For binary fission,  $p$  must be distributed symmetrically about a mean of 0.5. If division is equal but with random error, the distribution of  $p$  will be Gaussian. If division is regularly unequal, the distribution of  $p$  will still be symmetrical, but the inequality will be reflected in a large negative value of the statistic  $g_2$ .

Table 1 shows the parameters of the distribution of  $p$ , calculated from the measurements of constricted cells. The distribution of  $p$  is compared to the Gaussian distribution in Fig. 1. The co-

efficient of variation of  $p$  is very small, and the distribution of  $p$  is not significantly different from Gaussian. Thus, cells of *E. coli* divide equally, with a very small random error in the division of cytoplasm between the two daughter cells. For most purposes, it can be assumed that division is exactly equal.

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