Structural Polypeptides of Mumps Virus

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(Accepted 24 June 1978)

SUMMARY

The structural polypeptides of egg grown mumps virus were analysed by SDS-polyacrylamide-slab-gel electrophoresis. Mumps virions contained eight major polypeptides with mol. wt. of 75, 73, 71, 61, 47, 44, 42 and 40 × 10^3. The 75 K and 61 K polypeptides were glycosylated. In virions treated with pronase and trypsin, the 75 K glycoprotein was removed more readily from the virus than the 61 K glycoprotein. The gradual removal of the 75 K glycoprotein was paralleled by a decrease of haemagglutinating activity. The large glycoprotein was cleaved into a 40 K glycoprotein by trypsin treatment. Pronase and trypsin treatment also removed the smallest 40 K non-glycosylated polypeptide. Thus this polypeptide appears to be located on the outside of the virion and probably represents a cleavage product of the large glycoprotein.

Treatment of virions with 2% Triton-X 100 under alkaline conditions in the absence or presence of 2 M-KCl solubilized the two glycoproteins and a fraction of the 71 and 44 K polypeptides, but not the 73 and 47 K polypeptides. The two smallest polypeptides were solubilized by treatment with 2% Triton X-100 in the presence of 2 M-KCl. Since the 40 K polypeptide was interpreted to represent a cleavage product of the large surface glycoprotein the 42 K polypeptide was proposed to represent the membrane protein of mumps virus. The 44 K polypeptide co-migrated with Vero cell actin. The nature of the 47 K polypeptide could not be determined, but it is probably located in the central part of the virus. The 73 K polypeptide and in some experiments also the 71 K polypeptide were found in purified nucleocapsid preparations.

It is concluded that mumps virus has a general polypeptide composition similar to other paramyxoviruses. However, the molecular weights of the different polypeptides of mumps virus differ markedly from the corresponding polypeptides in Newcastle disease virus and Sendai virus.

INTRODUCTION

Mumps virus is a member of the paramyxovirus group by a number of different criteria (Kingsbury et al. 1978). Only a few biochemical investigations of the structure and replication of the virus have been carried out. East & Kingsbury (1971) demonstrated that the virus, like other paramyxoviruses, contains a parental genome of single stranded RNA sedimenting at 50S. Bernard & Northrop (1974) found an RNA-dependent RNA polymerase in the virion. The properties of the polymerase reaction were similar to those described for other paramyxoviruses. Recently two studies have been presented concerning
the structural polypeptides of egg grown mumps virus determined by sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE) in disc gels (Jensik & Silver, 1976; Huppertz et al. 1977). Six major polypeptides were found in the Jo Ann strain of mumps virus, ranging in mol. wt. from 40 to $64 \times 10^3$ (Jensik & Silver, 1976). The polypeptide pattern of mumps virus was interpreted to be similar to the polypeptide pattern of NDV and Sendai virus. By analogy with SV 5, NDV and Sendai virus, two different glycoproteins were identified in mumps virions. Huppertz et al. (1977) found seven major polypeptides in the Enders strain of mumps virus with mol. wt. from 47 to $68 \times 10^3$. The mol. wt. of the different polypeptides markedly differed from those obtained by Jensik & Silver (1976).

The aim of the present investigation was to study the structural polypeptides of mumps virus by the use of SDS-PAGE in slab gels. Efforts were made to characterize the different polypeptides with regard to their possible function and localization in the virion.

**METHODS**

*Viruses.* Two strains of mumps virus were used, the Enders strain of mumps virus and a strain isolated by the Department of Virology, National Bacteriological Laboratory, Stockholm. The viruses were propagated in the allantoic sac of 7- to 9-day-old chicken embryos. The virus-containing allantoic fluid was harvested after incubation for 5 days at 37 °C. After clarification by low speed centrifugations the virus was concentrated by differential centrifugation at 13 000 rev/min for 90 min in the GSA rotor of a Sorvall superspeed ultracentrifuge. The pelleted virus was washed five times with phosphate buffered saline (PBS). Further purification of the virus material was obtained by centrifugation in discontinuous sucrose gradients to the interphase between 30 and 60% (w/w) sucrose, as has been described previously (Örvell, 1976). Some materials were centrifuged in linear 10 to 50% sucrose gradients at 15 000 rev/min for 15 to 60 min in an SW 40 rotor. NDV (Montana strain) and Sendai virus were propagated in the allantoic sac of 10- to 12-day-old chicken embryos for 3 days at 37 °C. The purification procedure of these viruses was similar to that described for mumps virus.

*Labelling of mumps virus glycoproteins.* One hour after infection, eggs were inoculated into the allantoic sac with $^3$H-glucosamine, 50 µCi/egg (Radiochemical Centre, Amersham). The labelled virus material was purified in the same way as unlabelled material. Surface glycoproteins of purified virions were also labelled in vitro, using the method of Luukonen et al. (1977). Each purified virus sample containing 100 µg of protein in 200 µl of Dulbecco's phosphate buffered saline (PBS), pH 7.4, were incubated with 25 units of galactose oxidase (Sigma Chemical Company, U.S.A.). After 1 h of incubation at 37 °C, 200 µCi of $^3$H-sodium borohydride (Radiochemical Centre, Amersham) in 30 µl of 0.01 M-NaOH was added and incubated with the virus sample for 30 min at room temperature. The labelled virus was then layered on a discontinuous sucrose gradient composed of 2.5 ml 60% sucrose (w/w) and 7 ml 30% sucrose layers in 0.01 M-phosphate buffer, pH 7.2, and centrifuged at 30 000 rev/min for 45 min in an SW 40 rotor. Labelled virions banding at the interphase were collected.

*Pronase and trypsin treatment of virions.* Glycoprotein labelled purified virions in phosphate buffered saline (PBS) were divided into equal portions and treated with varying concentrations of pronase (Koch-Light Laboratories, England) or trypsin (Sigma) for 1 h at 37 °C. After the incubation period the different samples were tested for haemagglutinating (HA) activity and centrifuged on discontinuous sucrose gradients as described above.
Polypeptides of mumps virus

Virus material banding at the interphase between the sucrose layers was collected and analysed by SDS-PAGE slab gel electrophoresis.

Triton X-100 treatment of virus. Glycoprotein labelled purified virions were dialysed against 0.02 M-sodium bicarbonate buffers, pH 10, in the absence or presence of 2 M-KCl. The virus samples were then treated with 2% Triton X-100 (Fisher Scientific Company, U.S.A.) for 15 min at room temperature and centrifuged on discontinuous sucrose gradients as described above. Virus material banding at the interphase and top fractions were analysed by SDS-polyacrylamide-gel electrophoresis on slab gels.

Purification of nucleocapsids. Purified virions were dialysed against 2 M-KCl in 0.02 M-sodium bicarbonate buffer, pH 10.0, and were treated for 15 min at room temperature with 2% Triton X-100. After the treatment the material was centrifuged at 20000 rev/min for 30 min in an SW 50 rotor. The pellet obtained from the centrifugation was used for purification of nucleocapsids. The procedure used followed that described by Mountcastle et al. (1970). The pellet was washed and suspended in 0.005 M-tris-HCl, 0.05 M-NaCl, 0.001 M-EDTA buffer, pH 7.2, after which the material was treated with 1% Triton X-100 and 0.4% sodium deoxycholate (DOC) and centrifuged on discontinuous CsCl gradients (Mountcastle et al. 1970). The visible nucleocapsid band was collected, dialysed against 2 M-KCl in 0.02 M-sodium bicarbonate buffer, pH 10.0, and the whole purification procedure was repeated once or twice. The different preparations of nucleocapsids were analysed by electron microscopy and by SDS-PAGE.

Polyacrylamide gel electrophoresis (PAGE). The technique employed essentially followed that described by Laemmli (1970). All virus protein samples except detergent solubilized proteins were precipitated with 10% trichloroacetic acid (TCA). Solubilized proteins were precipitated by addition of 5 vol. of cold absolute ethanol and were kept at -20°C for a minimum time of 12 h (Jensik & Silver, 1976). The precipitated protein samples were centrifuged at 3000 g for 20 min at 4°C. After the centrifugation the TCA precipitated protein samples were washed with cold ethanol, cold 50% ether in ethanol (v/v) and cold ether. Ethanol precipitated samples were washed with cold ether. The protein film on the glass wall was dissolved in 1% sodium dodecyl sulphate (SDS), 2% β-mercaptoethanol and 10% glycerol in water and the samples were subjected to electrophoresis after 2 min of boiling in a water bath.

The slab gel apparatus was similar to that described by Studier (1973). The size of the gels were 8.0 × 12.0 × 0.15 mm. The spacer gel in the slab gels contained 4.5% acrylamide and 0.12% NN'-methylene-bisacrylamide (bis). The separation gel contained 10% or 15% acrylamide and 0.18% bis. If not otherwise mentioned the separation gel contained 15% acrylamide. Electrophoresis was performed for 6 to 8 h at 1-5 to 2-0 W with bromophenol blue as a front marker dye. The gels were stained with 0.25% Coomassie brilliant blue in 35% ethanol and 10% acetic acid and were destained in the same solution without the stain. After destaining, the gels were stored in 7% acetic acid.

Scintillation autoradiography. After protein staining and destaining and storage in 7% acetic acid the gels were equilibrated in dimethylsulphoxide (DMSO), impregnated with 20% (w/w) 2-5-diphenyloxazole (PPO) in DMSO and soaked in water (Bonner & Laskey, 1974). The gels were dried (Maizel, 1971) and exposed to Wicorx-RP film at -70°C. Exposed films were developed in Kodak liquid X-ray developer for 3 min, put in 1% acetic acid for 30 s and fixed for 3 min in Kodak rapid fixer. washed in water for 30 min and dried.
Fig. 1. SDS-polyacrylamide-slab gel electrophoresis of different mumps virus polypeptides stained with Coomassie brilliant blue in a 15% (a) and 10% (b, c, d, e) polyacrylamide gels. The following materials were included: purified mumps virions (a, b, e), isolated 75 K (c) and 73 K (d) polypeptides. In order to obtain a good separation of the 75 K and 73 K polypeptides in the 10% polyacrylamide gel the migration front marked by bromophenol blue was allowed to run out into the electrolyte buffer and the time of electrophoresis was prolonged for 2 h.
Polypeptides of mumps virus

The proteins and glycoproteins of mumps virus

The polypeptides of purified mumps virions were analysed on 15 and 10% polyacrylamide gels. Eight major polypeptide bands were identified. The mol. wt. of these polypeptides were 75 K, 73 K, 71 K, 61 K, 47 K, 44 K, 42 K and 40 K. In stained 15% polyacrylamide gels only seven major polypeptides could be identified (Fig. 1). However, a separation of a diffuse 75 K and a sharper 73 K polypeptide was obtained in 10% gels (Fig. 1). The 44 K polypeptide of mumps virus co-migrated with Vero cell actin which was included in the reference protein mixture. In some mumps virus samples an additional non-glycosylated polypeptide band was found. This band was located between the 61 K and 47 K polypeptides (Fig. 2, 3, 5). It occurred irregularly, but could be found after the samples had been stored in the dissociated state. The origin of this polypeptide could not be defined.

No significant differences of the mumps virus polypeptide pattern were observed in comparison of virus-containing pellets and virus purified once, twice or more times on discontinuous sucrose gradients. Virus purified in linear 10 to 50% sucrose gradients did
not significantly differ in its polypeptide pattern. The polypeptide pattern of the two strains of mumps virus were identical. Most work described in the present study was carried out with the mumps virus strain isolated at the National Bacteriological Laboratory, Sweden.

The glycoproteins of mumps virus externally labelled with $^3$H-sodium borohydride are shown in Fig. 2 and 3. By this method of labelling, a considerable part of the radioactivity remained at the top of the gels. However, there was concentration of two radioactive bands in the region of the stained polypeptides of mumps virus. The upper band had a mol. wt. of 75 K and appeared to be superimposed on the uppermost band in the stained preparation. The lower band of radioactivity corresponded to the 61 K polypeptide in the stained preparation. When $^3$H-glucosamine was used for labelling of glycoproteins all radioactivity was recovered in these two bands.

Effects of treatment with pronase and trypsin on the polypeptide pattern of mumps virus

Glycoprotein labelled purified mumps virions in PBS were treated with pronase at a final concentration of 0.004, 0.02, 0.1, 0.5 and 2.0 mg/ml for 1 h at 37 °C (Fig. 2). The smallest virus polypeptide (40 K) was removed by the treatment. Pronase treatment also affected the two glycoproteins of mumps virus. The 75 K glycoprotein was removed from the virus more readily than the 61 K glycoprotein. The effects on the large glycoprotein could be observed on the autofluorogram before the HA titre was affected (cf. lane d in Fig. 2).

Experiments of similar design were carried out with trypsin at a final concentration of 0.005, 0.02, 0.1, 0.5 and 2.0 mg/ml. The results were essentially similar to results obtained with pronase, but some additional findings were made (Fig. 3). The relative sensitivity between the large and small glycoprotein was more pronounced when trypsin was used (cf. Fig. 3 and 2). Further, the large glycoprotein appeared to be cleaved into a 40 K glycoprotein, corresponding in size to the smallest polypeptide of mumps virus. Both the 75 K and the 40 K glycoprotein disappeared in parallel at higher concentrations of trypsin. In addition to the 40 K glycoprotein small glycoprotein fragments were found when lower concentrations of trypsin were used. The 40 K non-glycosylated polypeptide was not removed in the experiment described in Fig. 3. However, in some experiments the non-labelled 40 K polypeptide was removed by trypsin activity. The relative amount of the 40 K protein appeared to vary in different preparations of purified virions (cf. Fig. 1, 5, 6 and 7).

Triton X-100 treatment of virions

Glycoprotein-labelled purified virions were treated with 2% Triton X-100 at pH 10 in the absence or presence of 2 M-KCl. Treatment with Triton X-100 in the presence of salt disrupted the virus more efficiently than in the absence of salt. The different solubilized and non-solubilized materials after the two treatments are presented in Fig. 4. The 75 K and 61 K glycoproteins and a fraction of the 71 K and 44 K polypeptides were solubilized by the two different treatments. In addition the 42 and 40 K polypeptides were solubilized in the presence of 2 M-KCl. A small amount of these two polypeptides were also found in the solubilized material in the absence of salt. The 73 and 47 K polypeptides were not solubilized by the two different treatments. The 42 and 40 K polypeptides were isolated according to the method described for isolation of polypeptides of SV 5 and NDV (Scheid et al. 1972; Scheid & Choppin, 1973). The isolated 42 and 40 K polypeptides of mumps virus are shown in Fig. 5.
Polypeptides of mumps virus

Fig. 3. Trypsin treatment of purified mumps virions. The stained polypeptides are shown to the left and the corresponding externally labelled glycoproteins identified in the scintillation autofluorogram are shown to the right. The following materials were included: untreated purified mumps virions (a), purified mumps virions treated with 0.02, 0.1, 0.5 and 2.0 mg/ml of trypsin for 1 h at 37 °C (b, c, d, e). The HA titre of the different samples after the treatment are marked in the lower part of the left hand photograph.

Nucleocapsid protein

Purification of the nucleocapsid protein imposed certain difficulties. In order to obtain material containing a single polypeptide the procedure of extraction and centrifugation had to be repeated once or twice. The polypeptide band(s) obtained from extensively purified nucleocapsids is seen in Fig. 6. It contained the 73 K polypeptide and in some experiments a small amount of the 71 K polypeptide. Relatively more of the 71 K polypeptide was found in less purified nucleocapsid preparations. Although the 47 K polypeptide was found
Fig. 4. SDS-polyacrylamide gel electrophoresis of purified mumps virions and different solubilized and non-solubilized materials after Triton X-100 treatment of purified virions (1 mg/ml) at pH 10 in the absence or presence of 2 M-KCl. The following materials were included: untreated purified virions (a), non-solubilized materials in the absence of salt treated for 15 and 60 min (b, d), solubilized materials in the absence of salt treated for 15 and 60 min (c, e) and non-solubilized and solubilized materials in the presence of 2 M-KCl treated for 15 min (f, g).

Fig. 5. SDS-polyacrylamide gel electrophoresis of purified mumps virions (left) and the two smallest polypeptides of mumps virus (right).
Fig. 6. SDS-polyacrylamide gel electrophoresis of whole virus (left) and purified nucleocapsids (right).

Fig. 7. Comparison of the polypeptide pattern of purified mumps (c), NDV (b) and Sendai virions (d) to reference proteins (a). The reference proteins were: phosphorylase A (90 K), bovine serum albumin (67 K), gamma globulin, heavy chain (55 K), actin (44 K), gamma globulin, light chain (23 K).
Table 1. Comparison of the molecular weights of four major polypeptides of NDV, mumps and Sendai virus

<table>
<thead>
<tr>
<th>Polypeptide</th>
<th>NDV</th>
<th>Mumps</th>
<th>Sendai</th>
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<tr>
<td>HN</td>
<td>74</td>
<td>75</td>
<td>71</td>
</tr>
<tr>
<td>NP</td>
<td>53</td>
<td>73</td>
<td>57</td>
</tr>
<tr>
<td>F</td>
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<td>61</td>
<td>49</td>
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<tr>
<td>M</td>
<td>36</td>
<td>42</td>
<td>36</td>
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associated with non-solubilized virus materials after Triton X-100 treatment (Fig. 4) it was not present in purified preparations of nucleocapsids. This polypeptide was probably removed by DOC treatment.

Comparison of the polypeptide pattern of mumps virus to the polypeptide pattern of NDV and Sendai virus

From the results described above it was evident that the principle polypeptide composition of mumps virus is similar to that of other paramyxoviruses. However, the mol. wt. of the different polypeptides of mumps virus differ markedly from the corresponding polypeptides of NDV and Sendai virus (Fig. 7). The mol. wt. of the large and small glycoprotein (HN and F glycoproteins), the nucleocapsid protein (NP) and the membrane protein (M) of the three viruses, as determined in the present study, are shown in Table 1.

DISCUSSION

As regards polypeptide patterns, SV 5, NDV and Sendai virus are the most thoroughly studied members of the paramyxovirus group. The corresponding polypeptides of the three viruses are markedly similar in their molecular weights. In the present study it was found that the mol. wt. of the different polypeptides of mumps virus differed markedly in comparison with mol. wt. of the corresponding structures NDV and Sendai virus.

SV 5, NDV and Sendai virus have two glycoprotein structures on the envelope. Also, mumps virus has recently been shown to contain two glycoprotein structures (Jensik & Silver, 1976). An exception to the rule of two glycoprotein structures appears to be measles virus (Mountcastle & Choppin, 1977; Tyrrell & Norrby, 1978), which only has one glycosylated structure on the envelope.

In this investigation it was confirmed that mumps virus has two glycoprotein structures on the envelope. However, the small glycoprotein of mumps virus is considerably larger than the corresponding structure of other paramyxoviruses (Table 1). The two glycoproteins of mumps virus were solubilized by Triton X-100. The large glycoprotein of mumps virus was much more sensitive than the small glycoprotein to the action of pronase and trypsin. In a previous study from this laboratory (Orvell, 1976), it was found that immunization of rabbits with pronase-treated mumps virions resulted in the production of haemolysis-inhibiting antibodies, whereas titres of haemagglutinating-inhibiting and neuraminidase-inhibiting antibodies were low or absent in these sera. Taken together, these different findings are interpreted to mean that the small glycoprotein of mumps virus is involved in haemolysis and fusion of cells. Recently obtained results lend further support to this conclusion (Orvell, 1978, previous paper).

The 42 and 40 K polypeptides were solubilized by treatment with Triton X-100 in the
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presence of salt. However, a small amount of the 42 and 40 K polypeptides were also found in the solubilized material by Triton X-100 treatment in the absence of salt. The smaller of the two polypeptides, the 40 K polypeptide, was removed by treatment of intact virions with proteolytic enzymes. It appears therefore to be located on the exterior of virions and must not be a true matrix protein. The membrane protein of mumps virus is therefore concluded to be the 42 K polypeptide. This protein is larger than the corresponding structure of NDV and Sendai virus.

The results obtained from trypsin treatment of virions suggest that the 40 K polypeptide of mumps virus is a cleavage product of the large glycoprotein. In these experiments it was shown that the large glycoprotein was cleaved into a small glycoprotein of 40 K mol. wt., which upon further treatment lost its label. It is not known if the remaining non-glycosylated polypeptide migrates in the 40 K region or is further degraded. One may speculate that a carbohydrate moiety is removed from the protein and that the non-glycosylated 40 K polypeptide found in egg-grown virions derives from the virus hemagglutinin. The variation in relative amounts of the 40 K polypeptide in different preparations of purified virions is consistent with the view that this polypeptide represents a cleavage product. Trypsin treatment of influenza virus of the orthomyxovirus group grown in tissue culture cells results in cleavage of the uncleaved glycoprotein HA (Klenk et al. 1975). In studies on Sendai virus it has been demonstrated that the virus grown in tissue culture cells has a fusion precursor protein (Fp), which, by the action of trypsin, is converted into the smaller active F glycoprotein of egg-grown virus (Homma & Ohuchi, 1973; Scheid & Choppin, 1974). This cleavage is essential for production of wholly infectious virus particles. The possible importance of cleavage of surface glycoproteins during maturation of mumps virus by proteolytic enzymes warrants further studies.

Actin is a host cell protein which appears to become incorporated into Sendai and measles virions (Lamb et al. 1976; Tyrrell & Norrby, 1978). Mumps virus also has a polypeptide of the same size as actin, the 44 K polypeptide, but in this study it was not actually proved that this polypeptide was actin. This might be demonstrated by tryptic digest analysis of the polypeptide. The 44 K polypeptide was not accessible to the action of proteolytic enzymes on intact virions and is therefore probably not exposed on the exterior of the virus. However, treatment with Triton X-100 in the absence or presence of salt solubilized a fraction of the polypeptide.

The nature of the 47 K polypeptide could not be determined in this study. It was not solubilized by Triton X-100 treatment of virions and it was not accessible to the action of proteolytic enzymes on intact virus particles. The two findings suggest that this polypeptide may be associated with the central part of the mumps virus.

The 73 K polypeptide and, in some preparations, the polypeptide 71 K were found to be associated with the ribonucleoprotein complex of the virus. Upon consecutive detergent treatments more of the 71 K polypeptide was released, leading to the conclusion that the 73 K polypeptide is the structural protein of nucleocapsids of mumps virus. The 71 K polypeptide might be the polymerase polypeptide of mumps virus. Its mol. wt. corresponds to those of other polymerases of paramyxoviruses.

The results obtained in the present investigation differ from the results obtained by Jensik & Silver (1976), both as regards the number of polypeptides and the mol. wt. of the different polypeptides. The polypeptide composition of the Enders strain of mumps virus reported in the present investigation was almost identical to that reported by Huppertz et al. (1977). However, in the study by Huppertz et al. (1977) seven major polypeptides were found, whereas eight major polypeptides were found in the present investigation. Also, in
the present study the mol. wt. of the eight major polypeptides ranged in size from 40 to \(75 \times 10^3\), whereas Huppertz et al. (1977) found that the corresponding size range was 47 to \(68 \times 10^3\). Although these differences may seem pronounced, they can at least be partially accounted for. In the study by Huppertz et al. (1977), previously determined mol. wt. of Sendai virus polypeptides were used as a reference standard, whereas in the present study the mol. wt. of both mumps and Sendai virus polypeptides were compared against reference standards. If only the comparison between mumps and Sendai virus polypeptides is taken into consideration, no major discrepancies were found between the two studies. In the high mol. wt. region three polypeptides with close mol. wt. were found in the present study, whereas only two polypeptides were found by Huppertz et al. (1977). It was shown in the present study that only two of the three polypeptides were discerned in standard experimental conditions.

In the present study it was shown that principally the same polypeptides which have been described for other paramyxoviruses can be identified in mumps virus. However, the mol. wt. of the different mumps virus polypeptides differed markedly from the mol. wt. of the corresponding polypeptides of NDV and Sendai virus. On the assumption that the 44 K polypeptide is actin and the smallest polypeptide is a cleavage product of the large glycoprotein, only six major polypeptides coded for by the virus genome remain. The total mol. wt. of these polypeptides would be approximately \(370 \times 10^3\). This value is within the expected coding capacity of the mumps virus genome.

The skilled technical assistance of Ms Mariethe Ehnlund is gratefully acknowledged. Dr Lendon Payne was helpful in electron microscopic work. The author conveys special thanks to Dr Gösta Winberg, who has introduced me into the technique of SDS-polyacrylamide slab gel electrophoresis. This work is supported by the Swedish Medical Research Council (Project No. 16X-116).

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(Received 11 October 1977)