The Study Group finds it appropriate that viruses which have as their host cyanobacteria (blue-green algae) should be grouped within the well-categorized families of the bacterial viruses. Thus, the term cyanophage is adopted as a synonym for the vernacular name BGA virus (BGAV) originally given to this virus type [1]. Where the nucleic acid and structural components of cyanophages have been characterized, all possess a single piece of double-stranded DNA and the characteristic head-tail morphology of the bacteriophage. This permits their placement in one of the three families of tailed phages incorporated in the taxonomic scheme approved by the International Committee on Taxonomy of Viruses (ICTV) [2]. Names proposed by the Bacterial Virus Subcommittee of ICTV for each of the families have also been applied to the cyanophages. They are: (i) the family Myoviridae, which includes phages with a central tube and a contractile sheath separated from the head by a neck; (ii) the family Styloviridae (alternative proposal: Syphoviridae), which comprises phages with long, noncontractile tails; and (iii) the family Podoviridae, which contains those phages with short tails. A cyanophage type species has been established in each family and is illustrated in figure 1. They should not be confused with the present scheme of coli-phage type species already set up by ICTV. Unlike the bacteriophage, where host ranges generally can be expected to be genus-specific, many cyanophages have been common to more than one genus. However, this poly-generic host range seems to stem from inherent deficiencies in generic assignments in the present system of blue-green algal taxonomy. Cyanophage LPP-1, for example, has as its host spectrum members of the genera Lyngbya, Plectonema and Phormidium, yet in another, more recent, taxonomic scheme all are classified as ecophenes of a single species Schizothrix calcicola [3].

The present classification has been limited to established cyanophages that have been well defined with regard to both morphology and host range. The cyanophage literature, like that of the bacteriophage, has had its share
These correspond to the bacteriophage groups A, B, and C of Bradley [29].

comparative data have been insufficient to determine the uniqueness of some widely published cyanophages. As the Bacterial Virus Subcommittee of ICTV [4] has pointed out, the problem has been exacerbated by the extensive practice of embellishing a new virus isolate as though it were a new virus.

The classification proposed here represents the first comprehensive scheme set forth for viruses of cyanobacteria. Because a complete documentation for each cited cyanophage would result in too extensive a bibliography, no more than two key references have been included for each. However, an in-depth coverage of published reports on cyanophages [5] has been submitted to the ICTV Bacterial Virus Subcommittee and is available on request.

1 Family: Myoviridae.

1.1 Main characteristics: Long, complex tail with a central tube and a contractile sheath separated from the head by a neck.

1.2 Genus: Cyanomyovirus

Derivation of name: Cyan from Greek _kyanos_ ‘blue’ and myo from Greek _mys, myos_ ‘muscle’.

Description: Cyanophages with contractile tails.

1.3 Type species: Cyanophage AS-1 [6, 7].

1.3.1 Distinguishing characteristics:

Host range: Unicellular cyanobacteria of the genera *Anacystis* and *Synecho-coccus*.

Morphology: Isometric head with a diameter of 90 nm and an extended tail of $244 \times 23$ nm contracting to 93 nm; short tail pins are attached to a base plate, 40 nm wide.

Nucleic acid: Mol. wt. = $57 \times 10^6$; G + C content = 52–55%. Proteins: 30 structural proteins.

Physicochemical properties: $S_{20w}=754$; buoyant density in CsCl = 1.49 g/cm$^3$; no magnesium requirement to maintain stability.

Replication: Multiply in nucleoplasm; no major displacement of the photo-synthetic lamellae.

1.4 Other members of genus

1.4.1 Common name: CyanophageN-l [8,9]. Host range: Filamentous cyanobacteria initially assigned to the genus *Nos-toe*, subsequently reidentified as belonging to the genus *Anabaena*.

Morphology: Isometric head with a diameter of 61 nm and a 100 nm long contractile tail with rigid spikes at distal end; flexible fibers (commonly 2) connected to the neck of each particle where tail and head meet. Nucleic acid: Mol. wt. = $(41–45) \times 10^6$; G + C content = 37–41%.

Classification and Nomenclature of Viruses of Cyanobacteria

63
Proteins: 19 structural proteins, with the 37,000 and 14,000 mol.wt. species as main components.
Physicochemical properties: S20W = 539; buoyant density in CsCl = 1.498 g/cm³.
Replication: Multiply in peripheral region of host cell; no major displacement of the photosynthetic lamella.

1.4.2 Common name: Cyanophage A-l(L)[10,11].
Host range: Filamentous cyanobacteria of the genus *Anabaena*. Morphology: Isometric head with a diameter of 60 nm; an extended tail 82.5 nm long and 14 nm wide contracting to 49 nm and a base plate which is 20 nm wide and 14 nm long. Nucleic acid: G + C content = 37.3%.
Physicochemical properties: Requires magnesium to maintain stability. Replication: Multiply in peripheral region of host cell; no major displacement of the photosynthetic lamella.

1.4.3 Common name: Cyanophage A-2 [12,13].
Host range: Filamentous cyanobacteria of the genus *Anabaena*. Morphology: Isometric head with a diameter of 63 nm and a 100 nm long contractile tail.
Nucleic acid: Mol. wt. = 24.3 × 10⁶; G + C content = 50.0–52.4%.
2 Family: Styloviridae.
Main characteristics: Noncontractile tail as long or longer than the diameter of the maximum head dimension.
Genus: Cyanostylovirus.
2.2.1 Derivation of name: *Cyano* from Greek *kyanos* ‘blue’ and *stylo* from Greek *stylos* ‘pillar’.
2.2.2 Description: Cyanophages with long, noncontractile tails.
2.3 Type species: Cyanophage S-l [14].2.3.1 Distinguishing characteristics:
Host range: Unicellular cyanobacteria of the genus *Synechococcus*. Morphology: Isometric head with a diameter of 50 nm and a rigid noncontractile tail 140 nm long. Nucleic acid: Mol.wt. = (23–26) × 10⁶; G + C content = 70–74%. Proteins: 13 structural proteins; major structural proteins = molecular weights of 39,000, 11,000, and 10,000. Physicochemical properties: S20W = 353; buoyant density in CsCl = 1.501 g/cm³.
2.4 Other members of genus
2.4.1 Common name: Cyanophage S-2L [15,16].
Host range: Unicellular cyanobacteria of the genus *Synechococcus*. Morphology: Isometric head with a diameter of 56 nm and a flexible noncontractile tail 120 nm long and 10 nm wide with several short thin fibers at distal end.
Nucleic acid: Mol.wt. = 26 × 10⁶; 2,6-diaminopurine possibly substitutes for adenine; G + C content = 68.7%. Physicochemical properties: No magnesium requirement to maintain stability. Replication: particles at the poles of the cells; no major displacement of the photosynthetic lamella.
2.4.2 Common name: Cyanophage SM-2[17,18].
Host range: Unicellular cyanobacteria of the genera *Synechococcus* and *Microcystis*.
Morphology: Isometric head with a diameter of 50–55 nm and a flexible noncontractile tail 130–140 nm long. Replication: Multiply in nucleoplasm; no major displacement of photosynthetic lamella.
3. Family: Podoviridae.
Main characteristics: Short tail, generally less than one-half the diameter of the maximum head dimension.
Genus: Cyanopodovirus.

Derivation of name: Cyano from Greek kyanos ‘blue’ and podo from Greek pous, podos ‘foot’.
Description: Cyanophages with short tails.
3.3 Type species: Cyanophage LPP-1 [19,20].
3.3.1 Distinguishing characteristics:
Host range: Filamentous cyanobacteria of the genera Lyngbya, Plectonema, and Phormidium.
Morphology: Isometric head with a diameter of 59 nm and a tail 15–20 nm long and 15 nm wide.
Nucleic acid: Mol.wt. = 27 × 10^6; G + C content = 53%.
Proteins: 10 structural proteins; major head proteins = molecular weights of 39,000 and 13,000; major tail protein = molecular weight of 80,000. Physicochemical properties: S20W = 548; buoyant density in CsCl = 1.48 g/cm³; requires magnesium to maintain stability.
Replication: Multiply in peripheral region (virogenic stroma) of host cell; lateral displacement of photosynthetic lamellae first morphological change observed.
3.4 Other members of genus
3.4.1 Common name: Cyanophage LPP-2[21,22],
Host range: Same as cyanophage LPP-1.
Morphology: Isometric head with a diameter of 57 nm; general characteristics indistinguishable from cyanophage LPP-1.
Nucleic acid: Mol.wt. = 28 × 10^6; G + C content = 52%.
Proteins: 14 structural proteins; major structural proteins = molecular weights of 11,000 and 42,000. Physicochemical properties: S20W = 490; buoyant density in CsCl = 1.48 g/cm³; requires magnesium to maintain stability; serologically unrelated to cyanophage LPP-1.
Replication: Multiply in virogenic stroma and/or nucleoplasm.
3.4.2 Common name: Cyanophage SM-1[23,24].
Host range: Unicellular cyanobacteria of the genera Synechoccus and Microcystis.
Morphology: Isometric head with a diameter of 67 nm and a very short collar with a protruding thin appendage which could be a tail. Nucleic acid: Mol.wt. = 56 × 10^6; G + C content = 66%.
Proteins: 12 structural proteins; major structural proteins = molecular weights of 25,000 and 40,000. Physicochemical properties: S20W = 820; buoyant density in CsCl = 1.48 g/cm³; no magnesium requirement to maintain stability.
Replication: Multiply in nucleoplasm; no major displacement of the photo-synthetic lamellae.
Classification and Nomenclature of Viruses of Cyanobacteria
65
3.4.3 Common name: Cyanophage A-4(L)[25,26].
Host range: Filamentous cyanobacteria of the genus Anabaena. Morphology: Isometric head with a diameter of 56 nm and a short tail less than one-fourth the diameter of the head. Physicochemical properties: No magnesium requirement to maintain stability. Replication: Multiply in nucleoplasm.
3.4.4 Common name: Cyanophage AC-1[27,28].
Host range: Unicellular cyanobacteria of the genera Anacystis and Chroococcus.
Morphology: Isometric head with a diameter of 62.5 nm and a tail 25 nm long.
Replication: Multiply in nucleoplasm; no major displacement of the photo-synthetic lamellae.

References


Kozyakov, S. Y.: Cyanophages of series A(L), specific for blue-green algae Anabaena variabilis; in Gromov, Experimental algology, pp. 151–171 (Biological Scientific Research Institute, Leningrad State University 1977).
Leach, J.E.; Lee, K.W.; Benson, R.L.; Martin, E. L.: Ultrastructure of the infection cycle of cyano-
66
Safferman/Cannon/Desjardins/Gromov/Haselkorn/Sherman/Shilo