Amino Acid Sequences containing Cysteine or Cystine Residues in Ovalbumin from Eggs of the Quail Coturnix coturnix japonica


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Abstract

Ovalbumin isolated from eggs of the Japanese quail, C. c. japonica, was subjected to limited proteolysis by subtilisin to give plakalbumin and then fractionated on Sephadex G75 in acid-urea to give plakalbumin S-protein and S-peptide. The plakalbumin peptide was recovered, oxidized with performic acid, and the sequence of amino acids determined from the peptides formed by enzyme digestion. There were two cysteine residues in the 33-residue sequence. The ovalbumin was also oxidized with performic acid and digested with thermolysin and pepsin before isolating, from a sulfonated polystyrene column, the acidic cysteic acid peptides, as well as acetylated N-terminal peptides and phosphorylated peptides, and determining their amino acid sequence. Additional peptide sequences containing cysteine or half-cystine were characterized.

Quail ovalbumin was reduced and carboxymethylated with [2-14C]iodoacetic acid. Peptides containing labelled S-carboxymethylcysteine residues were isolated from thermolytic digests of the carboxymethylated ovalbumin by paper ionophoresis and chromatography. Their amino acid sequence was determined and five different sequences involving labelled S-carboxymethylcysteine residues were established.

The presence of two half-cystine residues and the location of the disulfide bond were shown by blocking the cysteine residues with non-radioactive iodoacetic acid, reducing the disulfide bond and labelling the half-cystine residues with [2-14C]iodoacetic acid. After thermolytic digestion of the protein, radioactive peptides were isolated by paper ionophoresis and chromatography. These studies have thus shown that quail ovalbumin contains one cystine residue and three cysteine residues, which is one residue of cysteine less than in ovalbumin from the hen (Gallus gallus domesticus). There is strong homology in the amino acid sequences of hen ovalbumin and quail ovalbumin determined in these investigations.

Introduction

The ovalbumin from the egg of the hen Gallus gallus domesticus has recently had its covalent structure fully elucidated (McReynolds et al. 1978), including the location of the disulfide bond (Thompson and Fisher 1978a; Webster and Thompson 1980) among the six cysteine and half-cystine residues. The number of such residues in different ovalbumins shows considerable variation (Smith and Back 1970) and the present studies aim to define the number of thiol and disulfide groups in ovalbumin from eggs of the quail Coturnix coturnix japonica, and the amino acid sequences around them.
Plakalbumin is a modified ovalbumin formed by limited proteolysis of ovalbumin by subtilisin (Ottesen 1958) which cleaves relatively few peptide bonds and releases only small molecular weight peptides (Ottesen and Wollenberger 1952). It also enables dissociation in acid–urea solution, of a 33-residue fragment (Smith 1968) called plakalbumin S-peptide that contains two of the four cysteine residues of hen ovalbumin. The isolation and determination of amino acid sequence of plakalbumin S-peptide (Thompson et al. 1971) is a convenient way of studying the location and homology of amino acid sequences around these cysteine residues in ovalbumins from different species. The amino acid sequences around these and the other cysteine and half-cystine residues can also be determined using peptides from enzyme digests of reduced ovalbumin that has been radioactively labelled with $[2^{14}\text{C}]$iodoacetate. By first blocking the cysteine residues with non-radioactive iodoacetate, followed by reduction and labelling of the half-cystine residues with $[2^{14}\text{C}]$iodoacetate (Webster and Thompson 1980), the location of the disulfide bond is established.

By studying the acidic peptides in enzyme digests of performic acid-oxidized ovalbumin (Thompson and Fisher 1978a), additional information of the amino acid sequence is obtained, including the sequences of peptides containing cysteic acid, the acetylated $N$-terminal sequence, and the phosphorylated peptide sequences.

**Materials and Methods**

The methods of cellulose acetate electrophoresis, ultracentrifugation, peptide mapping, amino acid analysis, sulfhydryl group estimation, cyanogen bromide cleavage, sequence determination by the dansyl-Edman procedure, and digestion with trypsin, thermolysin and pepsin were substantially the same as previously described (Air and Thompson 1969, 1971; Beard and Thompson 1971; Nash and Thompson 1974; Fisher and Thompson 1979). Phosphate analyses of 6 M HCl hydrolysates of ovalbumin were done by the method of Taussky and Shorr (1953). $^{31}\text{P}$-n.m.r. studies on a JEOL FX-100 spectrophotometer at 40·25 MHz were done with complete proton decoupling in $\text{D}_2\text{O}$ at pH 5·5 uncorrected for isotope effects.

For the isolation of cysteic acid peptides and other peptides acidic at pH 2, from plakalbumin protein or ovalbumin, performic acid oxidation and fractionation on sulfonated polystyrene were the same as previously described (Thompson and Fisher 1978a).

The preparation of labelled SCM-ovalbumins and the labelling of disulfide-linked half-cystine residues followed the methods of Webster and Thompson (1980).

**Preparation of Ovumalbumin**

Fresh quail egg-white from 48 eggs was dialysed against 0·1 M ammonium acetate, pH 3·7, for a long period at 4°C, then centrifuged to remove the small insoluble precipitate. A portion of the dialysed material equivalent to 15 g of egg-white was chromatographed (Rhodes et al. 1958) on a column (12 by 3·4 cm) of carboxymethylcellulose equilibrated with the same buffer and eluted with a pH gradient of 0·1 M ammonium acetate buffers from pH 3·7 to pH 5·5 in a linear gradient device (500 ml each chamber). At the conclusion of the gradient, a further gradient from pH 5·5 to 10 (0·2 M Na$_2$CO$_3$ in buffer) was applied. The peak containing ovalbumin was dialysed against water and freeze-dried. The ovalbumin was characterized by its mobility on cellulose acetate ionophoresis, amino acid composition and sedimentation coefficient in comparison with hen ovalbumin.

Further purification of samples of the ovalbumin for amino acid analysis was by chromatography on a column (2·5 by 14 cm) of DEAE-cellulose in 8 M urea–thiol buffers (Thompson and O'Donnell 1966). The column was equilibrated with buffer containing 8 M urea–0·01 M Tris–HCl–0·001 M EDTA–0·05 M mercaptoethanol, pH 8, and loaded with 150 mg of the ovalbumin solution dialysed to equilibrium against the starting buffer. A linear gradient from 0 to 0·5 M NaCl in the buffer, 250 ml each chamber, was used. Fractions were recovered by freeze-drying after dialysis against water.
Preparation of Plakalbumin, S-peptide and S-protein

Plakalbumin was prepared by digestion with subtilopeptidase A under the conditions described by Smith (1968).

The plakalbumin S-peptide was separated from the S-protein by gel filtration on a column of Sephadex G75 equilibrated with 6 M urea–10% formic acid. The plakalbumin S-peptide has no absorption at 280 nm but can be detected by its phenylalanine absorption at 260 nm or by reaction of the cysteinyl residues with 5,5'-dithiobis(2-nitrobenzoic acid) as previously described (Thompson et al., 1971). After bulking the peptide fractions, 4 M trichloroacetic acid was added to precipitate the peptide before dialysis against water and recovery by freeze-drying. The dried peptide was oxidized with a 10-fold excess of preformed performic acid at 0°C for 4 h and then, after adding water to reduce the formic acid concentration to 5%, recovered by freeze-drying.

![Graph](image)

**Fig. 1.** (a) Chromatography of 35 ml (equivalent to three egg-whites) of dialysed solution of quail egg-white in 0·1 M ammonium acetate, pH 3·7, on a column (12 by 3·4 cm) of carboxymethylcellulose. After loading, and washing off the unadsorbed fraction, gradient elution with a linear gradient device (500 ml each chamber) was used from pH 3·7 to 5·5, followed by a second gradient from pH 5·5 to 10 (containing 0·2 M Na₂CO₃) applied at tube 96. Fraction size was 11·0 ml. The unadsorbed material usually contained some proteins from peaks 2 (ovomucoid), 3 (ovalbumin) and 4 (conalbumin). Peak 5 contained lysozyme. Fractions bulked for recovery of ovalbumin are indicated by a bar. (b) Electrophoretic patterns of fractions 1–5 on cellulose acetate at pH 8·6. Cross-hatched zones represent lesser amounts.

Results

The fractionation of proteins in quail egg-white is shown in Fig. 1. The ovalbumin was eluted as a single major peak by the pH gradient and was not resolved into fractions of differing phosphate content. Electrophoresis on cellulose acetate, however, showed the presence of three electrophoretic bands with mobilities similar to those of phosphorylated ovalbumins from the hen and presumably representing
the corresponding fractions of diphosphorylated, monophosphorylated and non-phosphorylated quail ovalbumin. In comparative experiments with hen ovalbumin, the phosphate content was found to be approximately the same as that of the sample of hen ovalbumin which is normally 1.8 residues per mole (Perlmann 1952). When examined by $^{31}$P-n.m.r., both hen and quail ovalbumin showed two prominent peaks in the same relative environment as hen ovalbumin, indicating two major phosphorylated sequences in quail ovalbumin.

Table 1. Amino acid composition of quail ovalbumin

Samples of ovalbumin or performic acid-oxidized ovalbumin were hydrolysed with 6 M HCl containing 0.1% phenol and 0.05% mercaptoethanol in sealed evacuated tubes at 110°C for 24 h. Values are given as moles per mole of protein relative to the content of the stable amino acids aspartic acid, proline, glycine, alanine, leucine and phenylalanine assumed to total 154 residues per mole. The values for threonine and serine have been corrected 5 and 10% respectively for destruction during hydrolysis. Tyrosine was estimated with ovalbumin, methionine and cysteine plus half-cystine residues as methionine sulphone, and cysteic acid with the performic acid-oxidized ovalbumin.

<table>
<thead>
<tr>
<th>Amino acid</th>
<th>Mean value</th>
<th>Preferred value</th>
<th>Hen ovalbumin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lysine</td>
<td>20.2</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>Histidine</td>
<td>7.2</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>Arginine</td>
<td>11.7</td>
<td>12</td>
<td>15</td>
</tr>
<tr>
<td>Cysteine+half-cystine</td>
<td>5.3</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>Aspartic acid</td>
<td>31.8</td>
<td>32</td>
<td>31</td>
</tr>
<tr>
<td>Threonine</td>
<td>22.0</td>
<td>22</td>
<td>15</td>
</tr>
<tr>
<td>Serine</td>
<td>39.6</td>
<td>40</td>
<td>38</td>
</tr>
<tr>
<td>Glutamic acid</td>
<td>45.6</td>
<td>46</td>
<td>48</td>
</tr>
<tr>
<td>Proline</td>
<td>11.6</td>
<td>12</td>
<td>14</td>
</tr>
<tr>
<td>Glycine</td>
<td>22.5</td>
<td>22</td>
<td>19</td>
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<tr>
<td>Alanine</td>
<td>33.4</td>
<td>33</td>
<td>35</td>
</tr>
<tr>
<td>Valine*</td>
<td>22.3</td>
<td>26</td>
<td>31</td>
</tr>
<tr>
<td>Methionine</td>
<td>14.1</td>
<td>14</td>
<td>16</td>
</tr>
<tr>
<td>Isoleucine</td>
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<tr>
<td>Leucine</td>
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<td>35</td>
<td>32</td>
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<td>Tyrosine</td>
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<td>20</td>
</tr>
<tr>
<td>Tryptophan*</td>
<td>3.3</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>

Total 381 385

* Values for valine and isoleucine will be low due to incomplete hydrolysis in 24 h. Similar hydrolysates of hen ovalbumin were low by 3.4 and 4.5 residues respectively for approximately the same content of these amino acids; the preferred values have been corrected up to a similar extent.

* Determined by the spectrophotometric method of Beaven and Holiday (1952).

A limited study of the amino acid composition of quail ovalbumin, using the reduced and performic acid-oxidized ovalbumin, gave the values shown in Table 1 in comparison with those for hen ovalbumin. There is a marked similarity in the total number of amino acids as well as in the relative proportions of the different amino acids when compared with hen ovalbumin.
Although the quail ovalbumin was eluted as a single peak in the gradient elution, the presence of ovalbumins of different electrophoretic mobility, presumably reflecting phosphate content, in the material when examined by cellulose acetate electrophoresis reveals a more limited fractionation than Rhodes et al. (1958) reported. These authors used hen ovalbumin with a similar column and buffer system but stepwise elution with buffers of different pH rather than a pH gradient. Some additional contamination, with another egg-white protein of higher cystine content, was found on analysis of the quail ovalbumin recovered from the peak material, which had a cysteic acid content after performic acid oxidation of 5.9 residues per mole. This contaminant was probably ovomucoid which elutes in the earliest fractions from carboxymethylcellulose columns, and is known to have a high cystine content. No stringent repurification was applied to the samples used for sequence work and no peptide amino acid sequences were found in recovered peptides, other than those that related to the sequences given in this paper. For good analytical results, however, it was necessary to fractionate the ovalbumin further. Because of the low cysteine values (2.3 residues per mole) obtained on material recovered after dialysis against tap water containing traces of copper, which probably catalysed oxidation reactions resulting in disulfide-bond formation, chromatography of the ovalbumin on DEAE-cellulose columns using 8 M urea–thiol buffers was used. The contaminant protein was eluted in the trailing fractions from the main peak, and after performic acid oxidation had a significantly higher cysteic acid content of 7.8 residues compared to 5.3 for the main peak.

The sedimentation coefficient for quail ovalbumin was 3.16, almost identical to that of hen ovalbumin (3.36) under the same conditions. The literature values of $S_{20,w}$ for hen ovalbumin range from 3.34 to 3.66 (Edsall 1953) for a molecular weight of 45000, suggesting a similar molecular weight for quail ovalbumin.

**Number of Half-cystine Residues in Quail Ovalbumin**

The number of half-cystine residues was two, judging by the quantitative results obtained on radioautography of peptide maps of thermolysin digests of S-carboxymethyl ovalbumin. This was prepared by blocking the thiol groups with unlabelled iodoacetate, followed by reduction of cystine residues and labelling with [2-14C]-iodoacetate according to the method of Webster and Thompson (1980), which minimizes disulfide interchange during the initial carboxymethylation. The major peptides, containing 85% of the radioactive label, were

\[
\text{Leu-Gln-CMCys}
\]

\[
\text{Phe-Gly-Asp-SerP-Ile-Glu-Ala-Gln-CMCys-Gly-Thr-Ser,}
\]

and its partial hydrolysis product,

\[
\text{Ile-Glu-Ala-Gln-CMCys-Gly-Thr-Ser,}
\]

indicating their presence in quail ovalbumin as half-cystine residue sequences. The sequences given are based on the sequence data on equivalent peptides given below, and homology with hen ovalbumin. The small amount of contaminant protein mentioned earlier did not affect the analytical results in the determination of the disulfide bond.
Sequences Involving Cysteine Residues

Quail ovalbumin was reduced before labelling the cysteine residues with [2-\(^{14}\)C]iodoacetate, and the labelled peptides in a thermolysin digest were isolated and identified. Three peptides additional to those listed above were obtained. They were

Leu-Phe-CMCys,

Phe-CMCys

(from the above sequence by partial hydrolysis as well as from the Phe-CMCys-Phe sequence), and

Phe-Gly-Arg-CMCys

which are identical in sequence to peptides previously identified in similar digests of hen SCM-ovalbumin (Webster and Thompson 1980).

Acidic Peptides in Digests of Oxidized Quail Ovalbumin

Acidic peptides containing cysteic acid isolated from peptic and thermolytic digests of performic acid-oxidized quail ovalbumin included

Ala-Ser-Mes\(^*\)-Glu-Phe-CySO\(_3\)H (pepsin),

Phe-CySO\(_3\)H-Phe (pepsin),

Phe-CySO\(_3\)H (thermolysin),

Asp-Lys-Leu-Pro-Gly-Phe-Gly-Asp-SerP-Ile-Glu-Ala-Gln-CySO\(_3\)H-Gly-Thr-Ser-Ala

(thermolysin),

Phe-Gly-Asp-SerP-Ile-Glu-Ala-Gln-CySO\(_3\)H-Gly-Thr-Ser

(Ile-Glu-Ala-Gln-CySO\(_3\)H-Gly-Thr-Ser

Leu-Gln-CySO\(_3\)H (thermolysin).

The large peptide was analysed and shown to have the composition

Lys\(_{1.0}\)CySO\(_3\)H\(_{1.2}\)Asp\(_{2.2}\)Thr\(_{1.1}\)Ser\(_{1.8}\)Glu\(_{2.1}\)Pro\(_{1.0}\)Gly\(_{3.1}\)Ala\(_{2.0}\)Ile\(_{1.1}\)Leu\(_{1.1}\)Phe\(_{0.9}\)

the same as the corresponding peptide from hen ovalbumin except for the substitution of an alanyl residue for a valyl residue.

Peptides not containing cysteic acid isolated in the acidic fraction and not adsorbed on sulfonated polystyrene, included the N-terminal acetylated peptide Ac-Gly-Ser (thermolysin) identified by mass spectrometry, and Ac-Gly-Ser-Ile-Gly (pepsin) and the phosphorylated peptides

Val-Val-Gly-SerP-Ala-Glu-Ala-Gly-Val-Asp (pepsin),

Val-Val-Gly-SerP-Ala-Glu-Ala-Gly (thermolysin),

Phe-Gly-Asp-SerP (thermolysin).

* Mes is an abbreviation for methionine sulfone.
The sequences of those not studied by the dansyl-Edman procedure have been given the sequence by homology with the known sequences in hen ovalbumin.

By amino acid analysis of the acidic peptide fraction from a CNBr digest of carboxymethylated ovalbumin (Ser$_2$-Hse$_0$-Gly$_{1-9}$-Ala$_{2-1}$-Ile$_{0-6}$), the N-terminal sequence of quail ovalbumin could be deduced to include two of the above peptides to give

\[
\text{Ac-Gly-Ser-Ile-Gly-Ala-Ala-Ser-Met-Glu-Phe-Cys-Phe} \xrightarrow{\text{thermolysin}} \text{Hen ovalbumin (cf. Thompson and Fisher 1978b).}
\]

### Table 2. Amino acid composition of peptic fragments of performic acid-oxidized quail plakalbumin peptide

Peptides were purified by paper ionophoresis at pH 1.9 followed by paper chromatography in butanol-acetic acid–water–pyridine (15:3:12:10 v/v). Hydrolysates were prepared with 6 M HCl for 24 h at 110°C. Values are not corrected for losses during hydrolysis or incomplete hydrolysis and are given as moles per mole of peptide, with values for amino acid sequence data in parentheses.

<table>
<thead>
<tr>
<th>Amino acid</th>
<th>P1</th>
<th>P2</th>
<th>Value P3</th>
<th>P4</th>
<th>P5</th>
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</thead>
<tbody>
<tr>
<td>Lysine</td>
<td></td>
<td></td>
<td>1.0(1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Histidine</td>
<td>0.8(1)</td>
<td></td>
<td>1.0(1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arginine</td>
<td>1.0(1)</td>
<td></td>
<td></td>
<td></td>
<td>0.9(1)</td>
</tr>
<tr>
<td>Aspartic acid</td>
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<td>0.9(1)</td>
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</tr>
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<tr>
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<tr>
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<td>1.1(1)</td>
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<td>Isoleucine</td>
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<tr>
<td>Leucine</td>
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<td>0.9(1)</td>
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<tr>
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</table>

Total 4 8 10 3 8

Amino Acid Sequence of Plakalbumin Peptide

The peptides isolated, analysed and sequenced to give the amino acid sequence of quail plakalbumin peptide are summarized in Table 2. The peptides can be placed in sequence by the strong homology to hen plakalbumin peptide, and there are overlaps as shown in Table 3 that confirm this order. The two cysteine residues in plakalbumin peptide have identical amino acid residues adjacent to them apart from the substitution of a valyl residue for an isoleucyl residue at position 15 in the hen ovalbumin sequence.

The assignment of side-chain amide and acidic groups in the plakalbumin peptide was easily made from the ionophoretic mobility of the small thermolytic peptides which often possessed only one acidic or amide residue.
Table 3. Amino acid sequence of the plakalbumin peptide from quail ovalbumin

Residues are numbered from the N-terminal residue and the positions of cleavage by pepsin (P), trypsin (Tp) and thermolysin (Th) shown by vertical arrows. Dotted arrows represent a partial cleavage. Residues identified by the dansyl-Edman procedure are underlined with an arrow. If no horizontal arrow is shown, the residue did not give a clear result or was not investigated. Before amino acid sequence studies, the peptide was oxidized with performic acid to convert the cysteine residues to cysteic acid residues.

<table>
<thead>
<tr>
<th>Residue</th>
<th>5</th>
<th>10</th>
<th>15</th>
<th>20</th>
<th>25</th>
<th>30</th>
<th>33</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ala-Thr-Glu-Glu-Phe-Arg-Ala-Asp-His-Pro-Phe-Leu-Phe-Cys-Val-Lys-Ile-Glu-Thr-Asn-Ala-Asn-Val-Phe-Leu-Phe-Gly-Arg-Cys-Val-Ser-Pro</td>
<td></td>
<td></td>
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<td></td>
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<td></td>
</tr>
</tbody>
</table>

P1  P2  P3  P4  P5

Tp1  Tp2  Tp3  Tp4

Th1  Th2  Th3  Th4  Th5  Th6  Th7  Th8  Th9  Th10

Th2+3
Discussion

Compared with hen ovalbumin, there is one less cysteine residue in quail ovalbumin, with a single intramolecular cystine residue linking half-cystine residues, with amino acid sequences around them identical to those in hen ovalbumin.

A comparison of the sequences of plakalbumin peptide from the hen and the quail is shown in Table 4. It is apparent that the subtilisin-sensitive region of the two ovalbumins is similar but not identical, the quail peptide commencing one residue nearer the C-terminal residue of ovalbumin, based on homology. An insertion in the sequence of the quail peptide relative to the hen peptide, however, results in the two plakalbumin peptides being of the same length.

Table 4. Comparison of the amino acid sequences of the plakalbumin peptide from the hen and the quail

Boxes enclose sequences that are identical

|-----|----------------------------------------------------------------|

The homology between the amino acid sequences reported in this paper compared with similar areas of hen ovalbumin is very high. Using the known numbered sequence of hen ovalbumin, these sequences include the N-terminal sequence (residues 1–12 of hen ovalbumin), the phosphorylated seryl residues (residues 65–68 and 341–350) and the sequences around the cysteine (residues 1–12, 356–367, and 379–385) and half-cystine (residues 60–77 and 118–120) residues. Although these sequences only represent a small percentage of the total sequence, the strong homology around these areas suggests that hen and quail ovalbumins share a common conformational structure.

Acknowledgments

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References


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