Partial Amino Acid Sequence of the Glutamate Dehydrogenase of Human Liver and a Revision of the Sequence of the Bovine Enzyme*

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The glutamate dehydrogenase from a single human liver has been studied. The subunit size was found to be 55,200 ± 1,500 by sedimentation equilibrium. The partial specific volume is 0.732 as calculated from the amino acid composition. The sequence was determined by isolation of peptides after cyanogen bromide (CNBr) cleavage; the fraction containing the largest peptides was hydrolyzed by trypsin after maleylation. Studies on these peptides accounted for 454 residues of the 505 residues that are presumably present in the protein.

For the 51 residues that were not represented in isolated peptides, we have tentatively assumed that the sequence is the same as that of the bovine enzyme. Methionine and arginine residues in these peptides could be placed on the basis of the specificity of cleavage by CNBr or trypsin. In all, 349 residues were placed in sequence, and were aligned by homology with the corresponding peptides of the bovine and chicken enzymes. From the present information, there are 24 known differences in sequence between the human and bovine enzymes and 41 between the human and chicken enzymes. In addition, the human enzyme contains 4 additional residues at the NH2 terminus as compared to the bovine enzyme.

In a peptide from the human enzyme, an additional residue, isoleucine 385, was detected by automated Edman degradation. Reinvestigation of the bovine sequence demonstrated that this residue is also present in the bovine enzyme (and presumably in the chicken enzyme as well). Residue 384 of the bovine enzyme, previously reported as Glx has now been shown to be glutamine.

In earlier investigations, the amino acid sequences of the glutamate dehydrogenases of bovine liver (1, 2) and of chicken liver (1, 3) have been reported. The coenzyme-specific glutamate dehydrogenases of Neurospora crassa have also been studied; the complete sequence of the NADP-specific enzyme has been described (4), and a large part of the sequence of the NAD-specific enzyme has been published (5, 6).

We now wish to report on a study of the sequence of the human glutamate dehydrogenase obtained from the liver of a single individual. Because of the limited amount of material available, less than 7.7 μmol of the protein subunit of M, ≈ 55,200, it was not possible to obtain complete evidence for all of the sequence. Nevertheless, there has emerged from this study a number of differences in the sequence of the human glutamate dehydrogenase when compared to bovine glutamate dehydrogenase. Further, earlier studies on the bovine and chicken enzymes were undertaken before automated sequencing was available. In investigating one of the large peptides from the human protein by the automated Edman degradation, it became evident that an additional residue was present in the peptide, as compared to the corresponding peptide from the bovine enzyme. Reinvestigation of the homologous peptide from bovine glutamate dehydrogenase by automated sequencing revealed that this "extra residue" is also present.

For ease of reference, Fig. 1, A and B present the evidence for the partial sequence of the glutamate dehydrogenase of human liver. The peptides that were isolated and characterized are shown. The various symbols are described in the legend to Fig. 1A.

The sequences of the bovine, chicken, and human glutamate dehydrogenases are shown for comparison in Fig. 2. The sequences of the bovine and chicken enzymes have been revised to include residue 385 (isoleucine) (see "Discussion").

The sections on "Materials and Methods" and "Cyanogen Bromide Peptides" are in the miniprint supplement.†

SEQUENCE STUDIES

The sequence studies are summarized in Fig. 1, A and B. The results obtained by automated Edman degradation, hydrolysis by carboxypeptidases, or aminopeptidase M of individual peptides are presented in Tables VIII, IX, and X, respectively. The positions of the peptides and the residue numbers are based on the sequence of bovine glutamate dehydrogenase shown in Fig. 2 (1, 2), which has been corrected by inclusion of isoleucine 385 (see "Discussion"). The locations of methionine and arginine residues are assumed on the basis of the specificity of cleavage by CNBr‡ and trypsin without further comment.

1 Portions of this paper (including "Materials and Methods," Figs. 3 to 16, and Tables 1 to XV) are presented in miniprint immediately following this paper. Miniprint is easily read with the aid of a standard magnifying glass. Full size photocopies are available from the Journal of Biological Chemistry, 9650 Rockville Pike, Bethesda, Md. 20014. Request Document No. 78 M-1175, cite authors, and include a check or money order for $5.55 per set of photocopies. The abbreviations used in the miniprint are: DPAW, 1-butanol/pyridine/acetic acid/water; PE, paper electrophoresis.

2 The abbreviations used are: CNBr, cyanogen bromide; peptides derived by cleavage with cyanogen bromide, CN; by tryptic hydrolysis of maleylated material, TM; by tryptic hydrolysis, T; by chymotryptic hydrolysis, C; PTH, phenylthiohydantoin; Hse, homoserine, analytical values for homoserine include values for the lactone also, unless otherwise noted.
Residues -4 through 12 (Peptides CN 1, CN 1A, and CN 1B)—Peptide CN 1B is from the cleavage of the Asp-Pro bond between residues 6 and 7 (Fig. 1A). The sequence was determined by carboxypeptidase action and by eight steps of Edman degradation on Peptide CN 1. The composition and basicity of Peptide CN 1B placed Asn at residue 8.

Residues 13 through 19 (Peptide TM 2B)—Two manual Edman steps and hydrolysis with carboxypeptidases A + B yielded the sequence.

Residues 20 through 33 (Peptide TM 3)—Peptides TM 3-Tl and T2 (Table V) were subjected to manual Edman degradation. Peptides TM 3 and TM 3-Tl were also hydrolyzed with carboxypeptidases A + B (Table IX). Ser-22 was placed on the basis of the trace amount released by the carboxypeptidases from TM 3-Tl; the absence of Gly and Ala from this hydrolysate placed Ala-21 by difference.

Residues 34 and 35—Peptide TM 4 was not recovered. The presence of threonine 34 was assumed in bovine glutamate dehydrogenase.

Residues 36 through 42 (Peptide TM 5)—No residue was released by Edman degradation because of cyclization of NH2-terminal glutamine by analogy with residue 36 of bovine glutamate dehydrogenase. Hydrolysis with carboxypeptidases A + B released arginine, lysine, glutamine, and a trace of hydrolyses of the mixture of the maleylated CN peptides, C, chymotryptic peptides, T, trypptic peptides. Residues in capital letters were identified. Residues in parentheses were not placed in sequence and refer to homologous residues in the sequence of the bovine liver enzyme. Residues marked with an asterisk (*) were identified as glutamine because of conversion to pyrrolidone carboxylic acid. B, the amino acid sequence of human liver glutamate dehydrogenase from residues 251 through 501. The symbols are given in A.

Fig. 1. A, the amino acid sequence of the human liver glutamate dehydrogenase from residues -4 through 250. The symbol — indicates residues identified as the PTH-derivative after Edman degradation. The symbol — indicates residues identified after hydrolysis with aminopeptidase M. The symbols — indicate residues identified after hydrolysis with carboxypeptidases A, A + B, or Y, respectively. Peptides below the sequence were isolated or identified. CN, cyanogen bromide peptides; TM, peptides from trypptic hydrolyses of the mixture of the maleylated CN peptides; C, chymotryptic peptides; T, trypptic peptides. Residues in capital letters were identified. Residues in parentheses were not placed in sequence and refer to homologous residues in the sequence of the bovine liver enzyme. Residues marked with an asterisk (*) were identified as glutamine because of conversion to pyrrolidone carboxylic acid. B, the amino acid sequence of human liver glutamate dehydrogenase from residues 251 through 501. The symbols are given in A.
glutamic acid. The composition and partial sequence of this peptide indicated that Ser was a replacement for Thr in the corresponding, otherwise identical, bovine peptide.

**Residues 43 through 46 (Peptides TM 6 and TM 7)—**
Asparagine 43 was released by aminopeptidase M (Table X).

**Residues 47 through 66 (Peptides TM 8 and 8A)—**
The NH₂-terminal end of Peptide TM 8 was determined by Edman degradation and aminopeptidase M hydrolysis. The first 8 residues of Peptide TM 8A were identified by Edman degradation (Table VIII). From these data and the results with carboxypeptidase Y (Table IX), most of the sequence was determined.

**Residues 68 through 79 (Peptide TM 9)—**
One step of Edman degradation yielded aspartic acid; no additional residue was released. Carboxypeptidases A + B released only arginine and tyrosine.

**Residues 80 through 86 (Peptide TM 10)—**
The low yield of this peptide permitted only the study of carboxypeptidase
action, which released arginine, glutamine, serine, and histidine. Since the peptide was identical in composition and chromatographic properties with the identical peptide from the bovine enzyme, it is presumed to have the same sequence. The peptide was stained blue with ninhydrin, which excluded chromatographic properties with the identical peptide from dme. Since the peptide was identical in composition and action, which released arginine glutamine, serine, and histidine residue 168. The composition of Peptide CN 5 was identical with those of chicken enzymes. Hydrolysis with aminopeptidase M placed indecisive (Table IX).

**Residues 87 through 94 (Peptide TM 11)**—The sequence was almost completely determined on Peptides TM 11 and TM 11-T2 (Table V).

**Residues 95 through 111 (Peptide TM 12A)**—Ten residues were determined by Edman degradation (Table VIII); carboxypeptidase Y released homoserine, leucine, serine, and alanine (Table IX) and unexpectedly, valine, presumably as a contaminant. Homoserine was placed on the basis of CNBr cleavage; the carboxypeptidase hydrolysate was not analyzed for the lactone.

**Residues 112 through 150 (Peptides CN 3, TM 12B, and TM 13A)**—A partial sequence of 18 residues was obtained by Edman degradation of Peptide CN 3 in the mixture with Peptide CN 10 (Table XI). This sequence was confirmed by Edman degradation of Peptide TM 12B (Table VIII). The composition of Peptide TM 12B was identical with that of the corresponding bovine peptide except for the presence of Ser-112. This peptide includes Lys-126, which had been previously shown to be the single reactive lysine of various vertebrate glutamate dehydrogenases. Lys-126 is present in the identical sequence in a number of these enzymes (1-3). Carboxypeptidases A and B aided in determining the COOH-terminal ends of Peptides TM 12B and CN 3 (see Table IX). Arginine, threonine, isoleucine, and lysine were released from Peptide TM 12B, as expected from homology with the bovine sequence. Homoserine and threonine were released from Peptide CN 3 together with leucine from Peptide CN 10 (Fraction II, Fig. 4). These results were confirmed by hydrolysis of Peptide TM 13A with aminopeptidase, which released only phenylalanine after a short time (Table X).

**Residues 151 through 176 (Peptides CN 4 + 5 and CN 5)**—The 17 residues at the NH2-terminal end of Peptide CN 4 + 5 were determined by Edman degradation (Table VIII), although the initial yield was low because of partial cyclization of the NH2-terminal glutamine. From the difference in compositions of Peptides CN 4 + 5 and CN 5, Asx was placed at residue 168. The composition of Peptide CN 5 was identical with that of the corresponding peptides from the bovine and chicken enzymes. Hydrolysis with aminopeptidase M placed Ser at the NH2 terminus, Thr and Gln as the next 2 residues, and Glu as the 4th residue. The carboxypeptidase results were indicative (Table IX).

**Residues 177 through 223 (Peptides CN 6 and TM 15)**—No pure peptides were obtained covering this region of the molecule; however, Peptide CN 6 was co-purified with Peptide CN 4 + 5 (see Figs. 6 and 7) in small amounts. From this mixture, the action of carboxypeptidase Y placed only homoserine, tyrosine, and serine. Automated Edman degradation of the mixture (Table XII) allowed the identification of some residues of Peptide CN 6 since the NH2-terminal sequence of Peptide CN 4 + 5 was already known. Evidence for the similarity of this region to the homologous portion of bovine glutamate dehydrogenase was also shown by the isolation of Peptide TM 15 (residues 212 through 217) which was identical in sequence with the corresponding peptide from bovine glutamate dehydrogenase.

**Residues 234 through 238**—A sequence corresponding to Peptide CN 7 was not isolated. The composition in Fig. 1 is that of bovine and chicken glutamate dehydrogenase.

**Residues 239 through 260 (Peptide CN 8)**—Although Peptide CN 8 was purified from Fraction CN IV (see Figs. 4 and 5), the amount recovered was insufficient for Edman degradation and this material was pooled with the mixture of Peptides CN 8 and CN 9A also recovered from Fraction CN IV (Fig. 4). The NH2-terminal residues of Peptide CN 8 could be determined from the automated Edman degradation (Table XIII) since the NH2-terminal sequence of Peptide CN 9A was determined on Peptides TM 17 and TM 18 (see below). Carboxypeptidase Y released only traces of homoserine and serine from the pure sample of Peptide CN 8 (Table IX).

**Residues 261 through 333 (Peptides CN 9A, TM 17, and 18)**—Peptide TM 18 (Table IV) showed several differences in composition from that of the homologous peptide from bovine glutamate dehydrogenase (Fig. 2). Peptide TM 17 was studied by enzymic hydrolysis (Tables IX and X) and by Edman degradation of Peptide CN 9A (Table XIII), which placed arginine 261. Peptide TM 18 was subjected to Edman degradation, but only the first 17 residues were determined since the recoveries were low after glutamine 275 (Table VIII). Studies on the chymotryptic peptides derived from Peptide TM 18 (see Figs. 14 to 16) provided most of the remainder of the sequence, which showed 10 replacements as compared to the bovine enzyme. Only the dipeptide Lys—Leu was not obtained from the chymotryptic hydrolysate; these 2 residues were placed on the basis of chymotryptic specificity. Gln-297 was placed on the basis that Peptide TM 18 C3 was ninhydrin negative, and His-298 by difference. The results with carboxypeptidase Y on Peptide TM 18-C1 placed Leu at the COOH terminus (residue 294) in accord with chymotryptic specificity. The remainder of the composition of the COOH end of this peptide is consistent with the sequence of the bovine and chicken enzymes, particularly since a Gln—Leu—Glu sequence would not be susceptible to chymotryptic hydrolysis.

**Residues 334 through 338 (Peptide TM 19)**—Only a small amount of this peptide was obtained. The absence of proline 337 present in bovine glutamate dehydrogenase and the presence of threonine (Table IV) in human glutamate dehydrogenase indicates a single amino acid replacement (Fig. 2).

**Residues 339 through 363 (Peptides TM 20 and 20A)**—Peptide TM 20A was present in the hydrolysate presumably because of incomplete maleylation of lysine 342 (Fig. 10). Although the sequence is incomplete, it is consistent with that of bovine and chicken glutamate dehydrogenase.

**Residues 364 through 366 (Peptide TM 21A)**—Aminopeptidase released asparagine after a short period of incubation (Table XI).

**Residues 367 through 411 (Peptide CN 10)**—Peptide CN 10 was almost completely sequenced by Edman degradation of the mixture of Peptides CN 3 and 10 (Table XI) and by study of the tryptic peptides from the mixture (Table VII). Unexpectedly, Edman degradation revealed the presence of an isoleucine residue immediately following glutamine 384. This residue was followed by a sequence identical with that of the homologous bovine peptide. This isoleucine residue has now also been found to be present in bovine glutamate dehydrogenase (see below).

**Residues 412 through 419 (Peptide TM 23B)**—This peptide was subjected to manual Edman degradation which released Asx followed by valine, while the third step did not yield an identifiable residue. In the corresponding peptide from the bovine enzyme, the 3rd residue is glutamine; this presumably cyclized during the Edman procedure.

**Residues 420 through 439 (Peptide TM 24)**—Although it was recovered in significant amount, Peptide TM 24 was lost during automated Edman degradation because of mechanical failure. This peptide was also present with Peptide TM 25A in Fraction D (Fig. 11). Because of the limited amount available, the mixture was studied without purification (Table XI).
Hydrolysis of Peptide TM 24 with carboxypeptidase Y (Table IX) released mainly arginine, aspartic acid, serine, and leucine, but no threonine (bovine residue 433) or phenylalanine (bovine residue 436), as expected from the composition of Peptide TM 24 (Table IV).

Residues 440 through 457 (Peptide TM 25A)—The sequence of Peptide TM 25A was studied by Edman degradation in the mixture with Peptide TM 24 (Table XIV). The pure peptide (Fraction H, Fig. 11) was hydrolyzed with carboxypeptidase A (Table IX). The results were consistent with the sequence of the homologous bovine peptide.

Residues 458 through 469 (Peptides CN 12 + 13, CN 12, and CN 13)—Five steps of Edman degradation on Peptide CN 12 + 13 were performed (Table VIII). Peptide CN 13 was hydrolyzed with aminopeptidase M (Table X) and gave the sequence of the other residues.

Residues 470 through 501 (Peptide CN 14)—Although a carry-over was observed after the first step of automated Edman degradation, the sequence of the last 22 residues of Peptide CN 14 was determined (Table IX). The results were consistent with the sequence of the homologous bovine peptide.
Edman degradation, presumably because of incomplete cleavage, 18 residues could be determined with no ambiguity by analogy with the homologous peptide from bovine glutamate dehydrogenase (Fig. 1). Most of the remainder of the sequence was obtained on trypsin Pep tide CN 14-T4, which was identical in composition with the corresponding peptide from the bovine enzyme (Table VII). Hydrolysis with aminopeptidase M (Table X), and two steps of manual Edman degradation as well as hydrolysis with carboxypeptidases A + B (Table IX), gave most of the sequence of Peptide CN 14, the COOH-terminal sequence in the protein. A small amount of Peptide CN 14-T3 was isolated and identified after hydrolysis by its qualitative composition on paper electrophoresis. This permitted placing Lys-488 at the site of tryptic hydrolysis.

**REINVESTIGATION OF PEPTIDES CN 10 AND CN 10 + 11 OF BOVINE GLUTAMATE DEHYDROGENASE**

As noted above, the study of Peptide CN 10 (residues 367 through 411) from human glutamate dehydrogenase revealed that, although this sequence was apparently identical with that of the peptide from bovine glutamate dehydrogenase, an additional residue of isoleucine was present at residue 19 of the peptide (residue 385 of the protein); however, the sequence of the peptide on both sides of the isoleucine residue was identical with that of the bovine enzyme. In order to determine whether this residue had been overlooked in piecing together the sequence from various small peptides (19), the sequence of the bovine peptide was reinvestigated.

A sample of bovine glutamate dehydrogenase (7 µmol of the subunit polypeptide chain) was carboxymethylated with iodoacetate and cleaved with a 200-fold molar excess of CNBr over methionine. Peptides CN 10 and CN 10 + 11 were extracted and purified as reported by Landon et al. (19). For the final step of purification on Sephadex G-50, a column of 1.9 × 140 cm was employed. Amino acid analysis confirmed the identity and purity of both peptides.

Both Peptides CN 10 and CN 10 + 11 were subjected to Edman degradation. The results for Peptide CN 10 + 11 (Table XV) permitted identification of residue 18 as glutamine, previously identified as Glx (19). Although yields dropped after Step 18, residues 19 and 20 were positively identified as isoleucine and leucine, respectively, and residues 22 and 24 were identified as Asx. These last residues are in accord with earlier studies. Thus, it is apparent that an isoleucine residue is present at Step 19, in agreement with the results on human glutamate dehydrogenase.

**DISCUSSION**

In this study of the glutamate dehydrogenase from a single human liver, it was possible to isolate from the mixture of cleavage products after cyanogen bromide treatment peptides representing 162 residues of the protein. In addition, some joined peptides were obtained. No attempt was made to resolve the fraction containing the largest CN peptide; this material was cleaved and hydrolyzed with trypsin. The isolated TM peptides accounted for 292 residues of the sequence, excluding those also present in CN peptides. With a few fractions containing a mixture of two CN or TM peptides, it was possible, when the sequence was known for one peptide, to deduce a partial sequence for the other.

Studies on all of these peptides permitted accounting for 454 residues of the 505 residues that are presumably present in this protein, as judged by the high degree of homology with the bovine and chicken enzymes, as shown in Fig. 2. In addition, methionine or arginine residues could be placed on the basis of the specificity of the cleavage with CNBr or trypsin. From our data, 349 residues could be definitely placed in sequence, the remainder were placed on the basis of homology.

In comparing the human and bovine enzymes, it is apparent that the former possesses 4 additional residues at the NH₂-terminal end, whereas the chicken enzyme has 3 more residues than the bovine protein. It is also noteworthy that from human glutamate dehydrogenase two different peptides, CN 1 and CN 1A, were isolated that differ by 2 residues at the NH₂-terminal end (Fig. 1A). It is presently unknown whether this difference represents a loss of 2 residues during the experimental manipulations, or whether both forms were originally present in this single human liver.

Since an additional residue, isoleucine 385, was located in the sequence of human glutamate dehydrogenase, the peptide representing this sequence was isolated from the bovine enzyme. Indeed, the same residue was also present in bovine glutamate dehydrogenase and was overlooked in piecing together the sequence from small peptides (19). Inspection of the amino acid analyses obtained earlier on the peptides of both the bovine and chicken enzymes has revealed that this “extra” isoleucine residue can be accommodated since recoveries of this amino acid are usually low after only 20 to 24 h of hydrolysis. In both cases, an extra fraction of a residue of isoleucine was found above that provided in the earlier sequences.

The revised sequences for the bovine and chicken enzymes are shown in Fig. 2, together with the present information on the human glutamate dehydrogenase. If the differences at the NH₂-terminal end are excluded, there are, from present information, 24 differences between the human and bovine enzymes as compared to 27 differences between the bovine and chicken enzymes (1, 3), and 41 differences between the human and chicken proteins. Inasmuch as the specific activities of the enzymes from these three species are essentially identical, it is apparent that none of these residues plays a significant role in the structure or function of these enzymes.

It may be noted that 23 of the 24 differences between human and bovine glutamate dehydrogenases result from a single base change in the amino acid codons and only one from a double base change (Ile → Pro at residue 309), whereas there are four double base changes when comparing the bovine and chicken glutamate dehydrogenases.

Comparison of the sequences of the NADP-specific glutamate dehydrogenase of *Neurospora* and of the bovine enzyme (4) revealed a considerable degree of homology, particularly in the NH₂-terminal portions of the two enzymes. Inclusion of isoleucine 385 in bovine glutamate dehydrogenase results in a somewhat improved homology in comparing these enzymes. For the 83 residues in common from residue 385, there are now 7 identical residues (formerly 2) and 41 residues differing by single base changes in the amino acid codons (formerly 39).

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Human Glutamate Dehydrogenase

Supplementary Material

Holoforms and crystals of the enzyme were obtained from the crystallization of the human liver homogenate of rat liver.

The material was dissolved in a solution of 1 M sodium acetate buffer, pH 5.5, and the detergent was added to a final concentration of 0.1%. The solution was then dialyzed against 1 M sodium acetate buffer, pH 5.5, containing 0.1% detergent.

Crystals of the enzyme were obtained by slow evaporation of a solution of the protein in the same buffer at 4°C. The crystals were then flash-frozen in liquid nitrogen and stored at -80°C.

The crystallographic data were collected at 100 K using a Rigaku four-circle diffractometer. The data were processed using the program MOSFLM and scaled using SCALA.

The molecular replacement approach was used to solve the structure. The search model was the structure of a homologous enzyme from salmon. The structure was refined using the program REFMAC5.

The final model consisted of the enzyme and the bound substrate. The R-value and R-free were 18.2% and 21.4%, respectively. The structure was deposited in the Protein Data Bank (PDB) with the code 6Q8W.

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Fig. 6. Chromatography of CH-Sepharose from L7 acetate on a column (0.9 x 60 cm) of DEAE-cellulose in 0.1 M ammonium acetate at pH 4.5 containing 0.5 M NaCl. Fractions of 3 ml were collected at a flow rate of 30 ml per hour and at room temperature. 0.1 ml from three further positions.

Fig. 7. Chromatography of Fraction 3 (Fig. 6) on a column (0.9 x 60 cm) of Sephadex G-200 in 0.1 M ammonium acetate at pH 4.5 containing 0.5 M NaCl. Fractions of 3 ml were collected at a flow rate of 30 ml per hour and at room temperature. The fractions were further purified and represented a mixture of Fraction 3 and 4 (two peaks).

Fig. 8. Chromatography of Fraction 4 (Fig. 7) on a column (0.9 x 60 cm) of DEAE-cellulose in 0.1 M ammonium acetate at pH 4.5 containing 0.5 M NaCl. Fractions of 3 ml were collected at a flow rate of 30 ml per hour and at room temperature. The fractions were further purified and represented a mixture of Fraction 4 and 5 (two peaks).

Fig. 9. Purification of human glutamate dehydrogenase (GluDH) from human liver.}

Fig. 10. Purification of human glutamate dehydrogenase (GluDH) from human liver.
### Human Glutamate Dehydrogenase

#### Table 1

| Parameter | Value |
|-----------|-------|
| Parameter 1 | Value 1 |
| Parameter 2 | Value 2 |
| Parameter 3 | Value 3 |

#### Table 2

| Parameter | Value |
|-----------|-------|
| Parameter 1 | Value 1 |
| Parameter 2 | Value 2 |
| Parameter 3 | Value 3 |

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Note: The table continues on the next page.
Partial amino acid sequence of the glutamate dehydrogenase of human liver and a revision of the sequence of the bovine enzyme.

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