The Subunit Structure of Phosphoglucose Isomerase from Bakers’ Yeast*

Stephen L. Lowe‡ and F. J. Reithel

From the Department of Chemistry, University of Oregon, Eugene, Oregon 97403

SUMMARY

Bakers’ yeast phosphoglucose isomerase was studied by both chemical and physical methods to determine its subunit structure. Gel filtration in 6 M guanidine HCl as well as acrylamide gel electrophoresis of sodium dodecyl sulfate-denatured phosphoglucose isomerase showed two species corresponding to one-half and one-fourth of the preparative molecular weight of 119,400 determined by equilibrium centrifugation. Further centrifugation studies showed that the enzyme could be completely dissociated to species of 30,000 molecular weight. Peptide maps of tryptic hydrolysates of denatured and chemically modified enzyme showed that the protein is composed of four identical or nearly identical subunits. The results of amino acid analysis, except half-cystine content, were compatible with identical subunits. The apparent partial specific volume and extinction coefficient were also determined.

Phosphoglucose isomerase (u-glucose 6-phosphate ketol-isomerase, EC 5.3.1.9) has been isolated from a variety of sources including bovine mammary gland (1), rabbit muscle (2), human muscle (3), brewers’ yeast (4), and bakers’ yeast (5). Extensive studies by Noltmann et al. (6-8) have shown that the rabbit muscle enzyme has a preparative molecular weight of 132,000 and is composed of two identical subunits.

In this study bakers’ yeast phosphoglucose isomerase was found to have a preparative molecular weight similar to that of the rabbit muscle enzyme, but was found by several different techniques to be dissociable to a polypeptide of 30,000 molecular weight. Peptide maps of tryptic digests of denatured and of modified phosphoglucose isomerase revealed very nearly the number of peptide spots to be expected if bakers’ yeast phosphogluco-isomerase is a tetramer composed of identical subunits.

* This investigation was supported by United States Public Health Service Research Grant 5R01 AM08128 from the National Institute of Arthritis and Metabolic Diseases. Abstracted from the Ph.D. dissertation S.L.L. submitted in partial fulfillment of degree requirements, University of Oregon, Eugene, Oregon, June 1974.

‡ Recipient of United States Public Health Service Training Grant 5T1 GM444-04.

EXPERIMENTAL PROCEDURES

Materials

The phosphoglucose isomerase used in this study was purchased from Boehringer Mannheim (New York, N. Y.) as a crystalline suspension in 2.4 M ammonium sulfate.

Protein standards for determination of polyacrylamide electrophoresis and gel filtration were bovine serum albumin and ovalbumin purchased from Pentex Inc. (Ranke, Ill.), and ribonuclease A and chymotrypsinogen A from Pharmacia (Fiscataway, N.J.).

Guanidine HCl (reagent grade, Matheson, Coleman and Bell) was treated repeatedly with activated charcoal until the absorbance at 280 nm was negligible.

Urea was purified by deionization followed by recrystallization from 60% (v/v) ethanol (9).

Pyridine and 1-butanol were refluxed with sodium hydroxide pellets and twice distilled before use in either thin layer chromatography or electrophoresis.

Dialysis tubing was washed with sodium bicarbonate, Na2EDTA, and hot distilled water.

Bovine pancreatic trypsin treated with L-1-tosylamido-2-phenylethyl chloromethyl ketone to destroy chymotryptic activity was purchased from Worthington Biochemical Corp. (Freehold, N. J.).

For thin layer plates, cellulose powder MN 300 was purchased from Machery, Nagel & Co., Duren, Germany.

Other materials were reagent grade and used without further treatment.

Methods

Extinction Coefficient—Evaluation of the extinction coefficient of phosphoglucose isomerase was made from optical density measurements taken with a Cary 15 recording spectrophotometer (Cary Instruments, Monrovia, Calif.) and dry weight measurements made using a vacuum microbalance (10).

Partial Specific Volume—Determination of the partial specific volume of phosphoglucose isomerase was made by measuring the protein concentrations and densities of varying dilutions of a stock solution. The protein concentrations were determined spectrophotometrically; the densities were measured using a magnetic densimeter built in this laboratory. The instrument and the method of calculation have been described previously (11, 12).

Chemical Composition—Amino acid analysis was performed by the modified method of Spackman et al. (13) on a Beckman model 120B amino acid analyzer using Bio-Rad ion exchange resins A4 and A5. Samples for analysis were hydrolyzed in 6 N HCl at 110° for times ranging from 6 to 96 hours. Cysteine plus cystine content was determined as cysteic acid following performic acid oxidation according to the method of Hirs (14). Calculations were

1 Dry weight determinations ordinarily would have been preferred, but the samples were in Tris buffer and would not readily dry to constant weight.
based) on a recovery of 96%; this value was obtained from a known sample of cysteine treated in the same manner as were protein samples. Cysteine was determined both according to the method of Boyer (15) with p-hydroxymercuribenzoate and according to the method of Ellman (16) with 5,5'-dithio-bis(2-nitrobenzoic acid). Tryptophan and tyrosine were determined spectrophotometrically in 6 M guanidine HCl by the method of Edelhoch (17).

Equilibrium—Equilibrium centrifugation studies were performed by both the conventional method as described by Chervenka (18) and the meniscus depletion method of Yphantis (19) were performed on a Beckman model E analytical ultracentrifuge. The instrument was equipped with an R1C temperature control and an electronic speed control. Rayleigh interference optics aligned by the method of Richards et al. (20) were used for all experiments. Photographs were taken by Kodak II-G spectrographic plates and read manually on a Nikon model 6 Shadograph microcomparator (Nippon Kogaku, Tokyo). Some plates from meniscus depletion experiments were scanned by a Grant comparator-microdensitometer (Grant Instruments, Berkeley, Calif.) interfaced with a Varian 620I computer (12).

When samples containing high concentrations of urea were run, blurring of the interference pattern usually occurred. This problem was alleviated by placing a Polaroid filter in the light path. This problem and its solution have been reported previously by Teller et al. (21).

The densities of all dialyzed for centrifuge studies were measured using a DMA 85C Digital Precision Densimeter (Anton Paar K.G., Graz, Austria).

Calculations for slow speed equilibrium runs were performed as described by Chervenka (18) using a computer program written by S. Lowe. Data from meniscus depletion experiments were processed with a program written by Dr. R. Tyson of Oregon State University and modified for our system (12).

Peptide Mapping—Thin layer (0.25 mm of cellulose) peptide maps were produced using electrophoresis in the first direction followed by chromatography in pyridine-1-butanol-acetic acid-water (10:15:3:12). Electrophoresis was performed either at pH 6.5 using a buffer containing 100 ml of pyridine and 4 ml of glacial acetic acid in 1 liter of distilled water or at pH 1.9 using a buffer containing 150 ml of glacial acetic acid and 50 ml of 88% formic acid in 1 liter of distilled water. Peptides were detected with 0.25% ninhydrin in acetone followed by the fluorescent reagent of Yamada and Itano (24) to detect arginine-containing peptides.

RESULTS

Extinction Coefficient—In 0.1 M NaCl adjusted to pH 7.5 the extinction coefficient, \(E_{1%}^{1cm}\), was found to have a value of 11.25

Partial Specific Volume—In 0.05 M Tris, 0.1 M KCl adjusted to pH 7.8 with glacial acetic acid at 20°C, the value of the apparent partial specific volume of phosphoglucose isomerase was found to be 0.732 ml per g using the magnetic densimeter. A value of 0.741 ml per g was obtained from the amino acid composition by the method of Cohn and Edsall (25). The former value was used for calculation of all molecular weights from the ultracentrifuge data.

Equilibrium Centrifugation of Phosphoglucoisomerase—Molecular weight determinations of phosphoglucose isomerase were performed both by the conventional and by the meniscus depletion methods in 0.05 M Tris-acetate, 0.1 M KCl, pH 7.8, at 20°C. For a conventional run at an initial concentration of 1.8 mg per ml and a rotor speed of 7,200 rpm, the least squares fit of the data gave an apparent molecular weight of 119,400 ± 400.

The results of a meniscus depletion experiment at an initial protein concentration of 0.2 mg per ml are shown in Fig. 1. An apparent weight average molecular weight of 119,500 ± 600 was obtained from the straight line fit of the In concentration versus In concentration for this run. The point values of the weight and number average molecular weights are close to this value and show no concentration dependence. This coincidence and the agreement between values obtained at very different initial concentrations by the two methods demonstrate that this preparation of phosphoglucose isomerase was homogeneous with respect to molecular size.
weight and did not readily undergo concentration-dependent association-dissociation reactions in the native state. Additional evidence of homogeneity was provided by acrylamide gel electrophoresis of native phosphoglucoisomerase which yielded a single band under a variety of conditions.

Chemical Composition—Amino acid analysis, performic acid oxidation, measurement of ultraviolet spectra in guanidine HCl, and titration with sulphydryl reagents were used to determine the total composition of phosphoglucoisomerase. Table I summarizes the results of these methods in amino acid residues per 119,400 g of protein.

Table I

<table>
<thead>
<tr>
<th>Amino acid composition of phosphoglucoisomerase</th>
<th>mol/119,400 g</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lysine</td>
<td>77.0 ± 3.6</td>
</tr>
<tr>
<td>Histidine</td>
<td>31.6*</td>
</tr>
<tr>
<td>Arginine</td>
<td>23.1 ± 0.8</td>
</tr>
<tr>
<td>Aspartic acid</td>
<td>120.9 ± 3.0</td>
</tr>
<tr>
<td>Threonine</td>
<td>74.4*</td>
</tr>
<tr>
<td>Serine</td>
<td>77.0*</td>
</tr>
<tr>
<td>Glutamic acid</td>
<td>103.8 ± 2.8</td>
</tr>
<tr>
<td>Proline</td>
<td>36.0 ± 2.2</td>
</tr>
<tr>
<td>Glycine</td>
<td>80.5 ± 2.6</td>
</tr>
<tr>
<td>Alanine</td>
<td>93.4 ± 4.9</td>
</tr>
<tr>
<td>Valine</td>
<td>77.7 ± 3.8</td>
</tr>
<tr>
<td>Methionine</td>
<td>15.8 ± 0.7</td>
</tr>
<tr>
<td>Isoleucine</td>
<td>55.3 ± 1.8</td>
</tr>
<tr>
<td>Leucine</td>
<td>88.3 ± 3.0</td>
</tr>
<tr>
<td>Tyrosine</td>
<td>29.8 ± 0.7</td>
</tr>
<tr>
<td>Phenylalanine</td>
<td>57.6 ± 2.3</td>
</tr>
<tr>
<td>Tryptophan</td>
<td>16.4*</td>
</tr>
<tr>
<td>Half-cystine</td>
<td>1.5*</td>
</tr>
</tbody>
</table>

* Extrapolated to zero time of hydrolysis.
* Spectrophotometric.
* As cysteic acid following performic acid oxidation.

Table II: The values obtained from amino acid hydrolysis represent averages of four or more determinations at a pH less than two with hydrolysis times except for serine and threonine. The values for these were extrapolated to zero time of hydrolysis and for histidine the values are the average of only the 96-hour determinations. Tryptophan and tyrosine were determined from the neutral spectrum in 6 M guanidine HCl. The value for tyrosine obtained by this method was essentially identical with that obtained from amino acid analysis. Calculation of tyrosine content by measuring the change in absorption at 295 or 300 nm during titration of tyrosyl residues yielded values approximately 10% higher. This difference appeared to be due to turbidity at the highly alkaline pH required for the titration. The value from this method was discarded.

The values obtained for titration of free sulphydryl groups of denatured phosphoglucoisomerase in either 8 M urea or 6 M urea or 6 M guanidine HCl ranged from 0.0 to 0.5 sulphydryls per 119,400 g of protein both with p-hydroxymercuribenzoate and with 5,5'-dithiobis(2-nitrobenzoic acid). Performic acid oxidation yielded approximately 1.5 cysteic acid residues per 119,400 g of protein.

Acrlylamide Gel Electrophoresis of Protein-Sodium Dodecyl Sulfate Complexes—Phosphoglucoisomerase denatured in sodium dodecyl sulfate in either the presence or the absence of 1% 2-mercaptoethanol yielded two bands during acrylamide electrophoresis. Increasing the incubation temperature from ambient temperature to 37°C or even 50°C did not result in a single band. From the straight line least squares fit of the calibration curve the two phosphoglucoisomerase bands were estimated to have molecular weights of 31,200 and 63,600. Within the error of the method these values correspond to one-fourth and one-half the preparative molecular weight, respectively.

Gel Filtration in 6 M Guanidine Hydrochloride—The discovery of two species upon denaturation of phosphoglucoisomerase with sodium dodecyl sulfate under reducing conditions prompted further investigation of the effects of denaturing agents on the enzyme. For this purpose the enzyme was first reduced in 6 M guanidine HCl with 2-mercaptoethanol, reacted with ethylene-imine to block free sulphydryls, applied to a calibrated Sepharose 6B column, and eluted with 6 M guanidine HCl. Once again two species were found. A plot of the logarithm of the molecular weight as a function of the ratio of the elution volume to the void volume (V/V0) is shown in Fig. 2 for protein standards and phosphoglucoisomerase. From this calibration curve two phosphoglucoisomerase components were estimated to have molecular weights of 27,900 and 58,700. Plotting V/V0 versus log molecular weight yielded a straight line in the applicable range. This fact and the inherent inaccuracy of the method did not justify more sophisticated treatment of the data. In order to determine whether the two bands represent incomplete dissociation or different subunits the experiment was repeated with increased concentration of 2-mercaptoethanol and higher incubation temperature. The elution curves for the two experiments are shown in Fig. 3. Incubation at room temperature with 0.1 M 2-mercaptoethanol gave a 49:51 ratio of the heavy to light peaks. For the sample incubated with 0.2 M 2-mercaptoethanol at 45°C, this ratio changed to 32:68. These results suggest that the two peaks are merely different aggregation stages.

Sedimentation Equilibrium Studies on Phosphoglucoisomerase in 8 M Urea—Further efforts to elucidate the subunit structure of phosphoglucoisomerase were carried out by meniscus depletion centrifugation studies in 8 M urea both in the presence of and the absence of reducing agents. These studies were repeated on both the heavy and light fractions obtained from gel filtration in 6 M guanidine HCl.

Plots of point weight average molecular weight versus concentration for two phosphoglucoisomerase samples in 8 M urea, 0.1 M KCl are shown in Fig. 4. The sample denatured in urea but not treated with any reducing agent shows point values for weight average molecular weight ranging from 47,000 near the meniscus up to 75,000 near the base of the cell. The values for the other sample which was first reduced with 0.2 M 2-mercaptoethanol and aminoethylated display less marked concentration dependence. Extrapolation of the weight average values to zero concentration yields an estimated molecular weight of 29,800. Reduction by 0.02 M dithioerythritol gave results similar to those obtained with 2-mercaptoethanol. Centrifugation in the presence of either reducing agent (rather than blocking of sulphydryls by aminoethylidyne) also gave comparable results.

Aliquots of both fractions obtained by gel filtration through Sepharose 6B were dialyzed against 8 M urea, 0.1 M KCl for centrifugation studies. Another aliquot of the heavy fraction
FIG. 2 (left). Calibration curve for determination of molecular weights by gel filtration in 6 M guanidine HCl. Log molecular weight versus the ratio of the elution volume to the void volume ($V_e/V_0$). Phosphoglucose isomerase is represented by vertical bars. The protein standards and their molecular weights are: 1, bovine serum albumin (68,000); 2, ovalbumin (43,000); 3, chymotrypsinogen (25,700); 4, ribonuclease (13,700) (22). The straight line is the least squares fit of the data for the first three standards.

FIG. 3 (right). Absorbance at 280 nm corrected for absorbance due to Blue Dextran 2000 versus elution volume ($V_e$) in grams. Solid line represents a sample incubated at ambient temperature in 6 M guanidine HCl, 0.1 M 2-mercaptoethanol, pH 8.6. Dotted line represents phosphoglucose isomerase incubated at 45° with 0.2 M 2-mercaptoethanol.

FIG. 4. Point weight average molecular weights as a function of concentration in fringes for phosphoglucose isomerase in 8 M urea, 0.1 M KCl, pH 8, at 20°. X, urea-denatured, 0.3 mg per ml, 30,000 rpm; Δ, reduced and aminoethylated in urea, 0.2 mg per ml, 36,000 rpm.

FIG. 5. Point weight average molecular weights as a function of concentration in fringes for phosphoglucose isomerase samples from Sepharose 6B column. Determined in 8 M urea, 0.1 M KCl, at 20°. A, heavy fraction, 26,000 rpm; B, light fraction, 34,000 rpm; C, twice reduced, aminoethylated heavy fraction, 36,000 rpm. Initial concentration of samples from 0.2 to 0.3 mg per ml.

was subjected to a second reduction with 0.1 M 2-mercaptoethanol followed by aminoethylation before dialysis against urea. The results obtained for all three samples are shown in Fig. 5. The point molecular weight values for the heavy fraction are highly concentration dependent; those obtained for the light fraction and the twice reduced, aminoethylated heavy fraction are much lower and only slightly concentration dependent. Extrapolation to zero concentration of these data yields values of 31,500 and 29,000 for the light and twice reduced fractions, respectively.

Peptide Mapping—To show whether the subunits of phosphoglucose isomerase are identical or nonidentical a series of tryptic peptide maps were produced. Heat-denatured, guanidine HCl-denatured, and aminoethylated, denatured samples all behaved well in tryptic digestion; all three initially were precipitates but were completely solubilized on digestion. On peptide maps aminoethylated, denatured phosphoglucose isomerase showed no material remaining at the origin.

On the basis of the content of lysine and arginine (77.6 ± 3.6 and 23.1 ± 0.8 mol/194,000 g of protein, respectively) and assuming that the enzyme is composed of identical polypeptide chains of 30,000 molecular weight, the expected yield from tryptic digestion would be 26 to 27 peptides (1 + 19.4 ± 0.9 lysine + 5.8 ± 0.2 arginine).

Fig. 6, A and B, shows peptide maps of digests of aminoethylated, denatured phosphoglucose isomerase at both pH 6.5 and pH 1.9. Fig. 7, A and B, shows peptide maps of digests of heat-denatured and guanidine HCl-denatured samples, respectively, both with electrophoresis performed at pH 6.5. Electrophoresis of either heat-denatured or guanidine HCl-denatured samples at pH 1.9 resulted in badly streaked maps. Since peptide maps of aminoethylated, denatured phosphoglucose isomerase obtained at both pH 1.9 and pH 6.5 showed essentially the same numbers of peptides, resolution at the higher pH was deemed satisfactory.
peaks partially overlap. The latter difficulty is exacerbated in aggregates.

tyrosine elutes near the end of the run, diffusion causes the peak phosphoglucose isomerase, whether from urea, guanidine HCl, additional evidence for identical subunits of 30,000 molecular weight is provided by the number of arginine peptides found; the expected yields shown in Table II are in close agreement.

The numbers of peptides obtained from these experiments and the expected yields shown in Table II are in close agreement. Additional evidence for identical subunits of 30,000 molecular weight is provided by the number of arginine peptides found; five strongly fluorescing spots were observed by the method of Itano (24) while six were expected.

Although the results of this set of experiments argue in favor of identical subunits, the half-cystine content from performic acid oxidation (0.4 mol/30,000 g) would suggest that the subunits are not identical. The values obtained for other amino acids present in low enough quantities to consider are compatible with identical 30,000 molecular weight subunits (7.9 histidines, 5.8 arginines, 9.0 prolines, 4.0 methionines, and 4.1 tryptophans per 30,000) except for tyrosine (7.5 per 30,000). Two difficulties affect the accuracy of tyrosine determinations. First, since tyrosine elutes near the end of the run, diffusion causes the peak to be low and broad. Second, the tyrosine and phenylalanine peaks partially overlap. The latter difficulty is exacerbated in this protein because the phenylalanine content is twice that of tyrosine. Whether the half-cystine content found is the true value or too low remains unclear.

**DISCUSSION**

The evidence presented in this paper demonstrates that bakers' yeast phosphoglucose isomerase has a preparative molecular weight of 119,400 ± 600 and is composed of four subunits. These subunits were found to be either identical or nearly so.

Equilibrium centrifugation in Tris buffer at pH 7.8 showed no concentration dependence of molecular weight over a wide concentration range; thus, the values of 119,400 ± 400 and 119,500 ± 600 found by the conventional and meniscus depletion methods, respectively, represent the molecular weight of a single entity rather than the average for a series of aggregates.

The finding of species corresponding to one-fourth and one-half the preparative molecular weight both from acrylamide gel electrophoresis of protein-dodecyl sulfate complexes and from gel filtration in 6 M guanidine HCl could have indicated either incomplete dissociation (or dissociation followed by reaggregation) or that phosphoglucose isomerase is composed of subunits of different molecular weights. A third possibility is that, since the validity of both of these methods depends on having the protein completely unfolded, anything causing a compact configuration of the subunit would cause an estimate of molecular weight far less than the true value. Equilibrium ultracentrifugation of aliquots of both the heavy and light phosphoglucose isomerase fractions obtained by gel filtration showed that the molecular weight of the light fraction was close to the estimate from the column, and that additional treatment of the heavy fraction could cause dissociation to the same molecular weight exhibited by the light fraction. Thus, phosphoglucose isomerase appears to be composed of polypeptides of approximately 30,000 molecular weight and the heavy fraction exists either because of incomplete dissociation or because of reaggregation. The failure of sodium dodecyl sulfate to cause complete dissociation is not unique to this protein (26, 27, 38).

Although reduction, or reduction followed by modification of free sulfhydryl groups, was required to produce complete dissociation to monomer, one need not assume the existence of interchain disulfide bonds in the native enzyme (8). Partial dissociation to monomer was observed after treatment of phosphoglucose isomerase with sodium dodecyl sulfate without reduction, and equilibrium centrifugation in 8 M urea without reduction gave point values of the weight average molecular weight near the meniscus approaching the monomer weight (Fig. 4). A possible explanation for the effect of reducing agents is that, while the native enzyme may contain reduced cysteines, they could be widely separated or sterically hindered and not able to come together to form disulfide linkages between polypeptide chains until the protein is denatured.

In 6 M urea, phosphoglucose isomerase has been shown by optical rotatory dispersion to have lost nearly all its helical structure (29); thus, the enzyme shows partial reassociation without regaining the secondary structure of the native state. In this respect phosphoglucose isomerase displays behavior analogous to the cyclic association-dissociation phenomena found by Contaxis and Reichel with urease and β-galactosidase (9, 30, 31). However, while both these proteins return to the native state with removal of denaturing agents, all attempts to renature phosphoglucose isomerase, whether from urea, guanidine HCl, or sodium dodecyl sulfate, resulted in formation of insoluble aggregates.
The aggregation of denatured phosphoglucomutase isomerase found in gel filtration is probably due to the high initial protein concentrations (10 to 12 mg per ml) used in those experiments. This hypothesis is supported by the finding that concentrating the same sample at a concentration of 0.3 mg per ml showed very little tendency to aggregate during centrifugation. In contrast, an aliquot of the light fraction from gel filtration to 1.5 mg per ml resulted in a strong tendency to aggregate during centrifugation (Fig. 5).

That the 30,000 molecular weight polypeptide chains obtained by dissociation of the reduced enzyme are identical, or nearly so, was shown by the peptide maps of tryptic digests both of denatured and modified phosphoglucomutase isomerase. The enzyme did not produce an insoluble tryptic core; therefore, the numbers of peptides obtained should be close to the theoretical yield. The numbers of peptides found clearly rule out a dimeric structure for the bakers' yeast enzyme. The results of amino acid analysis are for the most part compatible with the conclusion that the enzyme has identical subunits; however, the half-cystine content cannot be reconciled with truly identical subunits. Whether the half-cystine content is due to analytical difficulties or actual small differences in the subunits is unclear.

Rabbit muscle phosphoglucomutase isomerase has been well characterized by Noltmann et al. (6-8). In their studies the rabbit muscle enzyme was found to have a preparative molecular weight of 132,000 and was found to be composed of only two identical subunits. Given the vital role of phosphoglucomutase at the beginning of the glycolytic pathway, it seems probable that the differences between the yeast and the rabbit muscle enzymes are due to divergent evolution. One might hypothesize that at some point in time gene duplication occurred and was followed by a mutation linking the two chains to produce the longer chain found in the rabbit muscle enzyme.

Noltmann et al. have also found that the subunit size of brewers' yeast phosphoglucomutase isomerase is similar to that of rabbit muscle (32, 33). Although this result is surprising, it should be noted that bakers' and brewers' yeasts are different species (Saccharomyces cerevisiae and Saccharomyces carlsbergensis, respectively) and that the former is produced commercially under aerobic conditions while the latter is grown anaerobically.

The subunit sizes published for brewers' yeast, rabbit muscle, and other mammalian phosphoglucomutase isomerases are also in marked contrast to the results for most other aldose-ketose isomerases (34). It is possible that this change of subunit size may have significance with regard to the role of the enzyme in regulation of the relative rates of utilization of glucose by the glycolytic pathway and the pentose shunt.

Acknowledgments—We wish to thank Dr. G. Vaneeck for his invaluable instruction in the techniques of peptide mapping and for his critical reviews of the manuscript. We are grateful to Dr. S. Rogers for assistance in performing the initial amino acid analyses and to Dr. R. Wolfe for permission to use the instrument. We also thank R. Goodrich for his measurements of densities on the magnetic densimeter and his other technical assistance. In addition we would like to express our appreciation for other help provided by Dr. J. McIlvane (Department of Physics), Dr. J. Robbins, Dr. M. Lowe, and G. Lindly.

REFERENCES

The subunit structure of phosphoglucone isomerase from bakers' yeast.
S L Lowe and F J Reithel


Access the most updated version of this article at http://www.jbc.org/content/250/1/94

Alerts:
- When this article is cited
- When a correction for this article is posted

Click here to choose from all of JBC's e-mail alerts

This article cites 0 references, 0 of which can be accessed free at http://www.jbc.org/content/250/1/94.full.html#ref-list-1