Comprehensive Virology

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Newly Characterized Vertebrate Viruses

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Foreword

The time seems ripe for a critical compendium of that segment of the biological universe we call viruses. Virology, as a science, having passed only recently through its descriptive phase of naming and numbering, has probably reached that stage at which relatively few new—truly new—viruses will be discovered. Triggered by the intellectual probes and techniques of molecular biology, genetics, biochemical cytology, and high resolution microscopy and spectroscopy, the field has experienced a genuine information explosion.

Few serious attempts have been made to chronicle these events. This comprehensive series, which will comprise some 6000 pages in a total of about 18 volumes, represents a commitment by a large group of active investigators to analyze, digest, and expostulate on the great mass of data relating to viruses, much of which is now amorphous and disjointed, and scattered throughout a wide literature. In this way, we hope to place the entire field in perspective, and to develop an invaluable reference and sourcebook for researchers and students at all levels.

This series is designed as a continuum that can be entered anywhere, but which also provides a logical progression of developing facts and integrated concepts.

Volume 1 contains an alphabetical catalogue of almost all viruses of vertebrates, insects, plants, and protists, describing them in general terms. Volumes 2–4 deal primarily, but not exclusively, with the processes of infection and reproduction of the major groups of viruses in their hosts. Volume 2 deals with the simple RNA viruses of bacteria, plants, and animals; the togaviruses (formerly called arboviruses), which share with these only the feature that the virion's RNA is able to act as messenger RNA in the host cell; and the reoviruses of animals and plants, which all share several structurally singular features, the

most important being the double-strandedness of their multiple RNA molecules.

Volume 3 addresses itself to the reproduction of all DNA-containing viruses of vertebrates, encompassing the smallest and the largest viruses known. The reproduction of the larger and more complex RNA viruses is the subject matter of Volume 4. These viruses share the property of being enclosed in lipoprotein membranes, as do the togaviruses included in Volume 2. They share as a group, along with the reoviruses, the presence of polymerase enzymes in their virions to satisfy the need for their RNA to become transcribed before it can serve messenger functions.

Volumes 5 and 6 represent the first in a series that focuses primarily on the structure and assembly of virus particles. Volume 5 is devoted to general structural principles involving the relationship and specificity of interaction of viral capsid proteins and their nucleic acids, or host nucleic acids. It deals primarily with helical and the simpler isometric viruses, as well as with the relationship of nucleic acid to protein shell in the T-even phages. Volume 6 is concerned with the structure of the picornaviruses, and with the reconstitution of plant and bacterial RNA viruses.

Volumes 7 and 8 deal with the DNA bacteriophages. Volume 7 concludes the series of volumes on the reproduction of viruses (Volumes 2–4 and Volume 7) and deals particularly with the single- and double-stranded virulent bacteriophages.

Volume 8, the first of the series on regulation and genetics of viruses, covers the biological properties of the lysogenic and defective phages, the phage-satellite system P 2–P 4, and in-depth discussion of the regulatory principles governing the development of selected lytic phages.

Volume 9 provides a truly comprehensive analysis of the genetics of all animal viruses that have been studied to date. These chapters cover the principles and methodology of mutant selection, complementation analysis, gene mapping with restriction endonucleases, etc. Volume 10 also deals with animal cells, covering transcriptional and translational regulation of viral gene expression, defective virions, and integration of tumor virus genomes into host chromosomes.

Volume 11 covers the considerable advances in the molecular understanding of new aspects of virology which have been revealed in recent years through the study of plant viruses. It covers particularly the mode of replication and translation of the multicomponent viruses and others that carry or utilize subdivided genomes; the use of proto-

plasts in such studies is authoritatively reviewed, as well as the nature of viroids, the smallest replicatable pathogens. Volume 12 deals with special groups of viruses of protists and invertebrates which show properties that set them apart from the main virus families. These are the lipid-containing phages and the viruses of algae, fungi, and invertebrates.

Volume 13 contains chapters on various topics related to the structure and assembly of viruses, dealing in detail with nucleotide and amino acid sequences, as well as with particle morphology and assembly, and the structure of virus membranes and hybrid viruses. The first complete sequence of a viral RNA is represented as a multicolored foldout.

The present volume contains chapters on special and/or newly characterized vertebrate virus groups: bunya-, arena-, corona-, calici-, and orbiviruses, icosahedral cytoplasmic deoxyriboviruses, fish viruses, and hepatitis viruses.

Several subsequent volumes will deal with virus–host relationships and with methodological aspects of virus research.

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CHAPTER 1

Bunyaviridae

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1. INTRODUCTION

The Bunyaviridae are a relatively newly defined family of arthropod-borne viruses. Of the viruses that have been registered as of 1978 in the published and working *International Catalogue of Arboviruses* (Berge, 1975; Taylor, 1967; see Berge *et al.*, 1970, 1971; Karabatsos, 1978), 95 have been proposed as members of the genus Bunyavirus (Table 1), formerly known as the "Bunyamwera supergroup of viruses" (Calisher *et al.*, 1973; Casals, 1963, 1971; Fenner, 1976*a*,*b*; Murphy *et al.*, 1973; Porterfield *et al.*, 1973/1974, 1975/1976). Other genera of bunyaviruses have not yet been defined, although another 63 registered viruses are considered as possible members of the family. On serological criteria they have not been placed in the Bunyavirus genus (Table 2) (Porterfield *et al.*, 1975/1976). In addition, there are currently

TABLE 1

Proposed Serological Classification of Viruses of Family Bunyaviridae, Genus Bunyavirus

Anopheles A group[a]
- **Anopheles A**[b]
  - **CoAr 3624**[c]
- **Lukuni**
- **ColAn 57389**[c]
- **Tacaiuma (SP Ar 2317**[c]**)**
  - **CoAr 3627**[c] **(CoAr 1071**[c]**)**

Bunyamwera Group
- **Bunyamwera**
  - Germiston
  - Shokwe[c]
  - Batai (Calovo)
  - Ilesha
  - Birao
  - Tensaw
  - Cache Valley (Tlacotalpan)
    - Maguari
  - Northway
  - Santa Rosa
  - Lokern
- Wyeomyia
  - Taiassui[c]
  - Anhembi
  - Sororoca
- Main Drain
- Kairi
- Guaroa

Bwamba group
- **Bwamba**
  - Pongola

C group
- Caraparu
  - Caraparu (BeH 5546[c])
  - Caraparu/Trinidad[c]
  - Ossa
- Apeu
- Madrid
- Marituba
  - Murututu
  - Restan
- Nepuyo
- Gumbo Limbo
- Oriboca
  - Itaqui

California group
- California encephalitis
  - Tahyna (Lumbo[c])
  - Inkoo
  - San Angelo
  - La Crosse (snowshoe hare)
- Melao
  - Serra do Navio
  - Keystone
  - Jamestown Canyon (South River[c], Jerry Slough)
- Trivittatus

Capim group
- Capim
  - Guajara (Gu 71 u 350[c])
- Bushbush
  - BeAn 84381[c]
  - Gu 71 u 344[c]
- Juan Diaz

Capim group (*cont.*)
- Acara
  - Moriche
- BeAn 153564[c]

Guama group
- Guama
  - Moju
  - BeAn 109303[c]
- Mahogany Hammock
- Bimiti
- BeAn 116382[c]
- Catu
- Bertioga

Koongol group
- Koongol
  - Wongal

Mirim group
- Mirim
- Minatitlan

Olifantsvlei group
- Olifantsvlei
  - Bobia[c]
- Botambi

Patois group
- Patois
  - Shark River
- Zegla
  - Pahayokee

Simbu group
- Akabane
  - Yaba-7[c]
- Facey's Paddock[c]
- Shamonda
  - Sango
- Sabo
- Sathuperi
- Shuni
  - Aino (Kaikalur, Samford)
- Simbu
- Thimiri
- Nola
- Peaton[c]
- Manzanilla
  - Ingwavuma
  - Mermet
  - Inini[c]
- Buttonwillow
- Oropouche
  - Utinga[c]

Tete group
- Tete
  - Bahig
  - Matruh
  - Tsuruse
- Batama[c]

Unassigned members
- Gamboa
- Guaratuba
- Jurona
- Kaeng Khoi

[a] **The Anopheles A group was proposed as a group in the genus Bunyavirus (Calisher *et al.*, 1973); the group has not yet been officially accepted in the Bunyavirus genus.**

[b] **Viruses are classified in three steps indicated by degrees of indentation—complex, virus, subtype; viruses in parentheses are varieties.**

[c] **These viruses are not in the published or working *International Catalogue of Arboviruses* (Berge, 1975; Karabatsos, 1978).**

at least 34 viruses which are under study and consideration for candidacy (Tables 1 and 2).

1.1. Characteristics of the Bunyaviridae

The assignments of viruses to the Bunyaviridae family were initially made by serological studies (Casals, 1963). Such assignments were later confirmed by additional serological and morphological criteria (Berge, 1975; Casals, 1971; Murphy and Coleman, 1967; Murphy *et al.*, 1973). These assignments have been substantiated by molecular analyses which indicate that bunyaviruses are categorically different than other arthropod-borne viruses.

The principal characteristics of members of the Bunyavirus genus include the following:

1. The virus particles are spherical (90–100 nm in diameter) and enveloped.
2. The viruses have a single-stranded, three-segment, negative-sense RNA genome of total molecular weight of between 4 and 6×10^6. The viruses are capable of genetic reassortment. The viral RNA segments are designated according to their sizes, large (L), medium (M), and small (S).
3. Three circular, helical, viral nucleocapsids can be isolated from virus preparations. Each is composed of nucleocapsid protein (N) and a single RNA species (L, M, or S). The RNA species have 5′ and 3′ ends but can be extracted from nucleocapsids (or virus particles) as noncovalently closed circles.
4. Two virus-specific glycoproteins (designated G1 and G2) have been identified in all bunyaviruses so far analyzed; they are located on the outer surface of the virus particles.
5. Virus replication occurs in the cytoplasm of infected cells.
6. Virus particles are formed by budding primarily into the Golgi cisternae. Virions are liberated from infected cells by fusion of the intracellular vacuoles with the cellular plasma membrane and virus egestion, or by cell membrane disruption and discharge of the cell contents.

From the limited amount of available information, the same structural and genetic characteristics are attributable to at least some of the other possible members of the Bunyaviridae family.