

## POIKILOTHERM VERTEBRATE CELL LINES AND VIRUSES: A CURRENT LISTING FOR FISHES

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### SUMMARY

A survey of the literature and of work being done in vertebrate cell culture shows that there are currently in existence and available to investigators some 61 cell lines representing 17 families and 36 species of fish. The literature of fish virology shows that at least 17 fish viruses have been isolated and that at least 15 others have been visualized by electron microscopy. A minimum of four major virus groups—rhabdovirus, orthomyxovirus, iridovirus and herpesvirus—are known from fish. Original references, key reviews and sources of cell lines are given.

*Key words:* fish cell lines; fish viruses; poikilotherm vertebrate cell lines; poikilotherm vertebrate viruses.

### INTRODUCTION

A breakthrough was made in virology about 30 years ago when practical *in vitro* replication of animal viruses was realized. This development effected a synergism that resulted in a rapid growth in knowledge of both virology and animal tissue culture. Quite understandably, studies relating to human and veterinary medicine have predominated, and those relating to the lower vertebrates have received much less attention. Nevertheless, there is a significant body of information and a rich resource of research material dealing with poikilotherm vertebrate cell culture and virology. Much of the information has not been published, and many of the published reports are in journals that are fishery-oriented and not in the mainstream of health-oriented or tissue culture literature. Moreover, cell culturists and virologists concerned with man and other homeotherms and those concerned with the cold-blooded vertebrates can each benefit from overviews or reviews of their companion interests.

There are many advantages in, and much to be gained from, lower vertebrate tissue culture and virology. The lower vertebrates collectively constitute nearly three-fourths of the Phylum Vertebrata, and the fish alone account for nearly half of

all the vertebrates (Table 1). Although our perspective may be somewhat biased, we believe the fish could be considered as the most representative of the animals with backbones. The purpose, therefore, in compiling a listing of fish cell lines and viruses is to alert others as to what is available. Such information documents rich resources of potential applications in research, diagnostics and teaching. Additionally, the listing can help others avoid duplication—for example, the initiation of cell lines of species that have already been started. The listing also shows that major groups of animals have largely been neglected by cell culturists and virologists.

A major consideration for using lower vertebrate cell lines or viruses (or both) is the knowledge that can be gained from comparative studies. Because experimental conditions can be controlled, fundamental research could be carried out to determine significant phylogenetic differences and similarities in cellular metabolism. Comparative virological work could similarly be done. Herpesviruses and iridoviruses, for example, are known from fish and all higher classes of vertebrates. There are many opportunities for meaningful study of cell-virus interactions in the five major classes of vertebrates.

TABLE 1  
 PHYLUM VERTEBRATA, ESTIMATED  
 NUMBER OF SPECIES<sup>a</sup>

Class	Number of Species	Percentage
Mammals	4,420	10.6
Birds	8,600	20.6
Reptiles	5,770	13.8
Amphibians	2,300	5.5
Bony fishes	20,000	48.0
Sharks, skates, and rays	550	1.3
Cyclostomes	50	0.1
Total	41,690	99.9

<sup>a</sup> From Altman and Dittmer (1).

Characteristically, the lower vertebrate cell cultures grow through a greater range of temperatures than do homeotherm cultures. Some cells of poikilotherm vertebrates grow at the same temperatures as those of homeotherms but others—notably those of coldwater fish—grow and replicate viruses at temperatures a few degrees above 0° C. Some virus-cell interactions can take place at 0° C and others require temperatures of 15° C or less. Broad temperature manipulation is thus available for the study of lower vertebrate cells and viruses.

One of the greatest advantages offered by lower vertebrate cells or viruses becomes clearly evident in their use in teaching. Many lower vertebrate cell cultures grow at room temperature; optimal incubation is in the range of 20 to 25° C, and so they do not require special incubators. Instead, such cultures can be grown in vessels on bench tops, or in drawers or cabinets.

Furthermore, in contrast to the attention required by many homeotherm cell cultures, there is usually no need to change the medium on lower vertebrate cell cultures between the times they are passaged. This means that poikilotherm cell cultures require less time and attention than do homeotherm cultures. Lower vertebrate cell lines are undemanding and survive for many months without attention at temperatures normally used for their incubation—25° C or lower. One coldwater fish cell line, the RTG-2, has been grown and held at 4° C without a medium change for a total elapsed time of 2 years and it still retained viability. Similar long-term, low temperature storage probably can be endured by cell cultures from other lower vertebrates that inhabit cold environments.

Contrary to prevalent misconceptions, the usual handling of lower vertebrate cell lines is no

different from that of homeotherm cell lines. With only minor adjustments, such as dilution for amphibian cells and supplementation with NaCl for marine reptiles and marine teleost fish, lower vertebrate cells and tissues are routinely grown in Eagle's minimal essential medium, Eagle's basal medium, Medium 199 or Leibovitz Medium L-15. Thus cells of all vertebrates, from mammals to teleost fish, can be grown in media that were originally designed for mammalian cells and tissues.

Freezing lower vertebrate cells is done with the same procedures used for homeotherm cells, and storage may be at -65° C or lower. Optimal storage is in liquid nitrogen, vapor or liquid phase, but even at -80° C, the RTG-2 fish cell line has been recovered after 10 years of storage. Probably other lines are equally tolerant of long-term storage.

Poikilotherm vertebrate viruses known today are largely among the recognized viral groups; they respond to the usual virological manipulations and produce most of the effects that are known for the other animal viruses. There are two major exceptions. First, no fish virus has been shown to hemagglutinate unless it has been concentrated or at least partly purified, or both. Second, the embryonate avian egg is virtually unknown in any fish virus work; the relatively high temperature required for avian egg incubation has been a consideration that has deterred all but the most casual exploratory work.

As might be expected, the host specificity of lower vertebrate viruses is sufficiently different from that of homeotherms to provide a wide margin of safety for beginning students in virology—a feature that further contributes to the suitability of lower vertebrate cells and viruses for use in teaching. Certain of the fish rhabdoviruses, however, are able to replicate—albeit at reduced efficiency—in the mammalian BHK-21 and WI-38 cell lines incubated at reduced temperature Clark and Soriano (2).

At the risk of seeming facetious, we add that there is no evidence to date of a poikilotherm vertebrate cell being contaminated with HeLa cells. Admittedly, a counterpart cell may yet be found that creates problems of adulteration with cell lines from other cold-blooded vertebrates.

#### FISH CELL LINES

In the present survey, we collected information on 61 lines of fish cells representing 17 families

TABLE 2  
A LISTING OF TELEOST FISH CELL LINES, 1979

Family and Scientific Name	Common Name <sup>a</sup>	Tissue <sup>b</sup>	Cell Line Abbreviation	Cell Morphology <sup>c</sup>	Temperature Range/Optimum (° C)	Virus Susceptibility <sup>d</sup>	Original Reference
Anabainidae							
<i>Trichogaster trichopterus</i> <sup>e</sup>	Golden gourami	N-pectuncle	GP	E	15-39/30	?	3
Carangidae							
<i>Caranx mate</i>	Omaka	N-decapitated larvae	?	F	25-27/?	FV-3, IPNV	4,5
Centrarchidae							
<i>Lepomis macrochirus</i>	Bluegill	N-caudal trunk	BF-2	F	15-33/25	IPNV, IPNV, LV, TEV	6-8
<i>Micropterus salmoides</i> <sup>e</sup>	Largemouth bass	N-caudal trunk	LBF-2	F	15-33/25	BGV, LV, TEV	6,7
Cichlidae							
<i>Pterophyllum scalare</i> <sup>e</sup>	Angelfish	N-eyeball	AE	?	15-40/30	?	9
Clariidae							
<i>Clarias batrachus</i>	Walking catfish	N-gill	GIB	E	18-37/25	CCV	10
<i>Clarias batrachus</i>	Walking catfish	N-gonad	GD11	Mixed	18-37/25	CCV	10,11
<i>Clarias batrachus</i>	Walking catfish	N-kidney	K1K	F	18-37/25	CCV	10,11
Clupeidae							
<i>Alosa sapidissima</i> <sup>e</sup>	American shad	N-whole caudal trunk	ASF-1	F	15-20/15	?	12
Cyprinidae							
<i>Cyclopterus lumpus</i> <sup>e</sup>	Lumpfish	N-fin	?	F	18-20/?	LT-1 (= FV-3)	13
<i>Cyclopterus lumpus</i> <sup>e</sup>	Lumpfish	N-testis	?	F	18-20/?	?	14
Cyprinidae							
<i>Carassius auratus</i>	Goldfish	N-fin	CAR	F	20-25/25	GFA, IPNV	8,15
<i>Carassius auratus</i> <sup>e</sup>	Goldfish	N-fin	KGC-1	E	25-32/29	?	16
<i>Carassius auratus</i> <sup>e</sup>	Goldfish	N-fin	KGL-1	E	25-32/29	?	17
<i>Cyprinus carpio</i> <sup>e</sup>	Goldfish	N-fin	KGCP-1	E	25-32/29	?	18
<i>Cyprinus carpio</i> <sup>e</sup>	Carp	A-epithelioma	EPC	E	15-30/?	PFR, SVCV	19,20
<i>Cyprinus carpio</i> <sup>e</sup>	Carp	papiliosum cyprini					
<i>Carassius auratus</i> <sup>e</sup>	Carp/goldfish	N-epithelial cell	KGCF-1	E	25-32/29	?	16
<i>Pimephales promelas</i>	Fathead minnow	N-caudal trunk	FHM	E	0-36/34	ECHO-1, FV-3, IPNV, VSV	8,21
<i>Rhodeus ocellatus</i> <sup>e</sup>	?	N-fin	KGR-1	E	25-32/29	?	16
<i>Tinca tinca</i> <sup>e</sup>	Tench	N-ovary	TG	E	4-32/22-27	?	22
Esocidae							
<i>Esox lucius</i> <sup>e</sup>	Northern pike	N-fin epithelium	NPF	F	4-25/20-25	?	23
<i>Esox lucius</i> <sup>e</sup>	Northern pike	N-gonads	PG	F	15-25/20-22	IPNV, PFR, SVCV, VHSV	24
<i>Esox lucius</i> <sup>e</sup>	Northern pike	A-sarcoma	PS12	F	?/18	?	25
<i>Esox masquinongy</i> <sup>e</sup>	Muskellunge	A-lymphosarcoma	?	?	?	?	26
Ictaluridae							
<i>Ictalurus nebulosus</i>	Brown bullhead	N-caudal trunk	BB	E	4-34/25-30	CCV, IPNV	7,8
<i>Ictalurus punctatus</i> <sup>e</sup>	Channel catfish	N-ovary	CCO	F	20-30/30	CCV	27
Percichthyidae							
<i>Morone saxatilis</i> <sup>e</sup>	Striped bass	N-fry	SBF-1	Mixed	15-20/20	?	12
Percidae							
<i>Stizostedion vitreum</i> <sup>e</sup>	Walleye	N-whole eyed eggs	WF	?	4-25/?	?	23
<i>Stizostedion vitreum</i> <sup>e</sup>	Walleye	N-whole fry	WF-2	F	9-22/15	IPNV	28
<i>Stizostedion vitreum</i> <sup>e</sup>	Walleye	A-walleye dermal sarcoma	WC-1	F	10-30/22	IPNV, LT-1	29



and 36 donor species or hybrids of teleost (bony) fish; there were no cell lines from elasmobranch or more primitive classes of vertebrates (Table 2). Most of the lines are from freshwater or anadromous species; only eight, about 22%, are from strictly marine species. Because the impetus to initiate fish cell lines stems from the needs of virological research and diagnostics, about two-thirds of all the cell lines initiated have come from sport and commercial fish. Moreover, all but four or five of these fish are propagated to at least some extent. The Salmonidae—one of the most important families of sport and commercial fish—were the source of 18 (31%) of the extant fish cell lines. Age of the donor material varies from embryonic through juvenile or subadult to mature. Overwhelmingly, the apparent condition of starting tissue has been normal. However, the EPC line from the carp (*Cyprinus carpio*), the RTH and RTN lines from rainbow trout (*Salmo gairdneri*), the WC-1 line from walleye (*Stizostedion vitreum*) and the PS-12 from the northern pike (*Esox lucius*) were started from neoplastic tissues. Whether the cultured cells are actually the same as those of the original neoplasm is not known; however, the morphology of the cultured cells conforms with that of the original tumors. Sonstegard and Sonstegard (53) described the initiation, from the muskellunge (*Esox masquinongy*), of a lymphosarcoma cell line that grows in static suspension and is assumed to be neoplastic.

Judging from work with cell lines from homeotherms, it is likely that some of the fish cell lines derived from normal tissue have been transformed in culture. However, to our knowledge, demonstration of oncogenicity by inoculation of the donor species has not been reported.

The age of the fish cell lines varies from several months to 19 years for GF cells and 20 years for RTG-2 cells. The number of passages or transfers also varies, from fewer than 10 to more than 200 for certain lineages of the older established cell lines.

The survey includes six widely used cell lines that have been characterized and are designated as Certified Cell Lines (CCL); they are in the repository of the American Type Culture Collection (ATCC): brown bullhead BB (CCL 59); bluegill fry, BF-2 (CCL 91); goldfish, CAR (CCL 71); fathead minnow, FHM (CCL 42); grunt fin, GF (CCL 58); and rainbow trout gonad, RTG-2 (CCL 55). Several additional cell lines have been characterized and their descriptions have been

published, but most lines are neither adequately characterized nor given more than passing mention in reports.

The morphology of fish cell lines is either epithelial or fibroblastic, but nearly two-thirds of the lines are fibroblastic. Also, except for the culture of lymphosarcoma cells of the muskellunge, the fish cell lines were initiated as cultures that used or required a surface for attachment. However, Lidgerding and Schultz (54) recently succeeded in adapting FHM and RTG-2 cells to stirred suspension culture and showed that the FHM cells proliferate better than they do in static culture.

Fish cell line temperature-tolerance ranges from a low of 0° C for cold-water fish material such as that of salmonids to 37° C for some warm-water fish cells such as those of the goldfish. Although it is likely to occur, growth of salmonid or other cold-water fish cells at temperatures below 4° C has not been documented.

Media for growth of fish cells are almost universally unmodified formulations originally intended for homeotherm cell culture; they are Eagle's minimal essential medium, Eagle's basal medium, Medium 199, and Leibovitz Medium L-15. The usual supplement is 10% fetal bovine serum. The muskellunge lymphosarcoma cells that Sonstegard and Sonstegard (53) designate as TC H597 are grown with 20% calf serum.

Knowledge about the susceptibility of fish cell lines to virus is largely confined to viruses from teleosts and an icosahedral DNA agent from amphibians variously known as FV-3, LT-1 or TEV. The FHM cell line in addition to supporting growth of at least six fish viruses, has been found by Solis and Mora (55) to be susceptible to 11 homeotherm vertebrate viruses. It seems likely that, if appropriately tested, the viral susceptibility of other fish cell lines will be found to include agents from homeotherms.

Space limitations restricted the amount of information that could be given in Table 2. Readers interested in characteristics other than those listed are advised to consult the references. We list authors of cell lines whose characterization has been published. The originators of uncharacterized or unpublished lines have generally agreed to provide starter cultures to qualified investigators.

Methods for routine propagation of fish cell lines were described by Wolf and Quimby (56), and systematic management of animal cell lines was detailed by Wolf and Quimby (57) in a recent procedure of the *TCA Manual*.

## THE FISH VIRUSES

Providing that each is a distinct entity (that occurs only in one species), the literature of fish virology presently shows that there are at least 32 viruses; of these, 17 have been isolated in cell culture and the other 15 have been visualized—for

the most part rather convincingly—by transmission electron microscopy (Table 3).

Data given in the tabulation show that fish viruses are not unique but rather an extension of the known homeotherm vertebrate viruses. Some of the viruses have RNA and others have DNA genomes, but, like the viruses of homeotherms,

TABLE 3

## A LISTING OF CHLAMYDIA, RICKETTSIA, AND VIRUSES ISOLATED FROM, OR KNOWN TO OCCUR IN, FISH, 1979

Name of the Agent, or of the Disease it Causes, and Abbreviations	Major Grouping	Present Status	Selected References
<b>DNA viruses</b>			
Channel catfish virus (CCV) (ATCC VR 665)	Herpesvirus	Isolated	58-64
<i>Herpesvirus salmonis</i>	Herpesvirus	Isolated	65-66
Virus of <i>Epithelioma papillosum</i>	Herpesvirus	EM <sup>a</sup>	63,67-69
Turbot herpesvirus	Herpesvirus	EM	70,71
Lymphocystis virus (LV) (ATCC VR 342)	Iridovirus	Isolated	72-81
Piscine erythrocytic necrosis virus (PENV)	Iridovirus	EM	82-87
<b>RNA viruses</b>			
Bluegill virus (BGV) (ATCC VR 604)	Orthomyxovirus <sup>b</sup>	Isolated	88,89
Eel virus 2 (EV-2)	Orthomyxovirus <sup>b</sup>	Isolated	90,91
Eel virus-American (EVA)	Rhabdovirus	Isolated	90,92
Eel virus-European (EVEX)	Rhabdovirus	Isolated	90,92
Egtved virus (viral hemorrhagic septicemia: VHS)	Rhabdovirus	Isolated	93-105
Infectious hematopoietic necrosis virus (IHNV) (ATCC VR 714)	Rhabdovirus	Isolated	93,94,96,102,104-111
Spring viremia of carp (SVC) <i>Rhabdovirus carpio</i>	Rhabdovirus	Isolated	93,94,96,102,112-122
Pike fry rhabdovirus (PFR) = grass carp rhabdovirus	Rhabdovirus	Isolated	94,96,102,114-116,123-130
<b>Agents of provisional or unknown grouping</b>			
Pleuonectid papilloma virus	Ungrouped	EM	131,132
Walleye sarcoma virus	Ungrouped	EM	133,134
Walleye epidermal hyperplasia virus	Ungrouped	EM	133
White sucker virus	Ungrouped	EM	135
Brown bullhead papilloma virus	Ungrouped	EM	136
Atlantic salmon papilloma virus	Ungrouped	EM	137
Golden shiner virus (GSV)	Ungrouped (Reoviruslike)	Isolated	138
Infectious pancreatic necrosis virus (IPNV) (ATCC VR 299)	Ungrouped (Reoviruslike)	Isolated	98,99,104,105,139-148
Esocid lymphosarcoma virus	Ungrouped	EM	149-151
Eel virus 1 (EV-1)	Ungrouped	Isolated	90,91
Eel virus, European (EVE)	Ungrouped (Reoviruslike)	Isolated	90,92
Grunt fin agent (GFA) (ATCC VR 683)	Ungrouped	Isolated	152
Intraerythrocytic virus of rainbow trout	Ungrouped	EM	153
Carp gill necrosis virus	Ungrouped (Iridoviruslike)	Isolated	154
Atlantic salmon fibrosarcoma virus	Ungrouped (Oncoviruslike)	EM	155
Northern pike epidermal proliferation virus	Ungrouped	EM	156
Northern pike sarcoma virus	Ungrouped	EM	157
Epitheliocystis agent (bluegill, striped bass, and white perch)	Chlamydia or Rickettsia	EM	89,158-160

<sup>a</sup> EM = visualized by electron microscopy.

<sup>b</sup> Provisional placement.

fewer fish viruses have DNA than have RNA. Four herpesviruses and two, possibly three, iridoviruses are known from fish, but only two of the first group and one of the second have been isolated. There is, however, no evidence of an adenovirus nor of a poxvirus among fish. When some of the smaller agents are eventually isolated and characterized, representatives of papovavirus may be recognized.

The fish rhabdoviruses are the largest group of those known to have RNA; there are at least five. If the rhabdovirus EVEX proves to be a distinct entity, there will be six in the group. The bluegill virus (BGV) and one eel virus (EV-2) presumptively have been shown to have an RNA genome and are probably orthomyxoviruses. The golden shiner virus (GSV) and infectious pancreatic necrosis virus (IPNV) also have RNA, an icosahedral morphology and a size compatible with reoviruses. However, neither IPNV nor GSV are doubly encapsidated, and at best they can only be described as reoviruslike.

Placement of fish viruses that have only been visualized is at this time subject to speculation, but some generalizations are worth noting. At least eleven agents are associated with fish neoplasms, but no fish virus has been convincingly demonstrated to be oncogenic. That situation will probably change, and one of the most promising candidates for demonstrating oncogenicity is the virus associated with the lymphosarcoma of muskellunge. Another current generalization is that there are no arthropod-borne viruses among fish. Neither are there fish viruses that hemagglutinate without first having been concentrated or subjected to special procedures or conditions.

The temperature range for replication of fish viruses is different from that of homeotherm viruses, but that is to be expected. Viruses of cold-water fish such as salmon and trout are replicated *in vitro* and *in vivo* at temperatures that range from about 2 or 3° C to 12 to 20° C, depending on the agent. Warm-water fish viruses such as channel catfish virus (CCV), spring viremia of carp virus (SVCV), and lymphocystis virus (LV), grow at temperatures of 15 to 30° C.

The disease-producing potential of the fish viruses ranges from acute and virulent (CCV and IPNV) through chronic and virulent (*Herpesvirus salmonis*, Egtved virus) to benign (LV) and "orphan" status (bluegill virus and the grunt fin agent). Among those that produce serious disease [IPNV, SVCV, Egtved virus, infectious hematopoietic necrosis virus (IHNV) and pike fry

rhabdovirus (PFR)] the carrier state is either documented or circumstantially implicated. Infectious pancreatic necrosis virus has been shown to be transmitted vertically and that condition is suspected for *Herpesvirus salmonis*, CCV, IHNV and SVCV.

Six fish viruses are now available from the ATCC: lymphocystis virus (VR 342), infectious pancreatic necrosis virus (VR 299), channel catfish virus (ATCC VR 665), infectious hematopoietic necrosis virus (VR 714), bluegill virus (VR 604) and the grunt fin agent (VR 683). *Herpesvirus salmonis* and other isolated fish viruses are in the process of being accessioned.

The condition known as epitheliocystis disease is infectious. In some freshwater and marine hosts the presumed causal agent has the morphology of a chlamydia, but in other marine species electron microscopy shows a rickettsialike agent. No one has yet succeeded in isolating a rickettsia or a chlamydia from fish.

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