Bovine Secretory Component*

ISOLATION, MOLECULAR SIZE AND SHAPE, COMPOSITION, AND NH$_2$-TERMINAL AMINO ACID SEQUENCE

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Bovine free secretory component was purified from whey by salt precipitation, gel filtration, DEAE-cellulose and phosphocellulose chromatography, and immunoadsorption. It was obtained in immunologically pure form and in 55% yield. The Stokes radius of pure free secretory component was found to be 4.3 nm by gel filtration, and a $s_{20w}$ of 4.1 S was determined by the ultracentrifuge. The molecular weight was 79,000 by sodium dodecyl sulfate gel electrophoresis and by sedimentation equilibrium in the ultracentrifuge, using a $\theta$ of 0.73 determined by ultracentrifugation in D$_2$O and H$_2$O. A minimal axial ratio of approximately 5 was calculated. Amino acid analysis of bovine free secretory component showed remarkable similarity to that of human, dog, and rabbit but carbohydrate analysis showed significant differences. In contrast to the human, bovine free secretory component has 2 methionine residues/mol. The NH$_2$-terminal sequence was found to be Lys-Ser-Pro-Ile-Phe-Gly-Pro-Glu-Glu-Val. This sequence is identical with that of the human and dog. However, the poor immunological cross-reactivity between the dog, human, and bovine proteins suggests that significant structural differences will be found in other regions of the molecule.

SECRETORY IMMUNOGLOBULIN A IS THE PREDOMINANT CLASS OF IMMUNOGLOBULIN IN MUCOUS MEMBRANE SECRECTIONS (1). Unlike serum immunoglobulin A (IgA), it contains an additional specific polypeptide chain called the secretory component, which has been demonstrated in several species (for review see Ref. 2). The secretory component is synthesized in epithelial cells and becomes disulfide-linked to $\alpha$ chains of dimeric IgA as the IgA is transported across the epithelial mucous membrane (2). In addition to secretory component bound to IgA, this polypeptide chain is present in secretions unbound to other proteins, and this constitutes the free secretory component. The exact biological significance of the secretory component is not yet clear, but evidence is available suggesting that bound secretory component protects the secretory IgA molecules against proteolytic enzymes present in secretions (3-5). It has also been suggested that secretory component plays a role in the transport of IgA across the epithelial lining (6, 7) and, more recently, that it acts as a surface receptor for dimeric IgA and IgM in epithelial cells (8).

Chemical and physicochemical studies of both free secretory component and the released bound secretory component in human (9, 11), rabbit (12), and cow (13, 14), as well as studies on the binding of human and bovine free secretory component to IgA (15), suggest similarities of secretory component in different species. Although the bovine free secretory component is easily available in relatively large amounts, no detailed studies have been made on its structure, and data on its molecular weight vary considerably (2). In the present paper we report the isolation of highly purified free secretory component, its molecular weight and conformational properties, amino acid and carbohydrate composition, and the NH$_2$-terminal amino acid sequence. Interestingly, the amino acid sequences of the human and canine secretory component (16, 17) show almost complete identity to that of bovine secretory component in the NH$_2$-terminal 13 residues.

MATERIALS AND METHODS

Antisera—All antisera were prepared in rabbits by the subcutaneous injection of antigens into the foot pads in Freund’s adjuvant. The specificity of the antisera was tested by double diffusion in agar and by immunoelectrophoresis.

Preparation of Bovine Free Secretory Component—Fresh adult cow milk was collected, and 0.2% sodium azide was added immediately. Fat was removed by centrifugation, and casein was precipitated at pH 4.5. The resulting whey was dialyzed overnight against cold running water and made 33% saturated with ammonium sulfate. After centrifugation the supernatant was made 50% saturated, and the precipitate was dialyzed against 0.1 M ammonium bicarbonate and lyophilized. A solution of 1.0 g of the lyophilized ammonium sulfate fraction was dialyzed against 10 mM phosphate buffer at pH 7.4, applied to a DEAE-cellulose (DE52, Whatman) column (22 x 130 mm), and eluted with the same buffer. The unbound material was

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elution was carried out with 0.1 M ammonium bicarbonate. This was applied in succession to the immunoadsorbent column, and anti-secretory component (FSC) was absorbed with a crude preparation of Sephadex G-200 column in order to remove the anti-secretory component antibodies. The IgG fraction was precipitated from this serum with ammonium sulfate and linked to Sepharose 4B by cyanogen bromide (18). The fractions from the Sephadex G-200 column were pooled in five pools, as shown in Fig. 1, and concentrated by ultrafiltration through a PM-10 Diaflo membrane. Pool 2 (Fig. 1) was applied to a Sephadex G-200 column (110 x 2.5 cm) and eluted with 0.1 M ammonium bicarbonate solution. Two major peaks were obtained as shown in Fig. 2.

Antiserum raised against the 33% saturated ammonium sulfate fraction of whey (containing mainly anti-IgG antibodies and a trace of anti-secretory component) was absorbed with a crude preparation of immunoadsorbent column in order to remove the anti-secretory component antibodies. The y-globulins then were precipitated from this serum with ammonium sulfate and linked to Sepharose 4B by cyanogen bromide (18). The fractions from the Sephadex G-200 column in the second peak (Fig. 2, indicated by the area marked FSC), were applied in succession to the immunoadsorbent column, and elution was carried out with 0.1 M ammonium bicarbonate. This column was used to remove IgG. Effluent fractions having A\textsubscript{280} > 0.05 were pooled in three fractions, concentrated, and stored frozen.

**Gel Electrophoresis**—Disc electrophoresis was performed with 5% polyacrylamide gels at pH 8.5 (19). Staining was carried out with Coomassie Blue (20).

Polyacrylamide gel electrophoresis in acid urea was performed with 4% gels in 6.5 M urea at pH 3.2 (21), staining with Coomassie Blue solution in acid methanol (22). Some samples were reduced with 0.1 M dithiothreitol in 6.5 M urea at neutral pH for 8 hours at room temperature. For comparison, unreduced samples were similarly treated, but without dithiothreitol.

Polyacrylamide gel electrophoresis in the presence of sodium dodecyl sulfate was performed in 7.5% gels, as described by Weber et al. (22). For molecular weight determination, crystallized egg white lysozyme from Pentex Inc., catalase and chymotrypsinogen from Worthington Biochemical Co., twice crystallized ovalbumin from Schwarz/Mann, human albumin from Boehringer, and human plasma Cohn Fraction II were used as standards for calibration. Scanning of gels for determination of relative amounts of different bands was with a Gilford spectrophotometer model 240.

**Stokes Radius Determination by Gel Chromatography**—A Sephadex G-200 column (110 x 2.5 cm) equilibrated with 0.1 M ammonium bicarbonate was used for the determination of Stokes radius (23). The column was calibrated with normal human serum albumin and y-globulin, and the void volume was determined by the elution volume of IgM of human serum and of a y-globulin fraction of bovine whey, both agreeing exactly in several runs. Two equations were used for calculation of the Stokes radius \( a \), using the data obtained from six different preparations, (a) \( K_a = \frac{1}{a_M - a} \sigma \beta a \) (24), and (b) \( a = a_0 + b_s \sigma c \), where \( a = K_a = \frac{(V_s - V_T)(V_s - V_T - V_T)}{V_s - V_T} \) and \( a_0, \sigma, \beta, a_M, \) and \( b_s \) are constants determined by calibration. Stokes radii for human serum albumin (38 \AA) and y-globulin (55 \AA) were calculated from their diffusion coefficients (8.1 and 3.9, respectively, see Ref. 26) using the relation \( a = kT/6\pi \eta D \).

**Ultracentrifugation Studies**—Ultracentrifugation was performed at 20° in a Spinco model E ultracentrifuge equipped with a polymeric scanner. For sedimentation coefficient determination both schlieren optics and ultraviolet scanning were used at protein concentrations ranging from 0.3 to 3.0 g/liter. The results were corrected to water at 20° and extrapolated to zero concentration to obtain \( s_{20, w} \) values. Sedimentation equilibrium in D\textsubscript{2}O and H\textsubscript{2}O was used for determination of partial specific volume (\( \beta \)) and molecular weight (27). Densities were determined pycnometrically, and a \( k \) value of 1.015, corrected to correspond to 90% D\textsubscript{2}O, was used to correct for deuterium exchange by the protein.

**Amino Acid and Sugar Analysis**—Amino acid analyses were performed on a Beckman model 121 M microcolumn amino acid analyzer with computing integrator. Protein samples were hydrolyzed in constant boiling 6 N HCl in sealed, evacuated tubes at 110° for 24, 48, and 72 hours. Amino acid and sugar analysis was performed with a Beckman model 121 M microcolumn amino acid analyzer with computing integrator. Protein samples were hydrolyzed in constant boiling 6 N HCl in sealed, evacuated tubes at 110° for 24, 48, and 72 hours. Amino acid and sugar analysis was performed with a Beckman model 121 M microcolumn amino acid analyzer with computing integrator. Protein samples were hydrolyzed in constant boiling 6 N HCl in sealed, evacuated tubes at 110° for 24, 48, and 72 hours.
72 hours. For amino acids showing loss by hydrolysis the data were extrapolated to zero time, whereas for slowly liberated amino acids the 72-hour data were used. Methionine was determined as methionine sulfone, and cysteine (or cystine) as cysteic acid after performic acid oxidation (28). Tryptophan and tyrosine were determined spectrophotometrically in 6 M guanidine HCl (29) after correcting for cysteine absorption. Hydrolysis with mercaptoethanesulfonic acid for 22 hours (30) was also used for determination of tryptophan.

For amino-sugar determination hydrolysis by 4 N HCl for 6 hours at 100° and by 6 N HCl for 2 hours at 110° in sealed, evacuated tubes was used. Analysis was on the same amino acid analyzer, using a 20-cm column equilibrated at 49° with pH 5.36 citrate buffer (0.35 M in sodium).

Neutral sugar content was determined by the orcinol-sulfuric acid method as used by Francois et al. (31). Salic acid was determined by the thiobarbituric acid method as described by Sprio (32).

Amino Acid Sequence Studies—The NH₂-terminal amino acid of performic acid-oxidized free secretory component was determined by polyamide thin layer chromatography after dansylation1 in the presence of sodium dodecyl sulfate and hydrolysis with 6 N HCl as described by Gray (33). The NH₂-terminal amino acid sequence analysis was performed with a Beckman model 590 C Sequencer (34) using Quadrol buffer and a "fast" protein program (Beckman 072172C). For identification of each residue, gas-liquid chromatography of both PTH-derivatives as such, and after "on column" silylation, was performed.

RESULTS

Preparation and Purity of Free Secretory Component—Results of typical experiments and yields at different steps in the preparation of free secretory component are shown in Table I. It was important to accomplish these steps in as little time as possible to minimize protein loss. Freezing of the purified free secretory component solution was preferred for storage.

Immunoelectrophoretic examination (Fig. 3, well 6) of the final free secretory component preparation showed only one precipitation line with polyvalent antiserum against whole whey that reacted with at least eight components in whole whey (Fig. 3, well 1). Antiserum prepared by immunizing with these preparations showed only one line with whole whey, having the same electrophoretic mobility as the purified free secretory component. No reaction occurred with this antiserum against several whole bovine sera.

Immunoelectrophoresis (Fig. 3), immunodiffusion, and acid urea gel electrophoresis were used to assess the purity of the different purification steps. The 33 to 50% ammonium sulfate fraction was markedly enriched in free secretory component, and almost free of serum albumin, but contained α-lactalbumin and β-lactoglobulin (Fig. 3, well 2). The DEAE-cellulose effluent showed mainly IgG and free secretory component (Fig. 3, well 3), as well as several other minor components which were subsequently shown to be primarily lactoperoxidase and lactoferrin on antigenic analysis. The phosphocellulose column effectively removed lactoferrin and lactoperoxidase. Pool 2 of the phosphocellulose column showed only free secretory component and IgG on immunoelectrophoresis (Fig. 3, well 4), and these were partially resolved by the gel filtration step (Fig. 2). The remaining IgG was completely removed by immunoadsorption (Fig. 2A and Fig. 3, well 6).

Gel Electrophoresis Studies and Effects of Reduction—Disc gel electrophoresis at alkaline pH (Fig. 4, gel 1) revealed only one band even on loading with relatively large amounts of free secretory component. However, this band occupied the top 1 cm of the gel, and this is the same position as for IgG and lactoferrin. Gel electrophoresis in acid urea produced better resolution (Fig. 2A). It showed one heavy band in pure free secretory component preparations, whereas additional bands were seen with crude free secretory component preparations. Two faint, slightly faster bands were observed in some immunologically pure free secretory component preparations (Fig. 4, gel 2). The proportion of these bands in the late fractions obtained from the free secretory component peak on gel

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1 The abbreviations used are: dansyl, 5-dimethylaminonaphthalene-1-sulfonyl; PTH, 3-phenyl-2-thiohydantoin; FSC, free secretory component.

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TABLE I

| Step                                      | Volume | Protein |
|-------------------------------------------|--------|---------|
| 1. Whole whey                             | 500    | 4000    |
| 2. 33 to 50% ammonium sulfate fraction    | 25     | 1000    |
| 3. DEAE-cellulose column                  | 60     | 88      |
| 4. Phosphocellulose column (pool 2)       | 6      | 56      |
| 5. Superdex column (FSC pool)             | 70     | 32.5    |
| 6. Immunoadsorbed FSC pool                | 8      | 22.3    |
| Amount of FSC in starting material        |        | 40.0    |
| Final yield of FSC                        |        | 56%     |

a Calculated assuming a free secretory component concentration of 8 mg/100 ml as given by Mach and Pahun (35).
filtration was markedly higher than in the earlier fractions as quantitated by gel scanning. Reduced samples showed a marked decrease in mobility of the main band (Fig. 4, gel 3) and the appearance of more protein in the fast moving bands.

Gel electrophoresis in the presence of sodium dodecyl sulfate also showed one band in pure free secretory component preparations (Fig. 4, gel 4). Some faint fast bands were observed especially in gels of the last fractions of the free secretory component peak in gel filtration effluent. Reduced samples of the same preparations (Fig. 4, gel 5) showed some reduction in mobility as well as an increased amount of the fast bands. When samples of pure free secretory component were incubated at room temperature for 1 to 5 hours, the fast moving bands were detected in much larger amounts, representing up to 50% of the total protein (Fig. 4, gels 6 and 7), suggesting proteolysis.

**DISCUSSION**

Several methods have been used to purify bovine free secretory component (13, 15, 39) but, in our hands, the method

![Table II](https://example.com/table2.png)

| Physicochemical parameters | Present investigation | Literature |
|---------------------------|----------------------|------------|
|                          | No. | Average value ± range | Bovine Ref. 14 | Human Ref. 36 | Ref. 37 |
| Molecular weight | Sodium dodecyl sulfate gel electrophoresis after reduction | 10 | 79,000 ± 4,000 | 70,000 | 70,000 | 85,000 |
| Stokes Radius a | Gel filtration, in aqueous, non-denaturing buffers | 6 | 4.3 ± 0.1 nm | 4.6 | 4.4-4.6 |
| Molecular weight | Calculated from a | 100,000 ± 5,000 | 75,000 | 110,000 |
| D_20,w | 90.0 ± 1.2 µm² s⁻¹ | 47 | 47-49 |
| Molecular weight | Ultracentrifuge | 79,000 ± 1,000 | 86,000 | 74,000 | 83,000 |
| Partial specific volume (g) | Calculated from a, b, and c | 0.73 ± 0.01 ml/g | 0.724 | 0.710 | 0.712 |

* Value from Ref. 15.
* Assuming a linear relation between elution volume and log molecular weight. This is not strictly true due to differences in f/f₀.
* Literature values were obtained by other sedimentation equilibrium methods, and ɑ was calculated from composition.
partially degraded molecules in the preparation. Their further appearance of faster bands in sodium dodecyl sulfate gels in electrophoresis about 96% of the protein migrated as one band. The resolution of partially degraded free secretory component. was still necessary to first eliminate most of the IgG and allow component by gel filtrations alone. However, the gel filtration step makes it impossible to recover IgG-free free secretory component with lactoperoxidase or lactoferrin. Repeated precipitation with ammonium sulfate was used by Mach (15) to remove most of the lactoferrin, but from theoretical considerations (40) we did not expect this to be sufficient. On the other hand, chromatography on a phosphocellulose column was found to give good separation of these proteins, and no contamination of free secretory component preparations may not be solely a result of proteolysis, as their proportion is much higher in acid urea than in sodium dodecyl sulfate gel or acid urea gel electrophoresis (Fig. 4) is interpreted as showing that disulfide bridges help to maintain the compact structure of the free secretory component molecule, complete unfolding being achieved only after reduction. This is in agreement with the finding of larger Stokes radii for reduced protein molecules in denaturing solvents compared to the unreduced molecules with intact intramolecular disulfide links (43). However, the faster bands observed in acid urea gel electrophoresis of pure free secretory component preparations may not be solely a result of proteolysis, as their proportion is much higher in acid urea than in sodium dodecyl sulfate gels. This may be due to variations in charge as a result of differences in carbohydrate composition, which is common with many glycoproteins. Human free secretory component was found (37) to show marked microheterogeneity in isoelectric focusing, although other criteria showed 98% purity of the same preparation. Much of the variation in the data on molecular weight of bovine free secretory component (Table II) even using the same criteria showed 98% purity of the same preparation. Much of the variation in the data on molecular weight of bovine free secretory component (Table II) even using the same criteria showed 98% purity of the same preparation.

| Amino acid or sugar | Present Investigation | Literature Values |
|--------------------|-----------------------|-----------------|
|                    | Residues/mol (78,000 g) | Mol/100 mol amino acids | Mol/100 mol amino acids* |
| Lys                | 39.7                  | 5.90            | 6.01                  |
| His                | 10.1                  | 1.50            | 1.46                  |
| Arg                | 31.0                  | 4.61            | 4.76                  |
| Asp                | 87.0                  | 9.96            | 10.63                 |
| Thr                | 49.4                  | 6.00            | 6.54                  |
| Ser                | 57.9                  | 8.60            | 8.91                  |
| Glu                | 73.8                  | 10.97           | 10.63                 |
| Pro                | 37.4                  | 5.56            | 5.08                  |
| Gly                | 57.7                  | 8.57            | 8.82                  |
| Ala                | 38.8                  | 5.77            | 5.63                  |
| 1/2 Cys            | 22.8                  | 3.39            | 4.10                  |
| Val                | 70.5                  | 10.47           | 10.35                 |
| Met                | 1.6                   | 0.24            | 0.23                  |
| Ile                | 22.7                  | 3.57            | 3.33                  |
| Leu                | 43.6                  | 6.48            | 6.46                  |
| Tyr                | 24.5                  | 3.64            | 3.83                  |
| Phe                | 20.3                  | 3.01            | 3.21                  |
| Trp*              | 13.3                  | 1.90            | 3.19                  |
| Total             | 673.1                 | 100.92          | 99.98                 |
| Glucosamine       | 10.8                  | 1.61            | 2.16                  |
| Galactosamine      | 3.5                   | 0.52            | 0.80                  |
| Neutral sugars    | 12.8                  | 1.90            | 2.90                  |
| Sialic acid        | 1.0                   | 0.15            | 0.4                   |
| Mol/mol amino acid | 99.9                  | 99.9            | 91.8-110.0            |

* Range of data in these references
† Amino acids of bovine free secretory component were calculated from the molar ratio to glycine in Ref. 13, and amino sugars of rabbit free secretory component were calculated from the residues/mol in Ref. 12.
‡ Determined by mercaptoethanesulfonic acid hydrolysis; spectrophotometry gave slightly higher values.
§ From Ref. 14.
especially when repeated gel filtrations are used for preparation. Proteolysis may pass unrecognized because of intact disulfide linkages. However, collectively the data suggest that free secretory component of different species have similar molecular weights, close to 80,000. The relatively high frictional ratio determined in the present investigation for the bovine free secretory component (1.52 to 1.55), and by Björk and Lindh (36) for human free secretory component (1.57 to 1.6) explain their retardation on gel filtration compared to more globular proteins and consequent high estimates of molecular weights by this method if no correction is made for differences in frictional ratios. From the frictional ratio of the bovine free secretory component, a minimum axial ratio can be estimated as 4 to 6 assuming a hydration value of 1 to 0.4 g of water/g of protein (44).

The amino acid composition of the bovine free secretory component shows a close similarity to the human, rabbit, and dog (Table III). The variation of the different analyses of the human free secretory component in different laboratories (9–11) appear to be larger than the variation between the different species, with a few exceptions. Taking the range of the human free secretory component data as a basis for comparison, the only significant differences are the higher valine and lower leucine in the bovine, higher aspartic and and lower alanine in the dog, and higher histidine and proline in the rabbit free secretory component. However, the similarities are more remarkable, especially if we allow for substitution of some valine for leucine residues in the bovine free secretory component, both residues probably playing a similar role in protein structure. Importantly, methionine seems to be completely absent in the human free secretory component, whereas it ranges from 0.24 to 1.0 mol/100 mol of amino acids in cow, rabbit, and dog free secretory component. Because of its value in protein sequence studies, it was important to be sure that this small amount of methionine is not from a contaminant. Bovine lactoperoxidase and lactoferrin, two possible contaminants, are comparatively rich in methionine (45), but in the present studies both of these proteins were carefully excluded.

The similarity of the secretory component from various species is striking when their NH₂-terminal sequences are compared. Bovine, human, and canine secretory component show complete identity of sequence up to residue 11, and identity to residue 13 is present in the bovine and human species. However, immunological cross-reactivity of human and bovine free secretory component with rabbit antisera could not be detected by us, or by other investigators (46), and it therefore seems likely that significant differences will be found in the amino acid sequence of the remainder of the polypeptide chain of these species. The elucidation of the full sequence of the human component therefore seems likely that significant differences will be found and bovine free secretory component with rabbit antisera could not be detected by us, or by other investigators (46), and it therefore seems likely that significant differences will be found in the amino acid sequence of the remainder of the polypeptide chain of these species. The elucidation of the full sequence of the human component therefore seems likely that significant differences will be found and bovine free secretory component with rabbit antisera could not be detected by us, or by other investigators (46), and it therefore seems likely that significant differences will be found in the amino acid sequence of the remainder of the polypeptide chain of these species. 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Bovine secretory component. Isolation, molecular size and shape, composition, and
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