

Section A

Viruses of Vertebrates and Insects*

Acado virus (orbivirus subgroup of reoviridae).

Acute bee-paralysis virus, *see* bee acute paralysis virus.

Acute laryngotracheobronchitis virus (parainfluenza-type 2 virus).

ADENOVIRUSES (a uniform group or genus). Medium large nonenveloped particles of polygonal symmetry, 70–80 nm in diameter, of a density of 1.34 g/ml in CsCl and a particle weight of about 175×10^6 daltons, containing linear double-stranded DNA of $20\text{--}23 \times 10^6$ dalton molecular weight. The icosahedral protein shell consists of 240 hexons (each bound to 6 neighbors), and at the apices 12 pentons (each bound to 5 neighbors) which carry fibers. The pentons and hexons are round, 8 nm in diameter, the fiber 20×2 nm with a terminal knob 4 nm in diameter (see Electron micrograph I).

The virus is replicated and assembled in the nucleus. Many adenoviruses are oncogenic, particularly for newborn hamsters and rats, and transform cells in culture. There are 31 known serotypes pathogenic for man (of which types 12, 18, and 31 are highly oncogenic and types 3, 7, 8, 11, 14, 16, and 21 less so in hamsters). There are also many simian adenoviruses, of which SV1, 11, 20, 23, 25, 30, 33, 34, 37, 38, and SA7 are oncogenic, as is an avian serotype (celo) and a bovine serotype (type 3). Canine, porcine, and murine adenoviruses also exist. All mammalian strains share

* Many names of animal viruses start, like those of plant viruses, with the host's name (bovine, feline, avian, human, etc.), and frequently this adjective is omitted. The reader is advised to search under both names, with and without this prefix adjective. Also, some general features of virus groups are listed under the group name and not reiterated for each member of the group. Thus the reader is advised to look in both places.

one antigen. Except for the highly oncogenic strains, adenoviruses are very species-specific.

Infection in man may affect the respiratory system, the eyes, or the intestinal tract, often after a period of latency and rarely with serious consequences. Most adenoviruses cause hemagglutination of the erythrocytes of the host or species related to the host.

The nontumorigenic human strains of adenoviruses that have been studied chemically in detail appear very similar or almost identical by the methods used, but the difference between these and the highly oncogenic ones (types 12, 18, 31, which cause tumors in hamsters) is marked in several respects. These two groups will therefore be treated separately in describing structural detail. (Prage and Pettersson, 1971; Prage *et al.*, 1972.)

Human nontumorigenic serotypes (types 2, 4–6, 9, 10, 13, 15, 17, 19, 20, 22–30).

The virus particles (790 S) consist of 87% protein and 13% DNA; their density in CsCl is 1.34 g/ml. The DNA has a molecular weight of 23×10^6 and contains 56–60% (G+C). Its length is about 12 μ m. Type 1 adenovirus DNA was found to be slightly infectious for DEAE-treated human embryonic kidney cells.

The main protein, the hexon, amounting to half the weight of the virus, represents trimers of a protein of a molecular weight of 120,000; the other two proteins of the icosahedral shell, penton and fiber, are of dissociated molecular weight 70,000 and 62,000 respectively. The fiber of serotype 2 is 20 nm long with a 4 nm diameter knob. Its undenatured molecular weight is about 200,000.

The dense internal core of the virus (40 nm diameter) contains associated with the DNA about 1000 molecules of a protein rich in arginine (23%) and alanine (20%) of molecular weight 22,000, and less of another of molecular weight 45,000. Three other minor protein components of about 10,000 mol. wt. as well as the 22,000 mol. wt. protein may be host cell histones. For amino acid compositions, see Table 1.

Human tumorigenic serotypes (type 7A, 12, 18, 31).

Differences between the tumorigenic and the nontumorigenic adenoviruses were detected mainly in the DNA, in that the DNA of the tumorigenic strains has a molecular weight of only 21×10^6 and contains 47–49% (G+C); the weakly oncogenic strains (types 2, 3, 7, 8, 11, 14, 16, 21) contain 50–53% (G+C). The lower values of the more oncogenic strains are closer to those of host DNA.

Regarding the proteins, the tumorigenic strains differ from type 2 only in minor detail, suggestive of a few amino acid exchanges in most of the proteins of the virus. (Burlingham and Doerfler, 1972.)

Adeno-associated viruses (AAV) (defective parvoviruses). At least 4 serotypes are known.

Particles of 20–25 nm diameter; 7.5×10^6 particle weight; density in CsCl 1.38–1.44 g/ml. They contain single-stranded DNA of molecular weight 1.6×10^6 , either of the two complementary strands being encapsidated in the virion (type 2: A/G/T/C = 21/27/27/26 for one DNA strand and 25/27/22/27 for the other). The main protein, comprising 80%, has a molecular weight of 64,000; two others (10% each) are 77,000 and 90,000.

Adeno-associated viruses replicate in the nucleus only in the presence of certain adenoviruses (and possibly herpesviruses) but are unrelated to these helpers serologically and chemically. The virus is resistant to lipid solvents and many chemicals, as well as to heating (1 hour at 60°C). Types 1–3 do not hemagglutinate; type 4 does hemagglutinate human O erythrocytes at 4°C, but not at 37°C. (Berns and Adler, 1972).

Aedes iridescent virus of mosquitoes, *see* mosquito iridescent viruses.

Aerocystis agent, *see* swim bladder inflammation agent of carp.

African horse sickness virus (orbivirus subgroup of reoviridae). 60–80 nm diameter. Vector: *Culicoides* spp.

African swinefever virus (icosahedral cytoplasmic DNA virus or possibly iridovirus). Icosahedral particles of about 200 nm diameter but in contrast to iridoviruses covered with an ether-sensitive membrane. The virus contains a dense 80 nm nucleoid. Lethal in domestic pigs, symptomless in the natural host, wild warthogs. (Almeida *et al.*, 1967; Hess, 1971.)

Alastrim (vaccinia virus, subgroup of poxviruses). Very similar, if not identical, to variola minor virus.

Allerton virus, *see* bovine ulcerative mammillitis virus.

ALPHAVIRUS GROUP. Preferred name for group A arboviruses, members of the togaviridae. Spherical enveloped 40–70 nm diameter particles (240–280 S) containing about 5% single-stranded RNA of $3.4\text{--}4.5 \times 10^6$ daltons. Glycoproteins of $63\text{--}51 \times 10^3$ and capsid proteins of about 30×10^3 daltons have been reported. Prototype: Sindbis virus. Other members: Aura, Chikungunya, eastern equine encephalitis, Getah, Mayaro, Middleburg, Mucambo,

Ndumu, O'Nyong-nyong, Pixuna, Ross River, Semliki Forest, Una, Venezuelan equine encephalitis, western equine encephalitis, and Whataroa viruses. (Horzinek, 1973.)

Amapari virus (arenavirus).

Amphibian cytoplasmic virus (possible member of iridovirus group).

Amsacta poxvirus (insect poxvirus). Contains 1.5% DNA.

Apoi virus (flavivirus subgroup of togaviridae).

ARBO(R)VIRUSES. A classifying term which is no longer recommended, covering togaviridae and many other but not all *arthropod-borne* viruses.

ARENAVIRUS GROUP (or arenaviruses). Poorly defined group of serologically related enveloped RNA viruses 90–220 nm in diameter, with densely spaced surface projections, and dense internal 20–25 nm granules believed to be host ribosomes (see Electron micrograph II). Members: Lassa, lymphocytic choriomeningitis, Machupo, Tacaribe, Junin, Amapari, Pichinde, Parana, Tamiani, Latino, Pistillo viruses. Most arenaviruses cause chronic infections in rodents; some, e.g., Lassa virus, cause acute disease, often fatal, in man and other animals. (Rowe *et al.*, 1970.)

Argentina virus (a strain of vesicular stomatitis virus closely related to Cocal virus).

A-type particles. Particles with toroidal nucleoid resembling oncornaviruses and associated with tumors but not proven to be viral in nature. (Yang and Wivel, 1973.)

Aura virus (alphavirus subgroup of togaviridae). Related to western equine encephalitis virus. About 50 nm in diameter. Pathogenic for newborn mice.

Australian antigen, *see* hepatitis viruses. (Sukeno *et al.*, 1972)

Avian encephalomyelitis virus (picornavirus of chickens).

Avian herpesviruses (of pigeons, owls, parrots, cormorants); proposed name: phasianid herpesviruses.

Avian infectious bronchitis virus, *see* infectious bronchitis virus.

Avian influenza A virus (myxovirus). Serological differences noted in 10 strains (4 major groups) in regard to neuraminidases and hemagglutinin (*see* influenza viruses). (Madeley *et al.*, 1971.)

AVIAN LEUKOSIS VIRUSES (group of leukoviruses).* Similar in most respects to murine leukoviruses. Six subgroups have been identified. The properties of all these viruses are exemplified by the prototype, avian myeloblastosis virus (see below). They are transformation-defective and contain slightly smaller RNA molecules than nondefective strains causing tumors and focus formation (transformation) of fibroblasts (see Rous sarcoma virus).

Avian myeloblastosis virus (AMV) (prototype avian leukemia virus). Pleomorphic particles 80 nm in diameter (about 500×10^6 dalton particle weight), consisting of a dense 40 nm possibly icosahedral capsid, and a membrane or envelope studded with spikes or knobs. The envelope is largely derived from the host cell plasma membrane and is rich in the enzymes occurring in that membrane (e.g., ATPase). The virus capsid is assembled in the cytoplasm, but the RNA is probably replicated in the nucleus with an intermediate stage of DNA synthesis. Thus the virus, like all oncornaviruses, contains RNA-dependent DNA polymerase (reverse transcriptase).* The virus matures as it buds through the plasma membrane. Its lipids but not its envelope proteins are probably derived from that membrane. The virus is sensitive to ether.

The capsid contains single-stranded RNA, $10\text{--}12 \times 10^6$ daltons per particle, 60–65 S, as well as smaller RNAs (10–12 S, 5 S, 4 S). Upon heating or other means of separating paired bases, the large RNA is dissociated to 30–35 S, as well as smaller material (12 S–4 S). Thus the genome is believed to exist in 3 or 4 pieces of $2.5\text{--}4 \times 10^6$ mol. wt., held together by short H-bonded segments. The average composition is A/G/U/C = 25/29/23/23. The 3'-termini of the 30–35 S RNA are predominantly unphosphorylated adenosine with lesser amounts of cytidine and uridine. The 4 S RNA is probably in part tRNA.

The main proteins of the envelope are two glycoproteins (37,000 and 115,000 mol. wt.), the type-specific antigens. The purified core largely consists of a protein of 24,000–28,000 mol. wt. This and a protein of 12,000 mol. wt. represent the group-specific antigens.

The lipids of the envelope are qualitatively the same and quantitatively similar to those of the host cell's plasma membrane. The core retains most of the DNA-polymerase and reverse transcriptase activities characteristically occurring in all oncornaviruses. The core also is slightly infectious; it contains the RNA in the 62 S

* See footnote on page 34.

form but also some (< 5%) 27 S and 17 S cellular RNA and 4–5 S RNA.

Avian leukosis viruses cause widespread infection in domestic chickens, at times leading to visceral lymphomatosis, but often remaining symptomless. (Stromberg, 1972; Bolognesi *et al.*, 1972.)

Avian reticuloendotheliosis virus, *see* reticuloendotheliosis virus.

Avian sarcoma viruses, *see* Rous sarcoma virus.

B virus of monkeys (proposed name: cercopithecoid herpesvirus).

B 77 (nondefective avian Rous sarcoma virus strain).

B 1327 virus (orbivirus subgroup of reoviridae).

BACULOVIRUS GROUP. Proposed name for nuclear polyhedrosis and granulosis viruses; *see* under these names.

Bahig, Bakan, Banzi, Batai viruses (either flaviviruses or Bunyamwera supergroup, both subgroups of togaviridae).

Bat salivary virus, *see* salivary virus.

BeAr 35646, BeAr 41067 (orbivirus subgroup of reoviridae).

Bebaru virus (alphavirus subgroup of togaviridae).

Bee acute paralysis virus (nonoccluded insect picornavirus). 28 nm diameter particles (160 S) of buoyant density in CsCl 1.34 g/ml. Contains 25% single-stranded RNA (30 S), 2×10^6 mol. wt. A/G/U/C = 30/19/30/21. Infects only the adult insects. (Newman *et al.*, 1973.)

Bee chronic paralysis virus (unclassified insect virus). Ellipsoid particles 22×41 , 54, and 64 nm (97 S, 110 S, 125 S), not ether sensitive, containing RNA.

Bhanga virus (either flavivirus or Bunyamwera supergroup, both subgroups of togaviridae).

Birdpox viruses (subgroup of poxviruses, including fowlpox, canarypox, pigeonpox, turkeypox, etc.). Double-stranded DNA of 200×10^6 mol. wt.

Bittner virus, *see* mouse mammary tumor virus.

Bluetongue virus of sheep (orbivirus subgroup of reoviridae). Two types, 69 and 63 nm particles (550 S and 490 S), probably composed of a single shell of 32 capsomeres with a 23 nm central nucleoid (density 1.36 and 1.38 g/ml in CsCl). The virus contains

20% of double-stranded RNA, probably 10 components, 42% (G+C) on average. The largest component has a molecular weight of 2.7×10^6 , the total RNA of the particle being about 12×10^6 daltons. Four major and three minor capsid proteins ($110, 100, 58, 32 \times 10^3$; and $155, 72, \text{ and } 38 \times 10^3$) corresponding in molecular weight to respective RNA components. The smaller particles lack the 110 and 58×10^3 surface components. They are less infective but contain transcriptase, which is not detectable in the larger component. Transmitted by *Culicoides* spp. The virus replicates also in vector, causes severe disease in sheep. (Martin and Zweerink, 1972; Verwoerd *et al.*, 1972.) (The differences between orbiviruses and classical reoviruses are diminishing as more is being learned about them.)

Bovine adenovirus, *see* adenovirus.

Bovine diarrhea virus (unclassified, possibly flavivirus subgroup of togaviridae). 57 nm particles with 25 nm core. Sensitive to ether; density in CsCl 1.15 g/ml. Contains RNA.

Bovine enterovirus VG-5-27 (enterovirus subgroup of picornaviridae). 28 nm diameter particle (165 S); density in CsCl 1.34 g/ml; contains single-stranded RNA of 2.8×10^6 mol. wt. (35 S). Four equimolar proteins: 34,000, 28,000, 26,000, and 7300 mol. wt. The 75 S procapsid lacks the smallest protein component (*see* mouse-Elberfeld virus for viral architecture). (Martin and Johnston, 1972.)

Bovine ephemeral (or epizootic) fever virus (not yet classified). Bullet-shaped (140×80 nm) and conical (176×88 nm) particles. The virus has a density of 1.19 g/ml in CsCl; it is ether sensitive but it contains a 12 S double-stranded RNA. (Tanaka *et al.*, 1969, 1972.)

Bovine lumpy skin disease virus (paravaccinia virus subgroup of poxviruses).

Bovine mammillitis virus (bovid herpesvirus 2). 64% (G+C).

Bovine papilloma virus, *see* papilloma virus.

Bovine papular stomatitis virus (paravaccinia subgroup of poxviruses, related to orf virus).

Bovine parainfluenza virus (type 3 parainfluenza virus subgroup of paramyxoviruses). Many serotypes. 280–580 nm particles containing an 18 nm helical nucleocapsid. Causes shipping fever.

Bovine respiring syncytial virus (*see also* respiratory syncytial virus). Particles of 110 nm diameter with 15 nm projections, and helical

nucleocapsid of about 13 nm diameter (Malmquist *et al.*, 1969; Ito *et al.*, 1973b.)

Bovine rhinotracheitis virus, *see* infectious bovine rhinotracheitis.

Bovine ulcerative mammillitis virus (Allerton virus) (herpesvirus).

B particles, *see* B-type virus.

Brazil virus (strain of vesicular stomatitis virus).

Brazilian myxomavirus (myxoma subgroup of poxviruses).

Bryan strain of Rous sarcoma virus (replication-defective, usually contains RAV) (*see* Rous sarcoma virus).

B-type virus, *see* mouse mammary tumor virus.

Buffalopox virus (vaccinia virus). Closely related to cowpox virus, but distinguishable.

Bukalasa virus (flavivirus subgroup of togaviridae).

BUNYAMWERA SUPERGROUP VIRUSES (not yet clearly reclassified "arboviruses"). At least 9 serotypes, 60–120 nm diameter. Batai and Inkoo viruses are spherical enveloped particles, 60 and 55 nm in diameter, excluding 12 and 15 nm projections respectively. They contain a helical nucleocapsid, similar to that of Uukuniemi virus. These helices differentiate the Bunyamwera group from typical togaviruses (Semliki Forest and Sindbis viruses), and their appearance is also clearly different from the myxovirus nucleocapsids. (Holmes, 1971.)

Bussuquara, Bwamba viruses (togaviridae).

Cache Valley virus (member of Bunyamwera supergroup of togaviridae).

CALICIVIRUS GROUP (subgroup of picornaviridae). Larger than other subgroups (37 nm diameter, 175 S). Members: Vesicular exanthema and some feline viruses. Buoyant density in CsCl 1.37 g/ml (more than entero- and cardioviruses and less than rhino- and foot and mouth disease viruses). Contain 22% RNA and a 63×10^3 protein.

California encephalitis viruses (human alphaviruses or more probably members of the Bunyamwera viruses, exemplified by LaCross virus). Particles of 95 nm diameter. The 12 nm envelope matures during release of the virus. (Lyons and Heyduk, 1973.)

California myxoma virus (myxoma subgroup of poxviruses).

Canarypox virus (birdpox subgroup of poxviruses).

Candivu virus (togavirus).

Canine distemper virus (paramyxovirus). Closely related to measles and rinderpest virus. Pleomorphic particles of predominantly 200–250 nm diameter, with about 7-nm-thick outer membrane and 11 nm projections. The helical nucleocapsid has a diameter of 15–18 nm and a 5 nm axial canal. Buoyant density in CsCl 1.23 g/ml. The virus lacks neuraminidase. (Appel and Gillespie, 1972.)

Canine hepatitis virus (adenovirus).

Canine herpesvirus 61% (G+C).

Canine papilloma virus 300 S and 165 S for full and empty capsids.

CARDIOVIRUS GROUP (subgroup related to enteroviruses of picornaviridae). Members: Mengo virus, encephalomyocarditis virus, mouse-Elberfeld virus, etc. Density 1.32–1.34 g/ml, stable over the range of pH 3–10; 151–162 S. (Eggen and Shatkin, 1972.)

Carr-Zilber Rous sarcoma virus (nondefective avian sarcoma virus).

Celo virus, *see* chick embryo lethal orphan virus.

Central European tick-borne encephalitis virus (togavirus).

CH 9935 (orbivirus subgroup of reoviridae).

Chandiporna virus (human rhabdovirus).

Changuinola virus (orbivirus subgroup of reoviridae).

Channel catfish virus (herpesvirus). 175–200 nm particles of icosahedral symmetry, 162 capsomeres. The virus becomes enveloped at the nuclear membrane. (Wolf and Darlington, 1972.)

Chenuda virus (orbivirus subgroup of reoviridae).

Chick embryo lethal orphan virus (celo virus) (oncogenic avian adenovirus). 60–80 nm icosahedral particles, 252 capsomeres. Density in CsCl 1.35 or 1.32 g/ml. DNA, 17.3%, of 30×10^6 mol. wt. It is unique, nonpermuted, linear, and double-stranded, lacks cohesive ends, and contains 54% or 46% (G+C). The virions are 81% protein, similar to other adenoviruses, except that the pentons are quite different from those of human adenovirus and carry two fibers of 43 and 9 nm length. (For amino acid analysis of the hexon, *see* Table 1). (Laver *et al.*, 1971.)

Chicken herpesvirus 45% (G+C).

Chickenpox virus (human herpesvirus 3) *see* varicella-zoster virus.

Chick syncytial virus (oncornavirus, related to reticuloendotheliosis virus).

Chikungunya virus (alphavirus subgroup of togaviridae).

Chilo iridescent virus (insect iridovirus).

Citrus red mite virus (picornavirus).

Cocal virus (rhabdovirus of mite). 60×170 nm bullet-shaped particles. Genetically and serologically related to vesicular stomatitis virus; Indiana serotype.

Coital exanthema virus, equine herpesvirus 3.

Colorado tick fever virus (orbivirus subgroup of reoviridae). Not enveloped particles containing double-stranded RNA. Vector: *Dermacentor* spp. Host: man (virus replicates in both).

Columbia SK virus (cardiovirus subgroup of picornaviridae). Related to encephalomyocarditis, mouse-Elberfeld virus, etc.

Congo virus (togavirus).

Contagious pustular dermatitis virus (paravaccinia subgroup of poxviruses, related to orf virus).

CORONAVIRUS GROUP. Recently defined group of viruses resembling myxoviruses, the most marked distinguishing characteristics being 20-nm-long, widely spaced club-shaped or petal-shaped projections, instead of spikes, which give the particles their corona-like appearance. The entire virus maturation appears to occur in the cytoplasm, not through budding. Human prototype OC 43: 390 S particles, 80–160 nm in diameter, particle weight 112×10^6 daltons. The clublike projections are 15–20 nm long, 10 nm across the wide part (see Electron micrograph III).

The membrane appears to be double. The virus is ether and acid sensitive. Its buoyant density in CsCl is 1.19 g/ml. The 7–8 nm threadlike nucleocapsids (similar to those of myxoviruses) contain single-stranded RNA.

The proteins are a nucleocapsid protein (26%) of 30,000 mol. wt., and an envelope glycoprotein and protein of 104,000 (8%) and 47,000 (16%). Other proteins not yet located but surely mostly from the envelope are a glycolipoprotein of 191,000 mol. wt. (13%) and two glycoproteins of 60,000 and 15,000 (23% and 14%).

Besides many human serotypes (often found in association with common colds), other members of the corona virus group are avian infectious bronchitis virus, murine hepatitis virus, transmissible gastroenteritis and hemagglutinating encephalomyelitis viruses of pigs, pneumotropic virus of rats, etc. In man these viruses usually give respiratory symptoms. (Hierholzer *et al.*, 1972.)

Corriparta virus (insect orbivirus, subgroup of reoviridae). Host: *Culex mosquito*.

Coryza virus (rhinovirus subgroup of picornaviridae).

Cowbone ridge virus (flavivirus).

Cowpox virus (subgroup I poxvirus), *see* under poxvirus.

Coxsackie virus (enterovirus subgroup of picornaviridae). A: 24 serotypes; B: 6 serotypes. Particles of 153 S, 28 nm diameter, and a particle weight of about 7×10^6 , containing about 30% single-stranded RNA. A/G/U/C = 28/28/24/20. The particles consist of four proteins, like other enteroviruses. Serotype A7 is neurotropic in man. (Tannock *et al.*, 1970.)

C particles, *see* C-type viruses.

Creutzfeld–Jakob disease agent of man, *see* slow viruses, scrapie.

Cricket virus (picornavirus).

Croup-associated virus, *see* parainfluenza viruses.

Crystalline array virus of grasshoppers (picornavirus). Particles of less than 25 nm diameter.

C-type viruses, term used for all oncornaviruses with centrally located spherical nucleoid, i.e., all except the mouse mammary tumor virus (B-type).

Cytomegaloviruses (*see* human herpesvirus 5 and other herpesviruses). Associated with salivary gland of man, guinea pig, mouse, swine, vervet, horse. DNA of 100×10^6 daltons (55 S); composition of the human virus: 57% (G+C); vervet virus, 51% (G+C); mouse virus, 59% (G+C), 132×10^6 molecular weight. (Huang *et al.*, 1973.)

Cytoplasmic polyhedrosis viruses (occluded isometric diplornaviruses of insects, e.g., silkworm). Polyhedral inclusion bodies 0.5–15 μ m in diameter consisting predominantly of 2 proteins of 30,000 and 20,000 mol. wt. Embedded in this matrix are many icosahedral virus particles 60–65 nm in diameter, with large knobs, not en-

veloped. The virus is of about 400 S and 2.9×10^7 particle weight; its buoyant density in CsCl is 1.435 g/ml. The RNA of the *Bombyx mori* virus (12.7×10^6 daltons total) occurs in 10 double strands, all 3' terminating in U and C followed by a pyrimidine. Their molecular weights range from 2.7 to 0.37×10^6 daltons; average composition: A/G/U/C = 28/22/29/21. The RNA of the *Malacosoma distria* virus totals 20.3×10^6 daltons.

The virion proteins have molecular weights of 151, 142, 130, 67, and 33×10^3 , but the proteins of the polyhedron matrix may also be virus coded (molecular weight 122, 100, 48, 30, and 20×10^3).

The virions contain RNA polymerase which is able quickly to transcribe each of the RNA components. The virus hemagglutinates mammalian cells. (Lewandowski and Traynor, 1972; Shimotohno and Miura, 1973.)

D'Anguilar virus (orbivirus subgroup of reoviridae).

Dakar bat virus (flavivirus).

Deer fibroma virus (papilloma virus).

Defective viruses. Many different RNA and DNA viruses have been found to occur in lighter and noninfective forms, usually due to a deficiency of nucleic acid. Such phenomena have particularly been studied with influenza virus (von Magnus particles), Sendai virus, vesicular stomatitis virus, reovirus, adenovirus, and herpesvirus. Virions lacking nucleic acid ("top components") have also been observed, as well as virions containing host DNA instead of viral DNA (pseudoviruses). (Huang *et al.*, 1966; von Magnus, 1954; Schlesinger, 1969; Kingsbury *et al.*, 1970; Mak, 1971; Nonoyama *et al.*, 1970.)

Dengue virus (flavivirus subgroup of togaviridae). Four known serotypes: Dengue virus 2: spherical 50 nm particles with 26 nm core. Single-stranded RNA (45 S), A/G/U/C = 31/26/22/21. Nucleocapsid protein of 13,500 mol. wt. (lysine rich, histidine deficient); the envelope glycoproteins of 59,000 mol. wt.; and a membranous capsid protein tightly bound to the envelope of 8000 mol. wt. (Stollar, 1969; Matsumura *et al.*, 1971.)

Densonucleosis virus (*Galleria dense nuclear virus*) (insect parvovirus). Particles of 22 nm diameter consisting of 42 capsomeres; density in CsCl 1.440 g/ml; contains 37% DNA, probably single-stranded within the virion, of 2×10^6 mol. wt. and buoyant density of 1.711 g/ml in CsCl. (Kurstak *et al.*, 1973.)

DIPLORNAVIRUS GROUP. Not yet officially accepted name for double-stranded RNA viruses (reoviridae). This is a group of viruses occurring in man, mammals, plants, and insects (the latter not acting as vectors but regular hosts). The plant diplornaviruses (e.g., rice dwarf virus and wound tumor virus) will be dealt with in Section B; they are very similar in most respects to the diplornaviruses infecting animals and insects.

These viruses are characterized by single or more often double shells of protein, therefore of either about 60 or 80 nm diameter, of cubic symmetry, and lacking an envelope and thus not ether sensitive (see Electron micrograph IV). They contain 10–15 molecules of double-stranded RNA (diplo-RNA). The two animal subgroups of diplornaviridae known are the reoviruses and the orbiviruses (bluetongue virus). The diplornaviruses, like possibly all groups of RNA viruses except the picorna- and togaviridae, carry their own transcriptase.

Members of the animal and insect diplornavirus group are the reoviruses, African horse sickness, bluetongue, Changuinola, Colorado tick fever, Corriparta, epizootic hemorrhagic disease of deer, epizootic diarrhea of mice, Eubenangee, infectious pancreatic necrosis of trout, Kemerovo, etc., viruses.

Distemper virus of dogs, *see* canine distemper virus.

Drosophila P virus (insect picornavirus).

Drosophila sigma virus (insect rhabdovirus).

Duck hepatitis virus (enterovirus).

Duck infectious anemia virus (oncornavirus). Related to reticuloendotheliosis virus.

Duck plague virus, probably a herpesvirus (anatid herpesvirus 1). (Hess and Dardiri, 1968.)

Duck spleen necrosis virus (oncornavirus). Related to reticuloendotheliosis virus.

Eastern equine encephalitis virus (EEE) (alphavirus subgroup of togaviridae). 54 nm particles, 240 S, 58×10^6 particle weight; density in CsCl 1.21 g/ml; lipid-containing envelope. Single-stranded RNA, containing, as probably all togaviridae, poly(A) sequences, probably 3' terminal. Multiplies in cytoplasm, matures by budding, in vertebrates and arthropods. (Karabatsos, 1973.)

EB virus, *see* Epstein-Barr virus.

Echo viruses (enterovirus subgroup of picornaviridae) (enteric, cytopathic human orphan viruses). 30 serotypes. 27 nm diameter particles of 157 S. Produce no distinct disease.

Echo virus 10 (reovirus).

Echo virus 28 (rhinovirus subgroup of picornaviridae).

Ectromelia virus, mousepox virus (vaccinia subgroup of poxviruses).

Edgehill virus (flavivirus subgroup of togaviridae).

Egtved virus of rainbow trout (rhabdovirus). 65×180 nm bullet-shaped particles.

Encephalomyocarditis virus (EMC) (cardiovirus subgroup of picornaviridae). About 27 nm diameter particles, 160 S, 8.5×10^6 in particle weight. Density in CsCl 1.34 g/ml. Contains 31.7% single-stranded RNA of 2.6×10^6 mol. wt., A/G/U/C = 26/24/25/25. The RNA contains poly(A), about 58 residues long. Four probably equimolar proteins of 35,000, 28,000, 24,000, and 7000 mol. wt. For comparative data on amino acid composition of three main proteins of EMC and ME virus, *see* Table 1. One liter culture fluid yields 2-3 mg pure virus. Specific infectivity (particle/PFU) = 20 to 250. (Butterworth and Rueckert, 1972.)

Englebreth-Holm Rous sarcoma virus, *see* Rous sarcoma virus.

Entebbe bat salivary gland virus (flavivirus subgroup of togaviridae).

ENTEROVIRUS GROUP (subgroup of picornaviridae). Related to cardioviruses; of same physical properties and stability. Icosahedral particles of about 27 nm diameter; 8.6×10^6 daltons particle weight; 155 S; 1.34 g/ml buoyant density in CsCl; containing 29% single-stranded RNA of 2.6×10^6 daltons. Human, bovine, porcine, avian, and murine species are known.

Entomo poxviruses, *see* insect poxviruses.

Epizootic diarrhea virus of infant mice (related to reovirus).

Epizootic hemorrhagic disease virus of deer (orbivirus subgroup of reoviridae).

Epstein-Barr virus (human herpesvirus 4). Contains 9% double-stranded DNA of 95×10^6 daltons; density in CsCl 1.718 g/ml, 59% (G+C). Virus isolated from established cell lines of Burkitt

lymphoblasts, thus virus apparently associated with human malignancy. The virus is the causative agent of infectious mononucleosis. (Moss and Pope, 1972.)

Equine abortion virus, *see* equine herpesvirus 1.

Equine arteritis virus (probably alphavirus subgroup of togaviridae, similar to rubella virus). Enveloped, ether sensitive, 57 nm particles, buoyant density in CsCl of 1.18 g/ml. The 25 nm core contains RNA; there are 9 structural proteins (72,000 to 10,500), the major ones being 15,000 and 13,000 in molecular weight. This is similar to the protein pattern of flaviviruses, whereas rubella resembles alphaviruses more closely. (Hyllseth, 1973.)

Equine encephalitis virus, *see* eastern and western equine encephalitis viruses.

Equine herpesvirus 1 (equine abortion or rhinopneumonitis virus). Density of the DNA 1.717 g/ml, 92×10^6 mol. wt.; 58% (G+C). The virus contains about 20 proteins (13,000–115,000 mol. wt.), the nucleocapsid 3; three envelope proteins contain lipid, and four are glycoproteins.

Equine herpesvirus 2 (cytomegalovirus, possibly identical to equine infectious anemia virus). Density of DNA 1.716–1.717 g/ml; 57–58% (G+C).

Equine herpesvirus 3, coital exanthema virus.

Equine infectious anemia virus (possibly belonging to the slow virus group) (from horse leukocytes). Pleomorphic particles of 90–140 nm diameter, with a 40–60 nm core and a 9 nm envelope. Density 1.15 g/ml in CsCl. Ether sensitive. The virus contains RNA. (Nakajima *et al.*, 1970.)

Equine infectious arteritis virus, *see* equine arteritis virus.

Equine rhinopneumonitis virus, *see* equine abortion virus.

Eubenangee virus (orbivirus subgroup of reoviridae).

FAV-1, *see* frog adenovirus.

Feline ataxia virus (parvovirus).

Feline herpesvirus (probably identical with feline rhinotracheitis virus). 47% (G+C).

Feline leukemia-sarcoma viruses (oncornaviruses). 100 nm particles,

containing 75 S single-stranded RNA which upon melting becomes 37 S. A/G/U/C = 30/25/22/23. The 4 S RNA also associated with the virus shows A/G/U/C = 18/33/21/29. The major proteins (15,000, 18,000, and 33,000 mol. wt.) resemble those of murine leukoviruses more than those of avian myeloblastosis virus.

Feline panleucopenia virus (parvovirus).

Feline picornavirus. Density 1.38 g/ml.

Feline rhinotracheitis virus (feline herpesvirus 1). 46% (G+C).

Fibroma virus of rabbits, squirrels, hares (myxoma subgroup of poxviruses).

Fishpox virus (vaccinia subgroup of poxviruses).

Flanders (Hart Park) virus (rhabdovirus of birds and arthropods, not serologically related to others). 218 × 65 nm bullet-shaped particles.

FLAVIVIRUS (OR FLAVO) GROUP. Preferred name for group B arboviruses, subgroup of the togaviridae. Spherical enveloped particles of 30–55 nm diameter (200 S) containing 7–8% single-stranded RNA of $3\text{--}4 \times 10^6$ daltons. Glycoproteins of $65\text{--}51 \times 10^3$ and capsid proteins of about 16 and 9×10^3 daltons. (Horzinek, 1973.) Prototype: Yellow fever virus; others: Apoi, Banzi, Bukalasa bat, Bussuquara, Cowbone Ridge, Dakar bat, Dengue, Edgehill, Entebbe bat salivary gland, Ilhéus, Israel turkey meningoencephalitis, Japanese encephalitis, Kokobera, Kunjin, Kyasanur Forest, Langat, louping ill, Modoc, Montana myotis leukoencephalitis, Murray Valley encephalitis, Negishi, Ntaya, Omsk hemorrhagic fever (types I and II), Powassan, Spondweni, St. Louis encephalitis, Stratford, tick-borne encephalitis (subtypes central European and Far Eastern), Uganda S, salivary virus of bats (US), Usutu, Wesselsbron, West Nile, and Zika viruses.

Foamy virus of monkeys and chimpanzees (possibly related to slow viruses, oncornaviruses, or—less likely—togaviruses). At least 7 serotypes known. Type 1 and 2 (strain MK5) contain 35 nm nucleoid and 2 shells, 60 and 90 nm in diameter.

Foot and mouth disease virus (picornavirus). Rhinovirus subgroup of 7 known serotypes. Particles of 27–30 nm diameter of probably the same architecture as mouse-Elberfeld virus (ME); particle weight 8.5×10^6 (140 S). Buoyant density in CsCl 1.43 g/ml (with decomposition to 1.51 g/ml). Virus contains 30–32% single-stranded

RNA, of about 2.5×10^6 dalton molecular weight; A/G/U/C = 26/24/22/28. Four proteins build up the virion, probably in equimolar amounts (60 molecules of each per particle), about 34,000, 29,000, 26,000, and 7000 mol. wt., probably adding up to 96,000. Three different N-terminal amino acids (leucine, isoleucine, and threonine) were found in the virus. The C-terminals were for the three largest proteins, -Glu-Ala-Leu, -Leu-Glu, and -Ser-Glu. For amino acid analyses, see Table 1. The virus degrades at very low ionic strength and below pH 7. (vande Woude and Bachrach, 1971; Bachrach *et al.*, 1973.)

Fowlplague virus (influenza A subgroup of myxoviruses). Three glycoproteins in spikes; glycolipid and three proteins remain after removal of spikes. The hemagglutinin glycoproteins which arise through posttranslational cleavage are 49,000 and 32,000 in molecular weight (18 and 11%), the neuraminidase (7%) 45,000, and the nonglycoproteins (making up 34, 22, and 2%) 26,5000, 60,000, and 84,000. The first two of these represent the membrane and capsid proteins (*see* influenza virus). (Madeley *et al.*, 1971; Klenk and Rott, 1973.)

Fowlpox virus (birdpox subgroup of poxviruses). Contains 28 proteins, most of them identical in molecular weight to those of vaccinia virus.

Friend murine leukemia virus, *see* murine leukemia virus.

Frog adenovirus 1 (not serologically related to other adenoviruses, not oncogenic). (Clark *et al.*, 1973.)

Frog viruses 2 and 3 (FV2, 3) (polyhedral cytoplasmic DNA viruses, probably iridoviruses). Replicate in amphibian and mammalian cells below 37°C. Density of FV3 in CsCl about 1.27 g/ml. The virus consists of 56% protein, 14% lipid, and 30% DNA. The DNA is 57% (G+C), and about 130×10^6 in molecular weight.

In FV3 16 proteins were detected, the main components of which have molecular weights of 49,000, 13,000, 10,500, and 8500 (all 1300–2000 molecules per particle). Various enzyme activities are also found associated with the virion (e.g., ATPase) or with the core nucleocapsid (endonuclease). (Tan and McAuslan, 1971; Aubertin *et al.*, 1971.)

Frog virus 4 (ranid herpesvirus 2). This virus is associated with the Lucké adenocarcinoma virus in frog tumors. 55% (G+C). (Granoff, 1972.)

- Fujinami sarcoma virus** (oncornavirus).
- G 8886, G 15534** (orbivirus subgroup of reoviridae).
- Galleria dense nuclear virus**, *see* densonucleosis virus.
- Gallus adeno-like virus** (GAL virus) (chicken adenovirus).
- Gecko virus** (possibly a member of iridovirus group).
- Getah virus** (alphavirus).
- Gibbon leukosisvirus** (oncornavirus).
- Goatpox virus** (sheeppox subgroup of poxviruses).
- Gomphrena virus** (rhabdovirus).
- Gonometa virus** (insect enterovirus subgroup of picornaviridae). Particles of 32 nm diameter, 180 S, and density in CsCl 1.35 g/ml. Contains 37% RNA and four proteins of molecular weight of 37,000–12,000. Host: *Gonometa podocarp*. (Longworth *et al.*, 1973.)
- Graffi murine leukemia virus**, *see* murine leukemia virus.
- Granulosis virus** of insects (member of baculovirus group), similar to nuclear polyhedrosis viruses, but singly occluded. The granulosis virus of *Trichoplusia* contains closed double-stranded supercoiled circular DNA (95 S), relaxed circular DNA (74 S), and linear DNA (60 S). The molecular weight is 100×10^6 . (Summers and Anderson, 1972.)
- Gross virus** (transformation-defective strain of murine leukemia virus).
- Guineapig herpesvirus** (caviid herpesvirus). Icosahedral particle with double-layered membrane, 166 nm in diameter, with dense core of 101 nm diameter. DNA of density 1.716 g/ml (human herpesvirus 1: 1.728, host DNA 1.700). Always found together with C-type particles in leukemic guinea pigs.
- H-1, H-2, H-3 viruses** (hamster and rat osteolytic virus) (parvovirus). Particles of 19 nm diameter and buoyant density 1.400 g/ml in CsCl. Contain single-stranded DNA of 28 S (denatured 17 S) and density in CsCl of 1.72 g/ml, 1.7×10^6 mol. wt., A/G/T/C = 26/23/29/23 (like all parvoviruses and mammalian DNA, low in CpG sequence).
- Haden virus**, *see* hemadsorbing enteric virus.
- Hamster papilloma virus**, *see* papilloma virus.

Hare fibroma virus (myxoma subgroup of poxviruses).

Hart Park virus (rhabdovirus), *see* Flanders Hart Park virus.

Harvey sarcoma virus, *see* murine sarcoma virus.

Hemadsorbing enteric virus (haden) (bovine parvovirus). Particles of 22.5 nm diameter; density 1.425 g/ml (also a component of 1.45 g/ml and one of empty particles of 1.30 g/ml density). The main protein is of 67,000 daltons. (Johnson and Hoggan, 1973).

Hemadsorption virus 1, 2, *see* parainfluenza viruses.

Hemagglutinating encephalomyelitis virus of pigs (coronavirus). Isometric particle, about 150 nm diameter, including club-shaped 15-nm-long projections. (Clarke and McFerran, 1971.)

Hemagglutinating virus of Japan, *see* Sendai virus.

Hemorrhagic encephalopathy virus (HER) (parvovirus).

Hemorrhagic fever virus (arenavirus). Particles of 60–280 nm diameter with 20–25 nm electron-dense granules (possibly host ribosomes).

Hemorrhagic septicemia agent of salmon (rhabdovirus). (Bachmann and Ahne, 1973.)

Hepatitis viruses A and B (infective and serum hepatitis agents, respectively). Hepatitis B is associated with virus-like particles which have not yet been definitely shown to contain a nucleic acid. These 42 nm particles contain a 27 nm core which is able to bind antibody molecules from the serum of hepatitis patients. Relationship of hepatitis B virus to Australia antigen (hepatitis-associated antigen), a lipoprotein particle, is not yet clear. Viruslike particles of 27 nm diameter were found associated with hepatitis A. Relationship of hepatitis virus A to parvoviruses has also been suggested. (Dreesman *et al.*, 1972a; Feinstone *et al.*, 1973.)

Herpesvirus ateles of monkey. Oncogenic *in vivo* and possibly *in vitro*. (Meléndez *et al.*, 1971.)

Herpesvirus cuniculi (rabbit herpesvirus).

HERPESVIRUS GROUP. Large isometric particles of about 150 nm diameter, usually enveloped and ether sensitive; they contain 7% of double-stranded linear DNA of $80\text{--}100 \times 10^6$ daltons, 57–74% (G+C). The icosahedral capsid of 100 nm diameter consists of 162 hollow capsomeres. Many herpesviruses are or tend to become

oncogenic (*see* Lucké virus, herpesvirus saimiri, Epstein–Barr virus). While the protein is synthesized in the cytoplasm, synthesis of the DNA and assembly of the virion begins in the nucleus. The virus derives its inner envelope largely from the nuclear plasma membrane, including nonprotein host material. An outer envelope forms at the cytoplasmic membrane. Herpesviruses show great changes in virulence, in both directions, when infecting other than natural hosts. (*See also* under herpes simplex virus.)

Herpesvirus saimiri (cebid herpesvirus 2). Produces malignant lymphomas in adult primates. 69% (G+C).

Herpesvirus simiae, *see* B virus of monkeys.

Herpes simplex virus (prototype of herpesviruses). (Types 1 and 2, to be called human herpesvirus 1, 2; also called facialis and genitalis. There is about 40% homology in the nucleotide sequences of these two groups.) Large, enveloped, spherical particles, 160–200 nm in diameter; particle weight 1400×10^6 daltons. Irregular envelope around icosahedral capsid (100 nm diameter), composed of 162 capsomeres ($T = 16$), 150 hexagonal, 12 pentagonal. Particles without envelopes also occur naturally, as well as particles lacking DNA, leaving a hexagonal toroidal (hollow) core of 74 nm exterior diameter and 18 nm inner diameter and 50 nm high. The capsomeres are hollow prisms (10 nm in diameter, 12.5 nm long, with about 3 nm hole). The DNA content is 7%, the molecular weight probably 81×10^6 (55 S) for both subgroups 1 and 2, although their density in CsCl differs slightly, being 1.726 and 1.728 g/ml, corresponding to 67 and 71% (G+C). The isolated DNA is infective. Of the 33 proteins, ranging from 275×10^3 to 23×10^3 in molecular weight, almost half are glycoproteins. The capsid proteins are of 140×10^3 , 110×10^3 , 34×10^3 , and 20×10^3 daltons, the core protein of 44×10^3 mol. wt. (The amino acid compositions of several of these proteins have been reported.) The protein of molecular weight 110×10^3 is the main capsid protein in rabbits (Meléndez *et al.*, 1972; Dreesman *et al.*, 1972b; Gibson and Roizman, 1972.)

Herpesvirus sylvilagus (cottontail rabbit). Causes benign or malignant lymphoproliferative disease. (Hinze and Chipman, 1972.)

Herpesvirus tamarinus, a cebid (monkey) herpesvirus.

Herpes zoster (human herpesvirus 3), *see* varicella–zoster virus.

Hinze lymphoma virus, a rabbit herpesvirus.

Hogcholera virus, *see* swinefever virus.

Huacho virus (orbivirus subgroup of reoviridae).

Human adenoviruses, *see* adenovirus.

Human cytomegaloviruses (human herpesvirus 5).

Human papilloma virus (wart virus). The particle (56 nm diameter) consists probably of 72 capsomeres ($T = 7$) (12 pentamers, 60 hexamers), in skew right-handed configuration. 296 S and 168 S for full and empty capsids. DNA 41% (G+C). (*See also* under papilloma virus).

Human respiratory virus, *see* coronaviruses.

IbAr 22619 (orbivirus subgroup of reoviridae).

Ibaraki virus of cattle (orbivirus subgroup of reoviridae). Icosahedral particles of 55 nm diameter. (Ito *et al.*, 1973a.)

Icosahedral cytoplasmic DNA viruses. Newly defined group including African swinefever virus, frog virus 3, lymphocystis virus, etc. The name describes the common features of these viruses (Kelly and Robertson, 1973.)

Ilhéus virus (flavivirus subgroup of togaviridae).

Incomplete viruses, *see* defective viruses.

Infectious anemia virus of horses (unclassified). Particles of 90–140 nm width with 50 nm cores; buoyant density 1.18 g/ml in CsCl; ether sensitive; contains RNA. (Nakajima *et al.*, 1970.)

Infectious arteritis virus of horses, *see* equine arteritis virus.

Infectious bovine keratoconjunctivitis virus, infectious bovine rhinotracheitis virus (bovine herpesvirus X and 1). Serologically related to human herpesviruses, but not by DNA homology. The buoyant density of the DNA in CsCl is 1.730 g/ml. (Graham *et al.*, 1972.)

Infectious bronchitis virus of chickens (coronavirus). Particles of 70–120 nm diameter, density 1.15 g/ml, ether sensitive. Surface carries characteristic projections. The nucleocapsid is probably loosely helical (8 nm diameter). (Cunningham *et al.*, 1972.)

Infectious canine hepatitis and laryngotracheitis viruses (adenoviruses).

Infectious hematopoietic necrosis virus of salmon (rhabdovirus). (Bachmann and Ahne, 1973.)

Infectious laryngotracheitis virus of chickens (phasianid herpesvirus 1). 45% (G+C). (Lee *et al.*, 1972.)

Infectious pancreatic necrosis virus of trout (as yet unclassified; possibly a diplornavirus). Hexagonal particles of 60–74 nm diameter, lacking inner capsid structure. Density of particle 1.33 g/ml in CsCl. The virus contains double-stranded RNA of 14 S, three components of $2.55\text{--}2.85 \times 10^6$ daltons. The three proteins (3%, 68%, and 29%) are of 80, 50, and 30×10^3 daltons. (Kelly and Loh, 1972.)

Influenza viruses (orthomyxovirus) (*see also* under myxoviruses). Type A, of man, swine, horse, duck, chicken; B of man; C of man. The three subtypes of A (formerly WSN, Lee strain, etc.) are now termed A0, A1, and A2. Minor cross reactions exist between A0 and A1 hemagglutinins and neuraminidases. Particles not uniform in shape (pleomorphic), 100 nm diameter spheres predominating, about 300×10^6 daltons in particle weight. Filamentous forms also exist, up to 4 μm long. The approximate composition of the virion is 66% protein, 25% lipid, 8% carbohydrate, and 0.9% RNA.

Particles consist of an outer membrane or envelope with projections or spikes, and an internal flexible rod or thread-shaped nucleocapsid. The envelope is 7–10 nm thick, the regularly spaced spikes 8–10 nm long and 7–9 nm apart (about 2000 per virion). Ether disrupts the envelope, releasing the nucleocapsid threads (50 to 130 nm long, with a 1 nm axial channel and of varying lengths) (*see* Electron micrograph VI).

The total RNA of each virion (38 S, $3\text{--}3.9 \times 10^6$, though according to more recent estimates 5.0×10^6 daltons) is present as probably 7 molecules of varying but definite sizes, combined but not covered with capsid protein, the RNA being nuclease-sensitive, the protein relatively protease-resistant. Isolated nucleocapsids show, among others, two peaks at 56 S and 64 S containing mainly 15 S RNA and 18 S RNA respectively. The lengths of the nucleocapsids range from 20 to 110 nm (three size groups).

The average composition is A/G/U/C = 22/20/36/23. The RNA chains start (5') with ppp-A- and terminate mostly with 3'-unphosphorylated-U (doubtful). Differences in nucleotide sequences have been demonstrated between different RNA size groups.

The capsid (10% RNA, 90% protein) consists of two proteins,

one of a molecular weight of 53,000, 60,000, or 65,000 in different strains, or more likely in the hands of different investigators (about 1200 per particle), and another protein of 22,000–27,000 in equal to threefold quantity. It appears possible that the smaller represents the separate peptide chains and the larger a still disulfide-linked dimer. There also exist small amounts of two other larger proteins (80,000–90,000).

The envelope, including the spikes, consists largely of two biologically active proteins, the neuraminidase and the hemagglutinin, 10.8 S and 8.1 S, respectively. The neuraminidase consists of four identical glycopeptide chains, disulfide-linked in pairs, of about 63,000 mol. wt., and the hemagglutinin of two types of glycopeptide chains, of about 57,000 and 28,000 mol. wt., which are connected by disulfide bridges.

Influenza virus contains also an RNA polymerase.

For the amino acid composition of polypeptides isolated from influenza viruses, see Table 1. (Klenk *et al.*, 1972; Schulze, 1972; Laver and Baker, 1972.)

Inkoo virus (Bunyamwera supergroup). (Saikku *et al.*, 1971.)

INSECT VIRUSES. Viruses of almost all groups occurring in animals have been found in insects. Frequently insect viruses occur in large polyhedral inclusion bodies, and two large classes of occluded viruses have been distinguished, the cytoplasmic polyhedrosis viruses and the nuclear polyhedrosis viruses. The granulosis viruses are very similar to the latter; *see* under these listings.

Insect poxviruses. One originally isolated from larvae of the moth, *Amsacta*, grows on saltmarsh caterpillar. Many similar viruses have been found in beetles and other moths. 450 × 250 nm oval-shaped particle, in all detail similar to vaccinia (*see* melothonta poxvirus).

IRIDOVIRUS GROUP. Very large icosahedral DNA viruses, largely of insects. Tipula iridescent, sericestis iridescent, and chilo iridescent viruses, as well as possibly some frog viruses, African swinefever virus, Gecko virus, and lymphocystis virus of fish are members of the iridoviruses. The latter, in contrast to the insect iridoviruses, may be enveloped. All replicate in the cytoplasm (*see* Electron micrograph V).

Irituia virus (orbivirus subgroup of reoviridae).

Israel turkey meningoencephalitis virus (flavivirus subgroup of togaviridae).

Jaagsiekte virus, *see* sheep pulmonary adenomatosis virus.

Japanese B encephalitis virus (flavivirus subgroup of togaviridae). One glycoprotein (lipoprotein?) of 53,000 mol. wt. and two proteins of 13,500 (the nucleocapsid protein) and 8700. (Shapiro *et al.*, 1971.)

JC virus (human polyoma virus related to SV-40). Probably associated with progressive multifocal leucoencephalopathy (PML). The disease but not the virus shows similarity to slow virus diseases.

Junin virus (arenavirus).

Junoniavirus (insect parvovirus related to *Galleria* denonucleosis virus).

K-virus of rats and mice (polyomavirus). Isometric particles of about 45 nm diameter. Capable of transforming mouse cells *in vitro*.

KBSH-virus (parvovirus). Particles of 20 nm diameter, 105 S, 5.3×10^6 particle weight, density in CsCl 1.395 g/ml. The virus contains 26.5% of 24 S single-stranded DNA (18 S in alkali), 1.4 or more probably 1.7×10^6 in molecular weight, density 1.724 g/ml. (Siegl *et al.*, 1971.)

Kemerovo virus (orbivirus subgroup of reoviridae). Serologically unrelated to others.

Kern Canyon virus (rhabdovirus of myotis bats). Bullet-shaped particles of 73×132 nm containing three major structural proteins, of which the glycoprotein and the nucleocapsid protein (G and N) carry phosphate groups. The virion contains a protein kinase. Its proteins are similar to those of other rhabdoviruses. (Murphy and Fields, 1967; Sokol and Clark, 1973.)

Kilham rat virus (parvovirus). Isometric particles of 28 nm diameter, 6.6×10^6 particle weight (122 S), 1.43 g/ml density in CsCl (DNA lacking "top component" 1.32 g/ml); contains 27% of single-stranded linear DNA of buoyant density 1.715 in CsCl (16 S). The DNA of 1.6×10^6 mol. wt. is about 1500 nm long. A/G/T/C = 27/21/30/23. There are three major proteins, of 72, 62, and 55×10^3 daltons. The 62,000 mol. wt. protein represents 75% and is regarded as the capsid protein.

Kirk virus (rat parvovirus).

Kirsten virus, *see* murine leukemia virus.

Klamath virus (rhabdovirus of mice). 80×167 nm bullet-shaped particles.

Kokobera virus (flavivirus subgroup of togaviridae).

Kunjin virus (flavivirus subgroup of togaviridae). The 200 S particles, 48 nm in diameter, yield 143 S cores upon deoxycholate treatment, the same as for Sindbis virus cores (alphavirus subgroup). The RNA (38 S) of 4.2×10^6 daltons is said to disaggregate to half in 8 M urea (but newer data disagree with this interpretation). The major nucleocapsid protein is of 30,000 or 13,500 daltons, the envelope protein of 52,000 mol. wt. (earlier report: two smaller nucleocapsid proteins, adding up to 31,000). (Boulton and Westaway, 1972.)

Kuru disease agent of man, *see* slow viruses, scrapie.

Kyasanur Forest virus (flavivirus subgroup of togaviridae). Affects man.

LaCrosse virus (member of California encephalitis virus group). Enveloped particle of 98 nm diameter with electron-dense core. Contains single-stranded RNA of six molecular weights, the larger of which dissociate upon heating. Three proteins were detected, of 85, 45, and 26×10^3 mol. wt. (McLerran and Arlinghaus, 1973.)

Lactic dehydrogenase (elevating) (Riley) virus of mice (probably togavirus). 235 S elliptical particles (about 47–56 nm); buoyant density in CsCl 1.12 g/ml; ether sensitive. Infective RNA of $5-6 \times 10^6$ daltons (48 S). The nucleocapsid protein is of 13,000, the envelope proteins 17,000 and 28,000 daltons, the latter only containing glucosamine. (Darnell and Plagemann, 1972.)

Lagos virus (rhabdovirus of bats, serologically related to rabies virus).

Lake Victoria cormorant virus (fowl herpesvirus) (Lee *et al.*, 1972.)

Langat virus (flavivirus subgroup of togaviridae).

Laryngotracheitis virus (canine adenovirus).

Lassa (fever) virus (arenavirus).

Latent rat virus, *see* Kilham rat virus.

Latino virus (arenavirus).

LCV, L-cell virions (defective oncornaviruses). (Nichols *et al.*, 1973.)

Lebombo virus (orbivirus subgroup of reoviridae).

LEUKOVIRUSES. The approved name for the group also called RNA-tumor viruses, which, however, has not gained general acceptance. The author prefers oncornaviruses and likes best the term retraviruses (for reverse transcriptase). See under oncornavirus group for description and members.

LK virus (equine herpesvirus). DNA of 84×10^6 daltons.

L-S virus (rat parvovirus).

Louping ill virus (flavivirus subgroup of togaviridae). Causes a disease of sheep and cattle.

Lucké (frog adenocarcinoma) virus (ranid herpesvirus 1). A malignant, usually lethal frog tumor virus; contains DNA of 45% (G+C). (Granoff, 1972.)

Lumpy skin disease virus (cattlepox virus).

Lu III (parvovirus). Similar properties to, though serologically distinguishable from, KBSH virus.

Lymphocystis (tumor) virus, from the Atlantic croaker (icosahedral cytoplasmic DNA virus, possibly a member of iridovirus group or a herpesvirus?). 200–600 nm icosahedral particles, enveloped, with long attached filaments, ether sensitive. Probably DNA containing. Causes chronic disease and tumors in many fishes. (Zwillenberg and Wolf, 1968.)

Lymphocytic choriomeningitis virus (prototype of arenaviruses). Variable-size particles (about 120 nm in diameter containing several 20–30 nm diameter electron-dense granules. Density in CsCl 1.18 g/ml, about 500 S; contains seven single-stranded RNA species, of which two (23 S and 31 S) are virus-specific. The others may be from ribosomes which may represent the typical intraviral granules. Various light disease symptoms in many mammals. (Welsh *et al.*, 1972; Pedersen, 1973.)

M9 virus (orbivirus subgroup of reoviridae).

M25 virus, see parainfluenza virus type 4.

Machupo virus (arenavirus).

Maedi virus of sheep (slow virus, related to Visna virus). Shows many similarities to oncornaviruses; contains 62 S, 35 S, and 13 S RNA

as well as reverse transcriptase and DNA-dependent DNA polymerase. (Lin and Thormar, 1972.)

Malignant catarrh virus of cattle (herpesvirus).

Mammary tumor viruses, *see* mouse mammary tumor virus.

Marburg virus (rhabdovirus). Variably long (130 to 1200 nm, mean length 665 nm \times 80 nm) particles, often sharply bent. Simian (and human) pathogen. (Siegert, 1972.)

Marek's disease virus (phasianid herpesvirus 2). Double-stranded DNA, 56 S, 120 \times 10⁶ mol. wt. (in alkali 70 S, 60 \times 10⁶); density 1.705 g/ml; 46% (G+C). The protein pattern is similar to that of herpes simplex and pseudorabies virus. The virus shows serological relationship with common herpesvirus. Oncogenic in chickens, now controlled by vaccines. (Chen *et al.*, 1972.)

Mason-Pfizer monkey virus (unclassified oncornavirus). Buoyant density 1.155 g/ml in CsCl. Contains RNA of 70 \times 10⁶ daltons. (Manning and Hackett, 1972.)

Mayaro virus (alphavirus subgroup of togaviridae). Contains two proteins.

MC-29 virus (avian leukosis virus).

ME virus, *see* mouse-Elberfeld virus.

Measles virus of man (paramyxovirus). Closely related to canine distemper virus and rinderpest virus of cattle. 150 nm particles of buoyant density in CsCl of about 1.27 g/ml. Contains helical nucleocapsid of about 17 \times 1100 nm, 6 nm pitch, 11–13 protein subunits per turn (280 S). The RNA in the nucleocapsids (5%) is resistant to pancreatic ribonuclease.

The RNA of 52 S has a molecular weight of 6.4 \times 10⁶ daltons. The nucleocapsid protein has a molecular weight of 60,000. The virion contains five additional proteins of 76, 69, 53, 51, and 46 \times 10³ mol. wt., which are identical to those of canine distemper virus.

Measles virus hemagglutinates only primate erythrocytes and lacks neuraminidase, thus hemagglutinating optimally at elevated temperature. (Schluederberg, 1971; Hall and Martin, 1973.)

Melothonta (insect) poxvirus (occluded). Oval 400 \times 250 nm particles resembling poxviruses in all respects; *see also* under insect poxviruses. (Bergoin *et al.*, 1971.)

Mengo virus (cardiovirus subgroup of picornaviridae). 28 nm particles, 151 S, 8.5×10^6 particle weight (*see* mouse-Elberfeld virus for capsid architecture). 31% RNA, 2.6×10^6 mol. wt.; A/G/U/C = 26/23/26/25. Proteins: 34,000, 30,500, 24,000, and 7300 (plus a minor component of 40,000) mol. wt. (probably equimolar amounts; *see* mouse-Elberfeld virus). (Miller and Plagemann, 1972.)

Middleburg virus (alphavirus subgroup of togaviridae).

Milker's nodule virus (pseudocowpox) (paravaccinia subgroup of poxvirus).

Mink enteritis virus (probably a parvovirus).

Minute virus of mice (MVM) (parvovirus). 20–25 nm diameter, 1.42 g/ml density. Contains single-stranded DNA, 1.72 g/ml density in CsCl, 1.7×10^6 mol. wt., A/G/T/C = 27/19/33/21. (Tattersall, 1972.)

MM virus (cardiovirus subgroup of picornaviridae).

Modoc virus (flavivirus subgroup of togaviridae).

Molluscum contagiosum virus of man (poxvirus). Similar to vaccinia in DNA content (density 1.288 g/ml, vaccinia 1.287 g/ml, 5250 S vs. 5150 S). Oncogenic. (Pirie *et al.*, 1971.)

Moloney murine leukemia virus, *see* murine leukemia virus.

Monkeypox virus (vaccinia subgroup of poxviruses). The DNA has a molecular weight of 159×10^6 and 38% (G+C). (Yau and Rouhandeh, 1973.)

Mono Lake virus (orbivirus subgroup of reoviridae).

Montana myotis leukoencephalitis virus (flavivirus subgroup of togaviridae).

Mosquito iridescent virus (iridovirus). Two strains (RMIV and TMIV) which are serologically identical but differ in size and sedimentation rate. Isoelectric points pH 3.15 and 3.30. The 260/280 nm ratios are 1.20 and 1.21, and A_{\max} (0.1%) is 6.32 and 5.47, the diameters about 185 and 210 nm, the densities in CsCl 1.32 and 1.31 g/ml, the sedimentation coefficients 4041 and 3318 S, and the particle weights 2.75 and 2.1×10^9 daltons. (Wagner *et al.*, 1973; Stoltz and Summers, 1972.)

Mount Elgon virus (rhabdovirus of bats and mosquitos). Bullet-shaped in tissue, 226×688 nm. (Murphy *et al.*, 1970a.)

Mouse-Elberfeld (ME) virus (cardiovirus subgroup of picornaviridae). Virions of 24 nm diameter, 8.4×10^6 particle weight, 155 S. The nucleocapsid consists of 31% single-stranded RNA, molecular weight 2.6×10^6 , A/G/U/C = 25/24/27/24, and four proteins in equimolar amounts, 33,000 (α), 30,500 (β), 25,800 (γ), 7300 (δ), and varying small amounts of a 41,000 (ϵ) species (composed of $\beta + \delta$). The architectural principle of the picornavirus capsids consisting of four and at times five proteins was first established with this virus. It appears that both ($\epsilon + \alpha + \gamma$) and ($\alpha + \beta + \gamma + \delta$) add up to 96,000 in molecular weight. Since it is now well established for many picornaviruses, particularly poliomyelitis virus, that a large precursor protein is split in a specific manner, in part prior to capsid assembly and in part during virus maturation, it appears that all these capsids are built up as regular icosahedral arrays of 60 units composed of three (ϵ, α, γ) or, after the final proteolytic step, four peptide chains ($\alpha, \beta, \gamma, \delta$). For the amino acid composition of the polypeptide components of encephalomyocarditis and mouse-Elberfeld viruses, see Table 1. (Stoltzfus and Rueckert, 1972.)

Mouse hepatitis virus (coronavirus).

Mouse leukemia virus, *see* murine leukemia virus.

Mouse mammary tumor virus (Bittner virus, B-type particles) (oncoronavirus). Density of whole virus 1.17, nucleoid 1.24 g/ml. RNA content: whole virus, 1.9, nucleoid 4.4%. The envelope shows a smooth surface membrane, in contrast to C-type particles. The dense centrally located nucleoid contains nucleocapsid strands of 8–9 nm diameter containing S1 and S2, group-specific antigens. The S3–S5, type-specific antigens, are located in the envelope; all are synthesized in the cytoplasm. Proteins: 90,000, 70,000, 52,000 (the major nucleoid, S1), 33,000, 23,000 (the major membrane proteins, S3). (Sarkar *et al.*, 1971; Nowinski *et al.*, 1971.)

Mouse polyoma virus, *see* polyoma virus.

MP tumor virus (unclassified) (Molomut *et al.*, 1964.)

MP 359, MRM 10434 (orbivirus subgroup of reoviridae).

Mucambo virus (alphavirus subgroup of togaviridae).

Mumps virus (parainfluenza subgroup of paramyxoviruses). 150 nm diameter particles, containing an 1100 nm stretched-out nucleocapsid in helix of 6 nm pitch, about 12 protein subunits/turn. The RNA is of 50 S. The virus contains neuraminidase. (East and Kingsbury, 1972.)

Murine encephalomyelitis virus (picornavirus).

Murine hepatitis virus (coronavirus).

Murine leukemia virus (Rauscher, Friend, Moloney, Gross, Kirsten, Harvey viruses, etc.) (transformation-defective C-type oncornaviruses). Approximately spherical, enveloped particles, 106 nm in diameter upon freeze drying and negative staining, with 8 nm diameter weakly bound surface knobs. The core of 80 nm diameter of icosahedral symmetry consists of 6 nm subunits, 7.5 nm apart. The virions are of 1.18 g/ml density in CsCl, the cores (representing about 25%) of 1.226 g/ml density. There also can be seen one or two envelope membranes, 12 and 20 nm thick. The single-stranded RNA has been stated to be homogeneous after heating (although others report the presence of an 18 S component of different composition), 38 S, of about 3.8×10^6 mol. wt., it contains A-rich sequences. Among the five main proteins are the group-specific (capsid) antigen of 31×10^3 , a glycoprotein of 86, and proteins of 15, 12, and 10×10^3 daltons. Among various enzymes there is reverse transcriptase. (Moroni, 1972; Schäfer *et al.*, 1972.)

Murine sarcoma virus (replication-defective oncornavirus). Moloney and Harvey strains produce tumors in hamsters. The protein pattern of Harvey sarcoma virus is very similar to that of the Rauscher leukemia virus. (Moroni, 1972.)

Murray Valley encephalitis virus (flavivirus subgroup of togaviridae).

Myxoma viruses, subgroup of poxviruses, mostly of rabbits and related species. Largely oncogenic.

MYXOVIRUS GROUP (also called orthomyxoviruses. Members: influenza viruses types A [human, porcine, equine, and avian viruses] and B and C [only human types known]). Large (100 nm diameter), somewhat pleomorphic enveloped particles containing multiple chains of single-stranded RNA in helical nucleocapsids (about 6 [A,B] or 9 [C] nm in diameter) (see Electron micrograph VI). Sensitive to lipid solvents. Buoyant density in sucrose about 1.20

for A, B, and 1.18 for C. RNA synthesized in the nucleus, the envelope during passage through the plasma membrane. Filamentous forms also exist. Virions contain RNA polymerase. The envelopes carry spikes consisting of neuraminidase and hemagglutinin. Their lipid compositions reflect those of the plasma membrane of the host cell, except for the absence of neuraminic acid in the lipids—probably a consequence of the presence of the neuraminidase (*see influenza virus*).

Nariva virus (rodent paramyxovirus, unrelated to other known groups).

Ndumu virus (alphavirus subgroup of togaviridae).

Nebraska calf diarrhea virus (reovirus).

Negishi virus (flavivirus subgroup of togaviridae).

Nelson Bay virus (reovirus).

Newcastle disease virus (paramyxovirus of chickens). Roughly spherical, about 200 nm diameter, 500×10^6 dalton particle weight. The buoyant density in CsCl varies from 1.212 to 1.242. The spikes are less prominent than in influenza virus (8 nm long, 1.5 nm diameter, 8–10 nm apart). The helical nucleocapsid is about 1000 nm long and 18 nm in diameter. The virion consists of 67% protein, 24% lipid, 7% carbohydrate, and 1% RNA.

The single-stranded RNA is probably about 6×10^6 in molecular weight (56 S). The composition is A/G/U/C = 24/24/29/23.

The main envelope glycoproteins are 9.3 S and 6.1 S; the larger carries both the hemagglutinin and the neuraminidase activity (as is the case for other paramyxoviruses). They consist of peptide chains of 74 and 56×10^3 daltons. The main capsid protein (45%) is 56×10^3 and a membrane protein 41×10^3 daltons. Yield per cell: 0.1 PFU in mouse kidney cells to 100 in CV-1 monkey kidney cells. (Scheid and Choppin, 1973.)

Nodamura virus (insect picornavirus). 28 nm particle (140 S) of density in CsCl of 1.34 g/ml. Said to contain two RNAs of 22 S and 15 S (molecular weights 1 and 0.5×10^6), A/G/U/C = 22/28/23/27 and 25/23/24/28 respectively, and only one major protein of 46,000 daltons. Host and vector *Culex tritaeniorhynchus*, a mosquito; also a vertebrate, possibly swine. This appears to be the only animal covirus known (*see page 76*), the two RNA's being only cooperatively infectious. (Murphy *et al.*, 1970b; Brown and Hull, 1973.)

Ntaya virus (flavivirus subgroup of togaviridae).

Nuclear polyhedrosis viruses of insects, usually from silkworm (members of baculovirus group of rod-shaped occluded insect viruses). Virions are embedded in membrane-covered "crystalline" inclusion bodies of 0.5–15 μm ("polyhedra"). This matrix consists largely of 11 S protein. The rod-shaped virions are of complex structure, frequently with terminal protrusions, 40–70 \times 250–400 nm, covered with a membrane and containing a dense core. The virions are sensitive to ether. They contain double-stranded DNA, predominantly of 80×10^6 mol. wt. but ranging from 59×10^6 to 118×10^6 , with contour lengths from 30 to 60 nm, partly linear and partly open circular. The composition is 37–59% (G+C). They replicate in the nucleus. The silkworm (*Bombyx mori*) nuclear polyhedrosis virus (80 \times 330 nm rods) contains 8% DNA of 13.1 S, 41% (G+C). The isolated DNA is infectious. (Harrap, 1972.)

O-agent from cattle and sheep (orbivirus). Structurally indistinguishable from SA 11 virus, though serologically these are unrelated.

OC-43 (prototype coronavirus).

Omsk hemorrhagic fever virus of man (flavivirus subgroup of togaviridae).

ONCORNAVIRUS GROUP. Not yet officially accepted term for leukoviruses or RNA tumor viruses, all equally imperfect names.* Medium large (100 nm diameter) enveloped and ether-sensitive particles; studded in regular manner with projections and containing a dense eccentric nucleoid. The 60–70 S RNA (1.5%), of $10\text{--}12 \times 10^6$ daltons, dissociates with heat, DMSO, etc., to 30–35 S and smaller single-stranded RNA (10 S, 8 S, 7 S, 4 S, etc.). The partly helical nucleocapsids are 7–9 nm in diameter.

All oncornaviruses contain RNA-dependent DNA polymerase (= reverse transcriptase), also active as ribonuclease H which degrades only DNA-bound (= hybridized) RNA. Also other polymerases, nucleases, and many other enzymes occur in these viruses. The general protein pattern shows at least seven proteins of molecular weights 100,000, 70,000, 29,000, 19,000 (only in avian oncornaviruses), 15,000, 12,000, and 10,000. (For more detail, see under individual oncornaviruses.)

Members of the RNA tumor virus group are (A) Rous and other fowl viruses; RAV and RIF viruses; RPL 12; avian leucosis

* New proposal: retraviruses (for reverse transcriptase containing).

and myeloblastosis (AMV) viruses; osteopetrosis virus; Fujinami sarcoma virus, FAV-1; (B) murine leukemia and sarcoma viruses (Gross, Friend, Graffi, Moloney, Rauscher, etc.); (C) feline leukemia and sarcoma viruses; (D) mouse mammary tumor virus (Bittner) and nodule-inducing virus; (E) reticuloendotheliosis virus. All but (D) are also called C-type particles.

O'Nyong-nyong virus (alphavirus subgroup of togaviridae).

ORBIVIRUSES (one of two subgroups of reoviridae). Prototype: bluetongue virus. These are somewhat smaller than the reoviruses and more sensitive to low pH. They are slightly sensitive to ether. The surface architecture of the orbiviruses also differs from that of the reoviruses in that they may consist of a single shell of 32 capsomeres. However, the differences between orbiviruses and typical reoviruses are diminishing as more is being learned about them. These viruses, previously ungrouped or in minor serogroups, include bluetongue, epizootic hemorrhagic disease of deer, Eubenangee, IbAr 22619, B 1327, Colorado tick fever, African horse sickness, Irituia, Changuinola, BeAr 35646, BeAr 41067, Kemerovo, Chenuda, Tribec, Wad Medani, Mono Lake, Huacho, Lebombo, Palyam, D'Aguilar, G 8886, G 15534, Corriparta, Acado, MP 359, CH 9935, and MRM 10434 viruses. (Borden *et al.*, 1971; Murphy *et al.*, 1971).

Oregon sockeye disease virus (rhabdovirus of salmon).

Orf virus (contagious pustular dermatitis virus, "contagious ecthyma," paravaccinia subgroup of poxvirus). Infects sheep and goats (also man). Particles about 250×160 nm; nucleoprotein threads (7–9 nm) form characteristic lattice in transparent matrix. Some subtypes are enveloped and ether sensitive. Orf virus is antigenically as well as morphologically related to poxviruses.

Orteca virus, related to yaba and tanapox viruses.

Orthomyxoviruses, *see* myxoviruses.

Osteopetrosis virus (avian leukosis virus).

Owl herpesvirus (Lee *et al.*, 1972.)

P-virus of *Drosophila melanogaster* (picornavirus). About 27 nm in diameter. Symptomless. (Teninges and Plus, 1972.)

Palyam virus (orbivirus subgroup of reoviridae).

Papilloma viruses (the larger-sized subgroup of papovaviridae, including bovine, canine, human, rabbit papilloma, i.e., Shope rabbit papilloma virus, etc.). Generally cause benign warts, rarely cause transformation in tissue culture ($1/10^9$ for human, possibly $1/10^5$ for bovine papilloma virus) or cytopathic effects. Particles are of 53 nm diameter, 290 S, 47×10^6 dalton particle weight. The virion is of skew icosahedral structure, $T = 7$, 72 capsomeres (420 polypeptide chains, 60 hexamers, 12 pentamers) (see Electron micrograph VII). Contains 12% cyclic double-stranded DNA, 5×10^6 mol. wt. (density 1.711 g/ml); (G+C) content 41, 43, 46, and 47% for human, canine, bovine, and Shope rabbit papilloma virus DNA. The DNA has two sedimentation constants, due to its circular state, in part supercoiled, and in part relaxed through at least one break in one strand. Linear molecules, the result of both strands being broken near one another, also exist. (Klug and Finch, 1968.)

PAPOVAVIRIDIAE. Family of viruses including the *papilloma* and *polyoma* viruses, and *vacuolating agent*, i.e., SV-40. Medium small viruses of cubic symmetry (about 50 nm) containing double-stranded cyclic DNA of molecular weight $3-5 \times 10^6$. These viruses replicate in the nucleus; many of them are oncogenic.

PARAINFLUENZA VIRUSES (subgroup of paramyxoviruses). Four serotypes: (1) hemadsorption virus 2 (man); Sendai virus (mouse, pig, man?); (2) croup-associated virus (man); SV-5, SV-41 (monkey); (3) hemadsorption virus 1 (man); shipping fever virus (cattle), respiratory equine virus; (4) M25 (man), mumps virus. For structural detail, see SV-5, Sendai virus, etc.

Paralysis virus of termites (picornavirus). About 25 nm in diameter. Symptomless.

PARAMYXOVIRUS GROUP. Virions similar but larger (about 150 nm diameter, 700×10^6 particle weight) than those of myxoviruses. Contain about 1% of a single molecule of $6-7 \times 10^6$ single-stranded RNA (56 S) in a helical 18-nm-diameter, 1000-nm-long nucleocapsid, very similar in appearance to tobacco mosaic virus. The envelopes are similar to those of myxoviruses in structure, appearance, and origin (see Electron micrograph VIII). The viruses are ether sensitive. All paramyxoviruses hemagglutinate, but some (e.g., measles virus) lack the neuraminidase, a characteristic feature of all myxoviruses and many paramyxoviruses. Most paramyxoviruses cause fusion of host cells (polykaryons) at high

multiplicity of infection. Main members (all serologically interrelated): parainfluenza viruses 1-4, Newcastle disease virus, mumps virus. Measles, distemper, and rinderpest viruses represent a subgroup. The RNA of paramyxovirions, as those of rhabdo- and probably myxoviruses, represents the complement to the messenger strand; the term "negative strand" has been proposed.

Parana virus (arenavirus).

PARVOVIRUS GROUP (small DNA viruses; logical but not accepted name: picodnaviruses, analogous to picorna, small RNA viruses). Small, 18-22 nm diameter, icosahedral particles (buoyant density in CsCl 1.38-1.45 g/ml). The virion consists of probably 32 capsomeres of 2-4 nm diameter. They contain 18-34% single-stranded DNA of $1.2-2.1 \times 10^6$ daltons which in some are both of the complementary strands; then isolated DNA tends to anneal and appear double-stranded. Parvoviruses are partly infective (MVM, Kilham rat virus, etc.), partly defective and thus requiring infection by a helper virus (adeno-associated viruses). The viruses replicate in the nucleus; they are quite heat stable; several of them hemagglutinate widely.

Some certain or probable members of the parvoviruses are: H 1-3 and X-14 viruses, latent rat (Kilham) virus, minute mouse virus, porcine, bovine, and avian parvoviruses, denonucleosis and Junonia virus, mink enteritis, hemorrhagic encephalopathy, feline panleucopenia, and the defective adeno-associated viruses. (Tinsley and Longworth, 1973.)

Pichinde virus (arenavirus). The multiple single-stranded RNA species are probably in part from ribosomes (*see* lymphocytic choriomeningitis virus). The virus contains four proteins (two of 72,000, one of 34,000, and a minor component of 12,000 mol. wt. The second and third are glycoproteins). (Carter *et al.*, 1973.)

Picodnaviruses, *see* parvovirus group.

PICORNAVIRIDIAE. Large family of small RNA viruses characterized by icosahedral particles (25-30 nm diameter) consisting of usually four proteins forming sixty equal capsomeres and one molecule of RNA of 2.6×10^6 mol. wt. Both RNA and protein are replicated in the cytoplasm. The protein is split to form the four components amounting to 96,000 daltons (molecular weights about 35,000, 30,000, 24,000, and 7000), partly during assembly. The virions

contain no enzymes. The RNA serving directly as messenger carries 3'-terminal poly(A). Subgroups are the enteroviruses, cardioviruses, rhinoviruses, and foot and mouth disease virus (*see* poliomyelitis, encephalomyocarditis (EMC), mouse-Elberfeld (ME) virus, etc.). In a broader sense most plant and many bacterial viruses are picornaviruses (small RNA viruses), although these usually consist of only one or two proteins forming the icosahedral 20–30 nm nucleocapsid with usually one molecule of RNA of up to 2×10^6 daltons. (Brown and Hull, 1973.)

Pig enteroviruses (picornavirus). Ten serotypes (e.g., Talfan, Teschen, F43, etc.); 28 nm diameter particles.

Pigeonpox virus (birdpox subgroup of poxviruses).

Pistillo virus (arenavirus).

Pixuna virus (alphavirus subgroup of togaviridae).

PML-2 agent, *see* JC virus.

Pneumonia virus of mice (“meta” myxovirus, similar to respiratory syncytial viruses).

Pneumotropic virus (coronavirus of rats).

Poliomyelitis virus (enterovirus subgroup of picornaviridae). Three serotypes are known. Poliovirus is infectious only in primates. Its icosahedral particles have a 28 nm diameter; 158 S; density 1.34 g/ml; particle weight probably 8.4×10^6 . Virion contains 31% single-stranded RNA, 2.4×10^6 mol. wt. (2300 nm long?), A/G/U/C = 30/23/24/23. The RNA contains a 3'-terminal poly(A) sequence of about 89 adenylic acid residues, preceded by two guanylic acid residues, and 5'-terminal pA-. Proteins: 35,000 IV; 29,000 II; 25,000 III; 7300 I (and minor components of about 30,000). (Formerly reported percentages and molar ratios are probably erroneous.) Actually, by analogy to mouse-Elberfeld virus, mature poliomyelitis probably consists of four equimolar protein components. N-terminal are aspartic acid, glycine, and serine. (The roman numbers above indicate gene-map order, 5' to 3'). (Tannock *et al.*, 1970; Phillips, 1972.)

Polyhedral cytoplasmic DNA virus, *see* frog virus 3.

Polyhedrosis viruses, *see* cytoplasmic and nuclear polyhedrosis viruses.

POLYOMA VIRUSES (the smaller-sized subgroup of papovaviridae,

including polyoma virus, SV-40, rabbit kidney vacuolating virus, etc.). Icosahedral particles ($T = 7$) of 45 nm diameter, 240 S, particle weight 28×10^6 . Density of virion in CsCl 1.34 g/ml; of empty protein-only particles 1.29 g/ml (see Electron micrograph IX). Virus contains 12% of double-stranded DNA, 2.8×10^6 mol. wt., density 1.709 g/ml, 48% (G+C). The DNA is circular and consists of two or three density components due to the presence of hypercoiled (20.3 S) and relaxed circles caused by at least one break in one strand (15.8 S). Linear molecules, due to vicinal breaks of both strands, are 14.4 S (these also probably represent linear host DNA from pseudovirions).

The main protein (about 60%) has a molecular weight of 48,000; three others are 86,000, 35,000, and 23,000. Three small proteins (15,000–19,000) represent host cell histones. The architecture of the polyoma virus is still in dispute, with 72, 42, and 32 capsomeres being considered. The viruses are assembled in the nucleus. The polyoma virus is lytic in mouse cells and temperate, causing transformations, in hamster and rat cells (30–100 particles produce a plaque); compared to other DNA viruses, it is relatively efficient in causing transformation of cells ($1/10^5$ particles); it can be oncogenic in animals. (Roblin *et al.*, 1971; Friedmann and David, 1972.)

Powassan virus (of man) (flavivirus subgroup of togaviridae).

POXVIRUS GROUP. Very large brick-shaped particles (about 200×300 nm, 5000 S) containing about 6% of linear DNA of $160\text{--}200 \times 10^6$ mol. wt., 35–40% (G+C). The particles are of complex morphology, with several membranes, internal biconcave nucleoid or core, lateral bodies, etc. (see Electron micrograph X). The poxviruses are generally more or less ether resistant and relatively stable to heat and acid. They replicate in cytoplasmic “factories.” The virions contain many proteins, including many enzymes, such as the DNA-dependent RNA polymerase associated with the core, as well as nucleases, ATPase, etc.

Poxviruses frequently produce no apparent disease. Several strains hemagglutinate. Six subgroups have been identified as occurring in most vertebrates, besides very similar viruses detected in insects (entomopoxviruses). The poxviruses which cause diseases in man, birds, and mammals, but not usually tumors, are often transmitted by insect vectors. (Andrewes and Pereira, 1972.)

Members of Subgroup I, related to variola, are: variola, alastrim, vaccinia, rabbitpox, monkeypox, ectromelia, cowpox, buf-falopox.

Members of Subgroup II, related to orf virus, are: orf, milker's nodes (paravaccinia), bovine papular stomatitis.

Members of Subgroup III (other viruses affecting ungulates) are: sheeppox, goatpox, lumpy skin disease.

Members of Subgroup IV (avian poxes) are: fowlpox, canarypox, and other bird poxes.

Members of Subgroup V (viruses related to myxoma) are: rabbit myxoma, rabbit fibroma, hare fibroma, squirrel fibroma.

Members of Subgroup VI (unclassified poxviruses) are: molluscum contagiosum, swinepox, tanapox virus, yaba virus, horsepox, camelpox.

Prague virus (nondefective avian sarcoma virus).

Progressive multifocal leukoencephalopathy agent, see JC virus and SV-40.

Progressive pneumonitis virus (possibly the same as Maedi virus, a "slow" virus, seemingly related to oncornaviruses and specifically to Visna virus). Single-stranded 60–70 S RNA which becomes 35 S upon melting. Contains reverse transcriptase. (Stone *et al.*, 1972.)

Pseudocowpox virus (a poxvirus related to contagious pustular dermatitis virus).

Pseudorabies virus of swine (subgroup A herpesvirus). Related to herpes simplex virus, but lacking DNA sequence homology. The DNA is said to occur as two components of 26 S and 31 S [77% (G+C)]. The protein pattern is similar to that of Marek's disease virus. (Graham *et al.*, 1972.)

Pseudoviruses, see defective viruses.

Rabbit fibromavirus (myxoma-subgroup of poxviruses). Double-stranded DNA, 153×10^6 mol. wt., 40.4% (G+C), differs from vaccinia DNA, 35.5% (G+C). Oncogenic. (Jacquemont *et al.*, 1972.)

Rabbit kidney vacuolating virus (polyomavirus). The DNA of 2.8×10^6 mol. wt. is circular, partly hypercoiled, 43% (G+C).

Rabbit myxomavirus, see myxomavirus.

Rabbit (oral) papillomavirus, see Shope rabbit papillomavirus.

Rabbitpox virus (vaccinia subgroup of poxvirus).

Rabies virus of mammals (rhabdovirus). Bullet-shaped, 80×180 nm

particles (600 S), with lipid-containing envelope. Virus matures largely in the plasma membrane, and its lipid composition resembles that of the membrane, with relatively high cholesterol and sphingolipid content. Virus loses some lipid during purification, its density increasing from 1.14 to 1.16 g/ml in the process. The 1000-nm-long nucleocapsid (200 S, 120×10^6 daltons) consists of 1300 protein subunits and single-stranded RNA (45 S), 4.6×10^6 mol. wt.; A/G/U/C = 26/21/29/23. The envelope and spikes (7 nm long) consist of three proteins, 1783 molecules of 80,000 mol. wt. glycoprotein (G), the protein forming the spikes; 789 molecules of 40,000; and 1661 of 25,000. The nucleocapsid consists of 1713 molecules of protein of 62,000 (N) and 76 of 55,000 mol. wt. (Nm). The N protein was found to be a phosphoprotein. The virus hemagglutinates best at low temperature. The virion contains a protein kinase but no neuraminidase. Rabies virus replicates in many mammals. (György *et al.*, 1971; Sokol and Clark, 1973.)

Rat virus (RV), *see* Kilham rat virus.

Rauscher murine leukemia virus (transformation-defective murine leukemia virus).

RAV 0, 1-7, 49, 50, 60 (Rous associated viruses) (transformation-defective avian leukosis viruses).

RD 114 virus (transformation-defective oncornavirus). C-type virus isolated from human tumor cells, but derivation from a feline virus appears more probable.

Red disease agent of pike (rhabdovirus). (Kinkelin *et al.*, 1973.)

REOVIRIDIAE. Proposed name for the double-stranded RNA-containing viruses of animals (reo- and orbiviruses), plants, and insects. Preferred name, at least for the plant and insect viruses: diplornaviruses. (*See* diplornavirus group.)

REOVIRUSES (one of two subgroups of the animal diplornaviruses) (respiratory and enteric orphan viruses). First classified as echo virus 10. At least three serotypes are known.

Reovirus particles, 630 S, 100×10^6 in particle weight, consist of inner and outer protein shells. The core is 52 nm in diameter, the complete particle 76 nm (see Electron micrograph IV). Particles lacking the outer shell occur naturally and can be obtained by chymotrypsin treatment of the larger virion; they are infectious. The capsomeres in the outer shell are of 9 nm diameter, those of

the inner shell 4 nm. Both shells appear to be of icosahedral symmetry, consisting of 92 or 122 capsomeres of different size, with the core carrying 12 projections halfway into the outer shell (10 nm in diameter). The RNA (15%) is double-stranded, 43% (G+C) on average, and occurs in ten distinct molecular species of molecular weights ranging from 2.4 to 0.6×10^6 daltons. All ten segments start (5') with ppGp-pyrimidin and terminate (3') with unphosphorylated cytidine. Oligonucleotides also occur in the virion, one group starting with pppG- of lengths up to 9, and another of oligo-A of 2-20 residues, starting with pppA-. Both groups also exist with only one or two 5'-terminal phosphates.

The proteins of type 3 reovirus (Dearing strain) were found to be of molecular weight 155,000 (λ_1 , 113 molecules); 140,000 (λ_2 , 80 molecules; the major surface protein of the core); 80,000 (μ_1 , 23 molecules); 72,000 (μ_2 , 550 molecules); 42,000 (σ_1 , 31 molecules); 38,000 (σ_2 , 202 molecules); and 34,000 (σ_3 , 890 molecules); (5000-10,000?, about 500 molecules). Proteins μ_2 and σ_3 are located on the surface of the virion. Enzyme treatment, removing the outer shell (and the A-rich RNA), leaves only the two largest and the 38,000 mol. wt. protein. For amino acid composition, see Table 1. The amino-terminal sequence of μ_2 is Pro-Gly-Gly-Val-Pro-; all other proteins have blocked N-terminals. The C-terminal sequences of σ_3 is -(Val, Leu, Val)); those of μ_2 and λ_1 and λ_2 are -Arg preceded by different amino acids.

The RNA remains nuclease resistant in the core. The virion contains a latent RNA polymerase activated by heating or chymotrypsin treatment and thus present in the core. This enzyme may serve first as transcriptase and release messenger RNA, and later it may replicate both strands.

Relation to any human disease uncertain, but pathogenic upon inoculation. Newborn mice seriously affected by reovirus type 3. Reoviruses have been found in man and other mammals as well as in birds and mosquitoes, but no evidence for their multiplication in insect vectors has been found. Reoviruses, widely distributed in nature, cause marked cytopathic effects in tissue culture. They are nonenveloped and are thus resistant to lipid solvents. They agglutinate human erythrocytes, their receptors, in contrast to those of myxo- and paramyxoviruses, not being susceptible to the receptor-destroying enzyme of *Vibrio cholerae*. (Joklik, 1972; Pett *et al.*, 1973.)

Reptilian C-type virus (oncornavirus). (Gilden *et al.*, 1970.)

Respiratory equine virus, *see* parainfluenza virus.

Respiratory syncytial virus (human and bovine) (not yet classified; "metamyxovirus"). 80–120 nm diameter particles, with projections and helical nucleocapsids of 11–15 nm diameter. Does not hemagglutinate. (Ito *et al.*, 1973b.)

Reticuloendotheliosis virus, similar in morphology but not biologically and serologically related to avian leukosis or sarcoma viruses. Buoyant density in CsCl 1.20 g/ml (Rous sarcoma virus 1.24). The properties of the RNA show similarities to those of AMV. At least three proteins of 30, 20, and 12×10^3 and two glycoproteins of 65 and 18×10^3 mol. wt. have been observed, differing in molecular weight from those of RAV. The virus contains reverse transcriptase (Maldonado and Bose, 1972, 1973.)

RHABDOVIRUS GROUP. Medium large though somewhat variable bullet-shaped particles (e.g., 70×200 nm, 200×10^6 dalton particle weight). Lipid-containing envelope and 10 nm spikes can be seen as well as at times two transverse striation patterns of different periodicity. At least one of these is due to the helical nucleocapsid enclosing the simple molecule of $3.5\text{--}4.5 \times 10^6$ dalton RNA (2%). These viruses contain RNA polymerase and the RNA is the negative strand and must first be transcribed. They are ether sensitive. Prototype: Vesicular stomatitis virus. Others are: Cocal, Flanders Hart Park, Kern Canyon, rabies, and probably Egtved, Gomphrena, Lagos bat, Mount Elgon bat virus, possibly Marburg virus. *Drosophila* sigma virus represents an insect rhabdovirus. Also many plant viruses are rhabdoviruses, although these appear generally to be at least partly bacilliform rather than bullet shaped. It is not certain whether either form should be regarded as an artefact. (See Electron micrograph XI.)

Rhinopneumonitis virus, *see* equine abortion virus.

RHINOVIRUS GROUP (subgroup of the picornaviridae). More than 90 human serotypes known; also an equine and several bovine types (sd1, 181/v, C-07, EC11, RS 3X). There is little or no serological relationship or nucleotide sequence homology among the rhinoviruses. The human rhinoviruses are 22–28 nm particles of 158 S, 1.38–1.41 g/ml in density in CsCl (compared to enteroviruses 1.33–1.34 g/ml). Serotype 14 is of 25 nm diameter, 158 S (same as poliovirus), 7.1 (or more probably 8.4) $\times 10^6$ particle weight. The 260/280 absorbance ratio is about 1.71. The viruses contain 29.8%

(28 S) RNA of probable molecular weight 2.6×10^6 (same as poliovirus). The HGP strain is reported as 22 nm in diameter, 150 S. A/G/U/C = 34/20/26/20. The proteins are similar to those of other picornaviruses in molecular weight, all four occurring in equimolar proportion (34,000, 30,000, 26,000, 7000). *See* mouse-Elberfeld virus for architecture of picornaviruses. The rhinoviruses are stable at pH 6-8; they are more sensitive to acid than the enteroviruses and cardioviruses, but less than foot and mouth disease virus. (Medappa *et al.*, 1971; Stott and Killington, 1973.)

RIF (resistance-inducing factors) (transformation-defective avian leukosis viruses).

Rift Valley fever virus (unclassified arbovirus). 60-90 nm spheres, ether sensitive, density 1.23 g/ml (disease of sheep, goats, and cattle).

Rinderpest virus (bovine paramyxovirus). Closely related to canine distemper and human measles virus. The two animal viruses are serologically related. Rinderpest virus contains a helical nucleocapsid similar to all members of this group.

RNA tumor viruses, *see* oncornavirus group.

Ross River virus (alphavirus subgroup of togaviridae).

Rous sarcoma virus (avian oncornavirus). 80-120 nm particles (500-600 S) consisting of a dense nucleoprotein core (40 nm diameter) and a lipid-containing envelope with knoblike projections. The composition of the virion is 64% protein, 1.9% RNA, 1-2% carbohydrate; the rest is mostly lipid. The virus spectrum in 0.2% SDS, added to abolish the strong light scattering, shows a shallow maximum at 270 nm (260/280 absorbance ratio 1.15) A_{270} (0.1%) is about 2.0.

The phospholipid (31%) consists of sphingomyelin, phosphatidylcholine, and phosphatidylethanolamine, 1:1:1, similar but not identical to the phospholipid distribution in plasma membrane of infected and noninfected host (CEF) cells and of envelopes of Sindbis virus, Sendai virus, and Newcastle disease virus grown on the same cells. Thus the lipids are largely derived from, and determined by, the host.

The RNA (about 0.5% and containing about 2.5% poly(A)) is 60-70 S, corresponding to about 12×10^6 daltons per particle. Smaller RNA material also occurs in the virus (12-4 S, containing degradation products as well as 7 S, 5 S, and 4 S species). Upon melting (heat, dimethylsulfoxide, etc.) the large component be-

comes largely 35–30 S, believed to be due to release of unique molecules of RNA of $3\text{--}4 \times 10^6$ dalton molecular weight, held together by complementary H-bonded segments. A slightly larger and a smaller RNA component (a and b) have been found associated with nondefective viruses (producing foci in chick embryo fibroblasts) and avian leukosis viruses, respectively. The main proteins are two glycoproteins (105,000 and 36,000) in the envelope, probably making up the external spikes and carrying the type-specific antigens, and in the 50 nm diameter core proteins of 27,000, 19,000, 15,000, and 12,000 mol. wt., components of the group-specific antigen.

The glycoproteins differ slightly in size in a manner correlating with the presence of RNA components a and b. The glycopeptides obtained by exhaustive pronase treatment are of about 5700 and 3900 daltons, respectively.

The inner filamentous nucleoid liberated by Nonidet P40 (130 S, density in CsCl 1.34 g/ml) consists of only five of the eleven proteins detected in this study, the 28,000 protein predominating, and 20% RNA (30 4 S RNA molecules per 10^7 daltons of large-molecular-weight RNA). The nucleoid covered by an internal membrane represents the core of the virus.

Proteins associated with this membrane and the envelope are said to have molecular weights of 115 and 37×10^3 , the smaller ones present in greatest numbers (2000–6000 per particle). Only the 14,000 mol. wt. protein appears strictly associated with the RNA. The reverse transcriptase of the virus (Prague strain), less than 2% of the soluble proteins of the virus and not containing carbohydrate, was of 6 S (after RNase treatment), probably 110,000 in molecular weight.

RSV and other virulent RNA tumor viruses are produced and excreted by the cells they transform. (Bolognesi *et al.*, 1972; Lai and Duesberg, 1972; Hung *et al.*, 1971.)

RPL-12 virus (transformation-defective avian leukosis virus) (Davis and Rueckert, 1972.)

RT virus (parvovirus).

Rubella virus (alphavirus subgroup of togaviridae). Causes German measles in man, of particular danger during pregnancy. Only monkeys are susceptible. The pleomorphic enveloped lipid-containing 60 nm diameter particles contain a 150 S nucleocapsid with single-stranded RNA of about 3.4×10^6 daltons (39 S), of

density 1.634 g/ml. Three proteins of 62,500, 48,000, and 35,000 daltons have been detected, the first two representing glycoproteins and the last the capsid protein. This pattern resembles that of the alphaviruses. The virus hemagglutinates at low temperatures only. The virus is not arthropod-transmitted. (Liebhaber and Gross, 1972; Vaheri and Hovi, 1972.)

Russian tick-borne (or spring-summer) encephalitis virus (flavivirus subgroup of togaviridae). Related to louping ill virus.

R.V. (parvovirus). 3.6×10^6 dalton particles, containing 34% of single-stranded DNA (27 S) ($1.3 [?] \times 10^6$ mol. wt.).

SA 6 and SA 8 viruses (cercopithecoid herpesvirus 2 and 3).

SA 7 virus (oncogenic simian adenovirus).

SA 11 virus, from South African *Cercopithecus* monkeys (orbivirus subgroup of reoviridae). 72 nm enveloped particles. 57 nm in diameter when lacking outer shell, probably composed of 32 capsomeres. (Els and Lecatsas, 1972.)

Sacbrood virus (insect picornavirus similar but not related to bee acute paralysis viruses). Spherical particles, 28 nm in diameter (160 S). Contains 35% RNA (35 S), A/G/U/C = 32/19/31/18. Infects only bee larvae. (Newman *et al.*, 1973.)

Sacramento river chinook disease virus (rhabdovirus of salmon).

Salivary virus of bat (US) (flavivirus subgroup of togaviridae).

San Miguel sea lion virus, probably identical with vesicular exanthema virus of swine.

Schmidt–Ruppin virus (nondefective avian sarcoma virus).

Scrapie agent of sheep, member of a group of not typical viruses, also called unconventional viruses (Kuru and Creutzfeld–Jakob disease of man and transmissible mink encephalopathy; possibly viroids). (Marx, 1973.)

Semliki Forest virus (alphavirus subgroup of togaviridae). Spherical particles of 70–80 nm diameter (300–350 S), coated with a membrane and ether sensitive. Virus remains infectious after enzymatic removal of surface projections, but loses its hemagglutinating activity. The cores found in infected cells (40 nm diameter) (140 S) contain the RNA encapsidated in ribonuclease-resistant manner.

The RNA (6.3%) is 45 S and has a molecular weight of 4.1×10^6 . Its composition is A/G/U/C = 29/26/20/25.

The single core protein (12%) has a molecular weight of 32,000, N-terminal lysine, and a high content of hydrophilic amino acids. The surface protein (44%, 2.5 moles/mole capsid protein) occurs as spikes exterior to the lipid envelope. It contains sugars (14%) and is of 54,000 mol. wt. with N-terminal valine. A part of the protein particularly rich in hydrophobic amino acids is anchored to the lipid envelope. The bilayered lipids in the envelope resemble those of the host cell plasma membrane, infected or uninfected, but with much less fatty acids and more cholesterol (0.41 mg lipid/mg protein, 31% neutral, 61% phospholipid, 8% glycolipid). (Acheson and Tamm, 1970.)

Sendai virus or hemagglutinating virus of Japan (parainfluenza subgroup of paramyxoviruses). Infects swine, mouse, and man. 150 nm diameter particles containing a 1100-nm-long helical nucleocapsid (5.0 nm pitch, about twelve protein subunits/turn) (see Electron micrograph VIII). The RNA is 50 S, about 6×10^6 in molecular weight, and 6.5 μm long. (A report that it can be dissociated into smaller components has been corrected.) It contains poly(A). Its composition is A/G/U/C = 24/23/30/23. (Kolakofsky *et al.*, 1974.)

Two glycoproteins containing fucose, galactose, and glucosamine are 65 and 53×10^3 daltons. The main capsid protein is 60×10^3 daltons, and a membrane protein is 38×10^3 daltons. Three additional proteins are of 72, 57, and 46×10^3 daltons. Sendai virus, like all paramyxoviruses, causes at high-multiplicity rapid formation of polykaryons by fusion of cell membranes. Trypsin is said to release "monovalent" hemagglutinin and fully active neuraminidase of 124×10^3 daltons and 114×10^3 daltons, apparently dimers of the above-listed glycoproteins. The neuraminidase of Sendai virus shows considerable similarity, in enzymatic and serological respects, to that of Newcastle disease virus (Iida, 1972; Mountcastle *et al.*, 1971.)

Sericestis iridescent virus (insect iridovirus, related to tipula iridescent virus). Icosahedral particles with 86-nm-long edges; diameter about 130 nm; 760×10^6 particle weight; consisting of probably 1562 protein subunits in outer shell. Contains double-stranded DNA (18%) of 134×10^6 mol. wt. (Glitz *et al.*, 1968.)

Sheep enterovirus (picornavirus). 28 nm diameter particle.

Sheeppox virus (subgroup of poxviruses).

Sheep pulmonary adenomatosis virus (herpesvirus). Also termed Jaagsiekte virus.

Shipping fever virus, *see* parainfluenza viruses.

Shope fibroma virus, *see* rabbit fibroma virus.

Shope (rabbit) papilloma virus (prototype for papilloma virus subgroup of papovaviridae). Icosahedral particles of 53 nm diameter, about 50×10^6 particle weight. The architecture of the particle is probably the same as for polyoma virus: 72 capsomeres, $T = 7$; left-handed skew configuration. The sedimentation rates of the nucleocapsids and the empty capsids are 298 S and 172 S, respectively. The capsomeres are short (10 nm) hollow cylinders composed of five or six subunits. Double-stranded cyclic DNA of 5×10^6 mol. wt. and 48% (G+C). *See* under papilloma virus for more detailed information. (Klug and Finch, 1968.)

Sigma virus (rhabdovirus of *Drosophila*). 160×70 nm bullet-shaped particles.

Simian hemorrhagic fever virus (flavivirus subgroup of togaviridae). Unrelated to other known viruses. 40–45 nm particles.

Simian herpesviruses (several of them, e.g., type 8, deadly also to man), *see* herpesvirus ateles, saimiri, simiae, tamarinus.

Simian paramyxoviruses, *see* SV-5, SV-41.

Simian sarcoma virus type 1 (oncornavirus). Typical C-type particles containing RNA of 60–70 S, 28 S, 18 S, and 4 S, and reverse transcriptase.

Simian viruses, *see* under SV.

Simian virus SA-11, *see* SA-11 virus.

Sindbis virus (alphavirus subgroup of togaviridae, related to western equine encephalitis virus). Slightly pathogenic in man; transmitted by mosquitos. The 70 nm diameter particle contains a 40 nm core composed of 32 hexamer–pentamer morphological units ($T = 3$). The virus sediments with 273 S, the core with 173 S (*see* Electron micrograph XII).

The single-stranded RNA represents according to some authors

a single chain without breaks of 42 S and a molecular weight of 4.3×10^6 daltons. Others are equally insistent that this is the dimer of a 26–28 S RNA, although it now appears probable that the latter is the sedimentation rate of the messenger RNA, the complementary form to the virion RNA (or part thereof). The composition of the viral RNA is A/G/U/C = 30/26/20/25. Sindbis RNA also contains poly(A) sequences of various lengths.

The viral envelope was recently shown to consist of two rather than one glycolipoproteins. The lipid and to a lesser extent the carbohydrate compositions vary depending on host and culture conditions (like those of myxo-, paramyxo-, and oncornaviruses). Both glycolipoproteins are of approximately 53,000 mol. wt., the capsid protein 30,000. All proteins arise by posttranslational cleavage from a large precursor protein. (Boulton and Westaway, 1972; Schlesinger and Schlesinger, 1972.)

SLOW VIRUSES, a not well defined group of viruses which are intermittently or continuously present in appreciable quantities in the infected host, and may but need not cause diseases of usually very chronic and degenerative nature, often associated with the central nervous system. Some human diseases have been attributed to slow viruses. They are probably related to oncornaviruses since they contain reverse transcriptases. *See* Visna virus, Maedi virus, lactic dehydrogenase virus, possibly Creutzfeld-Jakob, Kuru, etc.

Spidermonkey herpesvirus, cebid herpesvirus 3

Spondweni virus (flavivirus subgroup of togaviridae).

Spring viremia virus of carp (rhabdovirus). Buoyant density in sucrose 1.16 g/ml. Contains 3 main proteins of 70, 40, and 19×10^3 daltons (9:4:4) and a small amount of a 150×10^3 species. Whether this agent causing infectious dropsy and the agent causing swim bladder inflammation are the same or closely related is as yet uncertain. (Bachmann and Ahne, 1973, Lenoir, 1973.)

Squirrel fibroma virus (myxoma subgroup of poxviruses).

St. Louis encephalitis virus (flavivirus subgroup of togaviridae). The RNA is said to be of 3.3×10^6 daltons. A/G/U/C = 31/26/21/22. The BHK strain contains three proteins: 63,000 and 8500 mol. wt. in the envelope and 18,000 for the capsid protein; the Vero and BS strains contain proteins of 52,000 and 14,000 respectively. (Qureshi and Trent, 1972.)

Stratford virus (flavivirus subgroup of togaviridae).

Subacute sclerosing panencephalitis virus (slow virus?, or paramyxovirus related to measles virus). However, papovavirus-like particles have also been found associated with this disease. Attacks central nervous system of children. Free nucleocapsids in infected tissue (both nucleus and cytoplasm) characterize this infection. They occur both in a helical form (18 nm diameter, 5–6 nm pitch, and 1.0 to 1.4 μm long) containing 4.3% RNA (density in CsCl 1.31 g/ml) and as granular 22–25 μm filaments. (Yeh and Iwasaki, 1972.)

SV-1 (oncogenic simian adenovirus).

SV-5 (simian parainfluenza subgroup of paramyxoviruses). The virus consists of 73% protein, 20% lipid, 6% carbohydrate, and 0.9% RNA. Its main protein components are a capsid and a membrane protein (61 and 41×10^3 daltons), and two glycoproteins (67 and 56×10^3) containing glucose, galactose, mannose, fucose, and glucosamine. Both neuraminidase and hemagglutinin activity were found associated with the larger of these two proteins (8.9 S). The glycolipid contains glucose, galactosamine, and galactose and lacks neuraminic acid. (Scheid *et al.*, 1972.)

SV-12 from monkeys, identical with human reovirus type 1.

SV-15 (nononcogenic simian adenovirus).

SV-20, 23, 25, 33, 34, 37, 38 (oncogenic simian adenoviruses).

SV-40 (simian polyoma virus). Particle dimensions and architecture as in polyoma virus (see Electron micrograph IX). The virus contains 12% double-stranded circular DNA of 3.2×10^6 mol. wt. (partly supercoiled), 41% (G+C), and one or possibly two capsid proteins of about 44×10^3 mol. wt. (75%), and two smaller proteins (32 and 23×10^3 , 9 and 10%), as well as lesser amounts of yet smaller proteins (some possibly cellular histones) of 14,000, 12,500, and 11,000, 6000, and 4000 mol. wt. The virus contains an endonuclease which causes nicks in the DNA. All the major proteins are said to be phosphoproteins. (See Table 1 for amino acid analyses.)

SV-40 is lytic in monkey cells, and temperate, causing occasional transformation, in mouse cells. The isolated DNA is able to infect and to transform susceptible cells. Evidence has been presented that the agent causing progressive multifocal leukoencephalopathy (PML-2) in man is a variant of SV-40. (Tan and Sokol, 1972.)

SV-41 (simian parainfluenza subgroup of paramyxoviruses). Very similar to SV-5.

SV-59 from monkeys, identical with human reovirus type 2.

Swim bladder inflammation agent of carp (rhabdovirus). (Bachmann and Ahne, 1973.)

Swinefever virus (flavivirus subgroup of togaviridae). Isometric virions of 40 nm diameter with a 29 nm core, 108 S, and of 1.17 g/ml density in CsCl. Contains RNA.

Swine influenza virus (myxovirus).

Swinepox virus (unclassified poxvirus).

Syncytium-forming (“foamy”) type 3 virus (member of slow virus group resembling oncornaviruses). Simian, feline, etc., types have been observed. The virus contains reverse transcriptase and causes extensive cell fusion. (See “foamy” virus.)

Takaribe, Tamiani viruses (arenaviruses).

Tanapox virus of primates, similar to Yaba virus.

Termite paralysis virus (picornavirus).

Theilen feline sarcoma virus, see feline leukemia sarcoma virus.

Tick-borne encephalitis virus (Central European and Far Eastern subgroups; flavivirus subgroup of togaviridae). Affects man.

Tipula iridescent virus (prototype of iridovirus of insects). Icosahedral particles of 130 nm diameter (2200 S), 82 nm edge length, probably containing 1472 protein subunits in outer coat (see Electron micrograph V). Double-stranded DNA of 126×10^6 mol. wt. (15%). Contains several proteins, little (9%) or no lipid. (Glitz *et al.*, 1968.)

TOGAVIRIDIAE. Family of very many viruses including most formerly called arboviruses. Subgroups, roughly corresponding to the A and B groups of the arboviruses, are the slightly larger (40–80 nm diameter) alphaviruses and the slightly smaller (30–50 nm diameter) flaviviruses.

The togaviruses are medium sized (usually 50–70 nm) enveloped viruses containing single-stranded RNA (see Electron micrograph XII). The RNAs of the togaviruses serve directly as messengers and appear to contain 3′-terminal polyadenylic acid sequences and no polymerases or transcriptases (RNA or DNA or reverse). The viruses mature by budding through the plasma membrane. They

hemagglutinate red cells. The nonhemagglutinating nucleocapsids of 40 nm diameter are probably icosahedral, with 32 capsomeres. The protein composition of the togaviridae is generally simple (about three, including the lipid-rich envelope proteins). (*See rubella, Sindbis, Semliki Forest virus, etc.*).

Toluca 1 virus (enterovirus). Serologically distinct from other known enteroviruses. Particles of 25 nm diameter.

Transmissible gastroenteritis virus of pigs (coronavirus).

Transmissible mink encephalopathy agent, *see* scrapie.

Tribec virus (orbivirus subgroup of reoviridae).

Turkey herpesvirus 1, used to vaccinate against Marek's disease.

Turkeypox virus (birdpox subgroup of poxviruses).

TVX virus (parvovirus). Same properties as, though serologically differentiable from, KBSH virus.

Uganda S virus (flavivirus subgroup of togaviridae).

Una virus (alphavirus subgroup of togaviridae).

US bat salivary virus (flavivirus subgroup of togaviridae).

Usutu virus (flavivirus subgroup of togaviridae).

Uukuniemi virus (togavirus, separate serological group). 450 S particles, density 1.20 g/ml; contains RNA of 18 S, 21 S, and 27 S (4.1, 1.9, 0.9, and 0.8×10^6 daltons), and at least one envelope protein (70,000 mol. wt.) forming 8-nm-long projections, and one capsid protein (25,000 mol. wt.), seemingly forming a helix upon release, with a 9 nm diameter. The phospholipid content of the envelope is very similar to that of Semliki Forest virus grown on the same cells. (Pettersson *et al.*, 1971.)

Vaccinia virus of man (vaccinia subgroup of poxviruses). The approximately 200×300 nm particles ($\sim 6000 \times 10^6$ daltons) of complex structure are composed of 92% protein, 3% DNA, 5% lipid (cholesterol 1.2, phospholipid 2.1, neutral fat 1.7%), and 0.2% nondeoxyribose carbohydrate (in glycoproteins) (*see* Electron micrograph X). The double-stranded DNA is of $160\text{--}200 \times 10^6$ mol. wt. and 36% (G+C). 31 proteins have been seen (mol. wt. 130,000–8000): 5 near surface; 17 including two main protein components in cores which make up half of the virion; 2 glycopro-

teins of uncertain location; 6 phosphoproteins. The cores contain an RNA polymerase which transcribes 15% of the genome. One of the phosphoproteins of molecular weight 11,000 is associated with the core. (Sarov and Joklik, 1972.)

Vacuolating virus (or agent) (polyoma virus). Simian and rabbit forms are known; *see* SV-40.

Varicella-zoster virus (human herpesvirus 3). The virus causes both chickenpox and herpes zoster. The particle is of 200 nm diameter, 100 nm when not enveloped, and contains a dense core. The DNA has a density of 1.705 g/ml (compared to 1.717 for herpes simplex virus and 1.697 for host cellular DNA). (Gershon *et al.*, 1973; Taylor-Robinson and Caunt, 1972.)

Variola (minor) virus, smallpox virus (vaccinia subgroup of poxviruses). Possibly identical with alastrim virus.

Venezuelan equine encephalitis virus (alphavirus subgroup of togaviridae). 60–75 nm particles with a 30–40 nm core. The phospholipid varies with and partially reflects that of the host's plasma membrane. There are considerable similarities among the lipids of different togaviruses. The lipids contribute to the relative heat resistance of these viruses. The RNA is of 40 S, 4.2×10^6 in molecular weight, and has a buoyant density in CsCl of 1.66 g/ml. (Heydrick *et al.*, 1971.)

Vesicular exanthema virus of swine (calicivirus subgroup of picornaviridae). Isometric 35–40 nm diameter particles, 207 S, of density 1.38 g/ml. Contains 20% single-stranded RNA ($2-3 \times 10^6$ mol. wt.; 37 S) and 80% protein. A/G/U/C = 29/21/25/25. Virus is ether resistant, sensitive to acid (pH 3), and heat (50°C); not inhibited by actinomycin D. (Oglesby *et al.*, 1971.)

Vesicular stomatitis virus of cattle (prototype of rhabdovirus group). Bullet-shaped enveloped particles of 290×75 nm (625 S). The buoyant density in CsCl is 1.18 g/ml, the particle weight 385×10^6 daltons. Indiana serotype: 64% protein, 13% carbohydrate, 20% lipid, 3% RNA (see Electron micrograph XI). The RNA of about 45 S and molecular weight 4.2×10^6 has the composition A/G/U/C = 27/21/31/22. The RNA is single-stranded.

The lipid composition, high particularly in phosphatidylethanolamine and sphingomyelin, is similar to that of other viral lipids (paramyxo-, myxo-, and togaviruses), and resembles the com-

position of the host cell plasma membrane more (but not entirely) than that of the entire host cell.

The glycolipid composition is similar to that of the host cell plasma membrane (neuraminic acid, galactose, glucose, ceramide) and represents host cell antigens. Most of the neuraminic acid is in the glycoprotein (G protein of about 69,000 daltons) making up the 10-nm-long spikes which is the major antigenic determinant of the intact virion, while the M protein (29,000–34,000 daltons) is situated in the underlying membrane.

The nucleocapsid is of 140 S, 3.5 nm long, and consists of 1000 protein subunits (density 1.32 g/ml). It contains 43 S single-stranded RNA of 4×10^6 mol. wt., which represents the “negative” strand and is thus noninfective when isolated. The RNA is transcribed by a virion RNA polymerase. The main protein of the nucleocapsid is the N protein (50,000–60,000 daltons). The largest protein (L, about 190,000 daltons) appears to represent the transcriptase, which does not also serve as replicase. The role of a “nonstructural” internal protein (NS, 40,000–45,000 daltons) is not clear; only the latter is a phosphoprotein. The virion also contains a protein kinase.

A comparative study of the two main serotypes (Indiana and New Jersey) as well as the Cocal virus indicates small differences between them. The molecular weight of the three major and one minor proteins are given in that study as about 62,000, 46,000, 27,000, and 38,000. Cocal is related more closely to the Indiana serotype.

The vesicular stomatitis virus replicates in mammals and arthropods. (Wagner *et al.*, 1972.)

Viral hemorrhagic septicemia virus (rhabdovirus of trout).

Visna virus of sheep (a member of slow virus group). A neurotropic variant of Maedi virus. The single-stranded RNA is about 63 S and 4 S, the former becoming about 35 S upon melting. The virus contains reverse transcriptase and DNA-dependent DNA polymerase activities. It transforms murine cells. Among its 11–14 proteins (mol. wt. 142,000–14,000) are at least 2 glycoproteins, the pattern resembling that of the oncornavirus proteins. (Mountcastle *et al.*, 1972.)

von Magnus virus (defective form of influenza virus), *see* defective virus.

Wad Medani, Wallal, and Warrego viruses (orbivirus subgroup of reoviridae).

Wart virus, *see* human papilloma virus.

Wesselsbron virus (flavivirus subgroup of togaviridae). Affects sheep.

Western equine encephalitis virus (alphavirus subgroup of togaviridae).
A/G/U/C = 30/22/23/25.

West Nile virus (flavivirus subgroup of togaviridae).

Whataroa virus (alphavirus subgroup of togaviridae). Related to Western equine encephalitis virus.

Woolly monkey sarcoma virus (oncornavirus).

X-14 virus (parvovirus).

Yaba virus of monkey (poxvirus). Double-stranded DNA has density of 1.6905, 32.5% (G+C). Oncogenic. Contains several enzymes. (Schwartz and Dales, 1971.)

Yellow fever virus (flavivirus subgroup of togaviridae).

Yucaipa virus (paramyxovirus). Symptoms range from inapparent disease to death. Contains neuraminidase.

Zika virus (flavivirus subgroup of togaviridae).

TABLE 1
Amino Acid Composition of Animal Virus Coat Proteins (Pure Single Chain Components)*

	Asp	Thr	Ser	Glu	Pro	Gly	Ala	Cys	Val	Met	Ile	Leu	Tyr	Phe	Lys	His	Arg	Trp	
Picornaviruses																			
EMC 1 (=α?)	8.9	7.0	13.0	10.7	5.3	15.1	6.7	ND	5.4	ND	3.1	6.3	1.7	4.4	4.9	3.0	4.4	ND	
EMC 2 (=β?)	10.1	10.0	10.0	9.5	8.8	10.5	7.3	ND	8.1	ND	3.6	8.1	3.4	8.1	5.2	2.1	4.1	ND	
EMC 4 (=γ?)	8.6	9.6	8.7	9.0	7.1	9.8	8.4	ND	7.0	ND	4.2	7.0	3.2	5.4	4.5	2.4	4.1	ND	
ME α	9.2	7.7	9.9	9.7	7.0	10.7	6.0	1.6	6.9	0.9	2.9	6.9	2.8	5.6	4.7	1.8	3.7	ND	
ME β	10.1	9.7	8.1	10.1	5.1	8.9	7.7	0.7	6.9	1.5	3.5	7.8	2.9	3.9	3.5	2.9	4.8	ND	
ME γ	7.5	10.1	10.1	7.1	8.3	9.2	8.8	1.2	5.5	2.1	5.2	6.7	4.2	4.4	4.0	1.1	2.9	1.6	
ME δ	19.6	4.2	16.6	8.5	4.3	9.0	7.6	0	2.9	1.0	3.7	8.7	3.1	4.2	2.2	0.3	2.0	ND	
Influenza virus																			
<i>Neuraminidase</i>																			
Lec strain (type B)	10.0	8.2	7.6	7.9	4.7	9.6	6.6	2.7	5.0	2.5	5.6	8.8	3.9	2.8	6.8	2.6	4.8	ND	
Bel strain (type A ₀)	11.9	6.1	9.5	10.5	4.7	9.4	4.5	2.4	6.7	0.9	8.6	6.3	2.5	3.9	6.3	1.8	3.9	ND	
X-7F ₁	14.5	7.1	10.3	8.7	4.9	9.1	3.8	2.6	7.3	1.1	8.5	4.7	2.4	3.3	4.5	1.2	6.1	ND	
A2,1957†	13.7	5.7	10.9	7.4	4.3	9.5	2.8	3.9	6.7	1.7	6.3	3.5	2.3	2.8	3.7	1.9	5.6	none	
<i>Hemagglutinin</i>																			
Lec strain, heavy chain	11.4	8.6	6.1	8.4	7.0	10.1	4.4	1.8	6.8	0.8	6.7	7.3	2.9	2.3	8.7	2.4	4.3	ND	
Lec strain, light chain	13.1	5.6	7.6	9.7	1.8	9.0	9.4	1.2	4.2	1.1	6.5	13.6	1.3	3.2	6.2	3.5	3.1	ND	
Bel strain, heavy chain	11.7	7.2	9.2	11.3	4.6	8.5	5.5	1.5	6.0	0.5	6.6	8.9	3.4	3.3	5.8	2.0	4.8	ND	
Bel strain, light chain	13.9	4.5	7.8	13.3	0.5	10.6	5.6	1.1	6.0	0.8	6.0	9.6	3.6	4.3	8.0	1.6	2.7	ND	

<i>Capsid</i>																		
Lec strain	12.0	6.0	7.3	9.9	3.4	8.9	8.3	0.0	5.2	1.9	7.5	9.6	1.8	3.5	8.8	0.9	5.1	ND
Bel strain	8.6	5.6	6.8	15.2	3.9	8.2	8.0	0.8	5.4	1.4	6.3	8.7	1.7	4.3	5.7	1.3	8.3	ND
Lec strain M†	8.2	3.8	6.6	12.2	1.8	8.8	9.0	1.4	4.8	3.8	5.2	12.0	2.0	3.1	9.5	2.1	5.6	ND
Bel strain M†	7.5	6.5	5.8	16.2	3.4	6.6	10.3	0.5	6.4	2.0	4.8	12.0	1.0	2.6	5.6	1.8	7.2	ND
Reovirus																		
$\lambda 1 + \lambda 2$	12	7.4	7.9	9.4	5.4	6.2	7.8	ND	7.1	3.4	6.0	9.3	4.1	4.2	2.8	1.7	5.3	ND
$\mu 2$	9.5	7.2	8.8	9.9	6.9	6.2	9.6	0.7	7.3	2.4	5.6	7.8	2.9	2.5	5.4	0.7	3.8	2.4
$\sigma 2$	10.7	7.2	8.0	10.7	4.3	8.3	9.5	ND	6.0	2.0	4.0	10.7	3.7	5.2	1.4	1.7	6.6	ND
$\sigma 3$	12.0	4.7	6.6	9.1	5.4	8.2	6.0	0.6	8.5	2.8	3.5	8.5	2.8	3.5	5.0	3.7	5.7	3.2
Adenovirus																		
Hexon	15	7.2	6.9	11	6.1	7.2	7.9	0	5.5	2.1	3.6	7.6	5.9	4.9	4.0	1.1	4.2	ND
Fiber	10	8.8	8.8	5.0	4.4	6.9	5.0	0.6	4.4	1.2	3.8	7.5	2.5	2.5	5.0	0.6	1.2	1.2
Major core protein (mol. wt. 18,000)	6.8	7.3	4.2	4.8	6.7	7.8	20	0	10	0.6	2.4	3.4	0.4	0.4	2.9	0.5	23	ND
Celo hexon	17	8.0	6.2	8.5	6.1	7.5	6.6	0	7.4	1.4	3.6	8.3	4.7	5.1	2.9	1.4	5.2	ND
SV-40 strain 777																		
<i>mol. wt.</i>																		
VP 1 ~ 43,000	10.6	7.6	5.7	11.5	6.5	9.7	6.4	0?	9.2	1.8	4.1	9.1	2.6	3.7	6.5	1.6	3.6	ND
VP 3 ~ 26,000	7.9	4.2	7.1	11.5	5.2	18.2	6.6	0?	6.9	1.9	3.2	8.6	3.1	3.2	5.2	1.4	5.7	ND
VP 4 ~ 16,000	7.5	5.7	7.2	9.8	4.7	13.5	9.6	0?	6.9	2.5	5.0	8.7	2.8	3.2	7.5	0.8	5.8	ND
VP 5 ~ 13,000	7.2	5.3	7.1	8.0	3.6	15.7	10.7	0?	6.8	1.1	4.4	7.5	2.0	3.1	8.9	0.8	8.0	ND
VP 6 ~ 11,000	7.9	5.3	7.1	9.5	4.1	16.2	8.2	0?	7.6	2.0	4.5	8.1	3.2	4.0	6.6	0.8	5.2	ND

* All given as mole-percentages. To obtain approximate residues/mole data each figure has to be multiplied by the protein molecular weight/11,500. ND means not determined.

† Glucosamine 1.1; no galactosamine nor tryptophan detected.

‡ Membrane protein.

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