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·综述·

中国水产动物病毒学研究概述

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摘要：本研究简要概述了过去几十年来中国水产养殖动物病毒学的代表性研究成果，主要涉及鱼类病毒、虾类病毒、两栖和爬行动物病毒等。此外，本研究还展望了水产动物病毒学研究的发展趋势，以有助于加深对中国水产养殖动物病毒学研究现状和未来发展的认识。

关键词: 水产动物病毒学；鱼类病毒；虾类病毒；两栖和爬行动物病毒；疾病诊断与防控

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水产养殖业的兴起被认为是百年来全球粮食生产中最深刻的变革之一[1-2]，也是满足当今人类需求最环保的、可持续发展的产业之一[3-4]。然而，几乎各种养殖水产动物都受到由病毒、细菌、寄生虫或其他新生和再生病原微生物感染的威胁[5]。病害流行已成为水产养殖业可持续发展的制约因素[6-8]，尤其是病毒病，发病快、死亡率高，潜伏期长短有异，一旦发病即无有效药物可治。由于病毒病是危害水生动物最普遍和严重的病害，长期以来，一直被作为研究的热点与难点[9-12]。近五十年来，研究者们已围绕水产动物病毒学开展了大量研究。本研究将简要介绍鱼、虾、蛙、鳖等不同水产动物病毒研究的现状及动态，并探讨我国水产动物病毒学研究的发展趋势。

1　水产动物病毒与病毒病

国内已解析的水产动物病毒基因组有数十种，而新分离鉴定的毒株则更多。为查阅方便，下面按水产养殖动物的种类，如鱼类、两栖类、爬行类、虾类、蟹类、贝类的病毒病及其报道的时间先后，简要概述相关研究。

1.1　鱼类病毒

本小节分别就鱼类呼肠孤病毒、鱼类虹彩病毒、鱼类弹状病毒、双节段RNA病毒及疱疹病毒等五类鱼类病毒进行介绍。

鱼类呼肠孤病毒　　我国报道的第一个鱼类病毒就是20世纪70年代末发现的草鱼出血病病毒(grass carp hemorrhage virus, GCHV)[13-14]。借助电镜观察、鱼类细胞培养等技术，对该病毒进行了分离鉴定[15-16]。在1988年出版的英文专著《鱼类病毒与鱼类病毒病》(*Fish Viruses and Fish Viral Diseases*)中引用了上述相关文献[15]，认为中国学者报道的草鱼呼肠孤病毒(grass carp reovirus, GCRV)是引起草鱼(*Ctenopharyngodon idella*)幼鱼急性出血病的一种新病原[17]。为了深入认识该病毒的病原性，并进行有效防控，人们现仍在继续改进草鱼呼肠孤病毒的诊断方法或尝试更有效的攻毒感染方式[18-19]。

水生呼肠孤病毒属(*Aquareovirus*)成员是具

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有11节段(S1–S11)双链RNA的基因组、双层衣壳、直径约75 nm的无囊膜(envelope)正20面体颗粒(ViralZone, Aquareovirus，https://viralzone.expasy.org/605?outline=all_by_species)。至2014年，在国内已分离鉴定的草鱼呼肠孤病毒就超过了30株[20]。经比较分析显示，不同草鱼呼肠孤病毒毒株对细胞的敏感性存在差异，其基因组结构或基因组图谱也不同[21-22]。近些年，不仅解析了新分离到的草鱼呼肠孤病毒毒株的基因组序列[23]，还分别对从淡水鱼、海水鱼中分离鉴定的呼肠孤病毒基因组序列进行了解析和深度比较，结合基因功能的分析，阐明大菱鲆呼肠孤病毒(turbot *Scophthalmus maximus* reovirus, SMReV)所编码融合相关小跨膜蛋白(fusion-associated small transmembrane protein, FAST protein)致宿主细胞病变作用及其分子机理[24]。经对鲈鱼呼肠孤病毒(larger mouth bass *Micropterus salmoides* reovirus, MsReV)基因组测序及7个结构基因级联序列进行多重比对，揭示鱼类呼肠孤病毒基因组结构与其宿主所生存的淡水、海水环境有关[25]。另外，还从养殖斑点叉尾鮰(*Ictalurus punctatus*)中也鉴定了一株呼肠孤病毒[26]。

利用冷冻电镜进行三维重构，解析了草鱼呼肠孤病毒近原子分辨率的完整结构[27]。鉴定了能与草鱼呼肠孤病毒外衣壳蛋白作用的草鱼蛋白，并阐明其相互作用分子机制[28-29]。开展了对草鱼呼肠孤病毒的感染及其宿主细胞的抗病毒免疫应答研究，报道鲫囊胚细胞系在经紫外线灭活处理的草鱼出血病毒GCHV作用后，能产生有活性、呈现抗病毒状态的干扰素(interferon, IFN)[30-31]。干扰素是脊椎动物抗病毒系统的标志物[32]。就实验鱼稀有鮈鲫(*Gobiocypris rarus*)对草鱼呼肠孤病毒感染的反应进行测试，结果显示，草鱼呼肠孤病毒能上调稀有鮈鲫鳃中干扰素相关基因的表达[33]。已查明，草鱼具备维甲酸诱导基因I (retinoic acid inducible-gene I, RIG-I)介导的抗草鱼呼肠孤病毒先天性免疫信号通路[34]。另外，证实草鱼呼肠孤病毒具有免疫逃逸能力，可通过利用病毒编码蛋白削弱或消除宿主干扰素应答[35-36]。草鱼呼肠孤病毒GCReV-109 基因S11节段所编码的VP33蛋白具有良好免疫原性，其抗体能抑制草鱼呼肠孤病毒的感染[37]，现已研发出草鱼呼肠孤病毒相应的核酸疫苗[38]。测试分析草鱼对不同呼肠孤病毒株反应的转录组数据，可分为温和型或强烈型，不同病毒株的毒力与其潜伏期长短、宿主免疫应答方式有关[39]。可见，草鱼呼肠孤病毒无疑是我国研究最早、也最为详细的水产动物病毒之一。

鱼类虹彩病毒　1996年，我国学者就从发病牛蛙[*Rana*(*Lithobates*)*catesbeiana*]中分离鉴定属于虹彩病毒科(*Iridoviri*dae)成员的沼泽绿牛蛙蛙病毒(*Rana Grylio* virus, RGV)[40]，这也是国内水产动物虹彩病毒研究的最早报道。随后，从包括鱼类、两栖类和爬行类在内的多种水产动物中都分离到虹彩病毒[41-42]。如鱼类虹彩病毒有：鳜鱼传染性脾肾坏死病毒(infectious spleen and kidney necrosis virus, ISKNV)[43]、大黄鱼虹彩病毒(large yellow croaker iridovirus, LYCIV)[44]、大菱鲆红体病虹彩病毒(turbot reddish body iridovirus, TRBIV)[45]等。

为了解牙鲆淋巴囊肿病毒中国株(lymphocystis disease virus isolated from China, LCDV-C)的感染性，经对13种鱼类细胞感染性测试，用LCDV-C攻毒后，在草鱼细胞系(grass carp ovary，GCO)中观察到明显补丁样病变[46]。随后在2004年，报道了淋巴囊肿病毒中国株LCDV-C的全基因组序列[47]，该基因组一直保持其脊椎动物虹彩病毒最大基因组的记录，直至2016年从金头鲷(*Sparus auratus*)中分离的淋巴囊肿病毒(lymphocystis disease virus-*Sparus auratus*, LCDV-Sa)株(KX643370)为止。对来自10个不同虹彩病毒株或物种的羟类固醇脱氢酶蛋白序列进行了比较和分析[48]，阐明LCDV-C与其他虹彩病毒分子特征[49]，研究并阐明LCDV-C所编码的合成与修复DNA酶——胸苷酸合成酶(thymidylate synthase, TS)能诱导鱼类细胞转化，提供了LCDV-C的TS对宿主细胞有转化作用及能诱导宿主鱼产生囊肿的直接证据[50]。另有对鱼类虹彩病毒入侵过程及感染机制研究的报道，阐明鳜鱼传染性脾肾坏死病毒(ISKNV)是依赖发动蛋白(dynamin)和细胞微管骨架，通过胞膜窖-小窝体-内质网轨迹运动而进入宿主细胞[51]。还借助病毒单粒子示踪技术，阐释新加坡石斑鱼虹彩病毒(Singapore grouper iridovirus, SGIV)能由网格蛋白介导、pH依赖的胞吞途径，通过巨胞饮途径进入宿主细胞，而不是经小窝蛋白介导的胞吞途径[52]。经对石斑鱼抗虹彩病毒作用分子机理研究，认为石斑鱼的关键磷酸激酶(TBK1)可通过调节干扰素免疫和炎

症反应，产生抗病毒活性[53]。

虹彩病毒具有大小为150~280 kb的双链DNA基因组，有囊膜、直径大小为150~200 nm的球形颗粒[54]。除了从淡水、海水患病养殖鱼类中检测和分离到虹彩病毒外，也从两栖类、爬行类等养殖的低等水产动物、甚至无脊椎动物中检测分离到虹彩病毒。本研究将在后续的“两栖与爬行动物病毒”章节中，还会涉及虹彩病毒的内容。

鱼类弹状病毒　20世纪90年代，养殖鳜(*Siniperca chuatsi*)突发疾病并大批死亡。在从采集的患病鳜组织中，电镜观察到弹状病毒(mandarin fish *Siniperca chuatsi* rhabdovirus, SCRV)、球形病毒(*Siniperca chuatsi* spherical virus, SCSV)及杆状病毒(*Siniperca chuatsi* baculovirus, SCBV)[55]，由此开始对鱼类弹状病毒研究。从患致死性出血综合征的胭脂鱼(*Myxocyprinus asiaticus*)中鉴定了能产生包涵体、两端都为尖头的胭脂鱼弹状病毒(Chinese sucker rhabdovirus, CSRV)[56-58]。从海水养殖鱼类中，鉴定了大菱鲆弹状病毒(turbot *Scophthalmus maximus* rhabdovirus, SMRV)和牙鲆弹状病毒(flounder *Paralichthys olivaceus* rhabdovirus, PORV)[59-61]。测定了这些鱼类弹状病毒基因组序列[62-63]，并经分析表明，鳜鱼弹状病毒SCRV和大菱鲆弹状病毒SMRV含5种主要结构蛋白，依次是核蛋白(nucleoprotein, N)、磷蛋白(phosphoprotein, P)、基质蛋白(matrix protein, M)、糖蛋白(glycoprotein, G)和RNA聚合酶(RNA polymerase，L)，属于水疱病毒属(*Vesiculovirus*)。而牙鲆弹状病毒属于诺拉弹状病毒属(*Novirhabdovirus*)，在基因组的G和L基因之间增加了非毒粒蛋白(non-virion protein，NV)基因, 使之基因组结构及编码蛋白的顺序为3’-N-P-M-G-NV-L-5’[64]。制备了不同鱼类弹状病毒的单克隆抗体[65-66]，并对鱼类弹状病毒与宿主细胞的相互作用及鱼抗病毒免疫等进行了研究，证实大菱鲆弹状病毒SMRV可诱导宿主细胞凋亡[67]，当受到弹状病毒刺激后，从鱼皮肤组织中也能检测到抗体[68]。由半胱天冬酶介导的鳜鱼弹状病毒SCRV N蛋白裂解，能显著降低感染子代病毒滴度[69-70]。比较了分别用弹状病毒糖蛋白G基因与核蛋白N基因疫苗注射的鳜所产生的抗病毒免疫效果，显示含鳜鱼弹状病SCRV糖蛋白G基因比含核蛋白N基因的核酸疫苗有更强的抗弹状病毒免疫作用[71]。

从患病鳢科鱼组织中，分离鉴定不同的弹状病毒。如杂交鳢弹状病毒(hybrid snakehead rhabdovirus-C1207，HSHRV-C1207)[72-74]、乌鳢水泡病毒(snakehead fish vesiculovirus, SHVV)和斑鳢弹状病毒(*Channa maculata* rhabdovirus, CHRV)等。对乌鳢水泡病毒SHVV与宿主的相互作用及致病机理也进行研究[75-76]，结果表明乌鳢水泡病毒能通过调节宿主细胞微小RNA分子miR-214而减少干扰素IFN-α的表达，从而逃避宿主先天性免疫，有利于子代病毒复制[77]。

鲤春病毒血症病毒(spring viremia of carp virus, SVCV)的P蛋白可作为宿主细胞关键磷酸激酶TBK1的诱饵，削弱干扰素调节转录因子3 (interferon regulatory transcription factor 3, IRF3)的磷酸化作用，从而抑制宿主干扰素表达，以助病毒免疫逃避[78]。已开展虹鳟(*Oncorhynchus mykiss*)抗传染性造血器官坏死病病毒(infectious hematopoietic necrosis virus, IHNV)的分子免疫学、抗病毒动力学及非编码小分子RNA (miRNAs)差异表达对病毒复制影响的研究，阐明胞内干扰素(intracellular IFN, iIFN)能诱导鱼体快速呈现抗病毒状态，还检测到差异表达的非编码小分子miRNAs能参与虹鳟抗传染性造血器官坏死病毒IHNV的免疫[79-80]。经对弹状病毒刺激的硬骨鱼抗原递呈系统进行分析，并对鲤春病毒血症病毒(SVCV)和草鱼呼肠孤病毒(grass carp hemorrhagic virus, GCHV)刺激宿主抗原递呈系统进行比较，阐释鱼类主要组织相容性复合体(major histocompatibility complex，MHC)的结构与作用[81]。

弹状病毒科成员(*Rhabdoviridae*)是基因组为单一负链RNA、有囊膜、呈子弹状或杆状、直径大小约为75 nm×180 nm颗粒的一大类病毒[82]。在2018年世界动物卫生组织须申报鱼类传染病名录中(2018年OIE-listed diseases, http://www.oie.int/en/animal-health-in-the-world/oie-listed-diseases-2018/)，列出3种鱼类弹状病毒, 包括传染性造血器官坏死病病毒(infectious hemntopoietic necrosis virus, IHNV)、鲤春病毒血症病毒(SVCV)和病毒性出血败血症病毒(viral haemorrhagic septicaemia virus, VHSV)。国内对这3种病毒开展了检测、感染性、致病性、分离及基因型分析等研究[83-89]。

双节段RNA病毒　2008年从患病牙鲆(*Paralichthys olivaceus*)中分离鉴定到一株双节段RNA病毒(*Paralichthys olivaceus*, POBV)，并已进行其基因组测序。该病毒基因组中节段A和节段

B的大小各是3 091 bp和2 780 bp，其中节段A编码PV2-VP4-VP3 和非结构蛋白VP5基因；而节段B仅编码VP1基因[90]。这是我国第一例非鲑鱼宿主来源的双节段RNA病毒完整基因组序列的相关报道。2017年报道了从虹鳟中分离的一株传染性胰腺坏死病毒基因组测序结果，其节段A和节段B的大小分别是3 099 bp和2 789 bp。经与已知虹鳟传染性胰腺坏死病毒(infectious pancreatic necrosis virus，IPNV)代表株 ChRtm213及日本株A9的基因组序列比对，显示有不同程度的变异[91]。有对虹鳟传染性胰腺坏死病毒IPNV的衣壳蛋白进行了克隆表达、单抗制备及检测的相关报道[92]。

双RNA病毒科(*Birnaviridae*)的成员基因组为双节段双链RNA，病毒为无囊膜、直径约 60 nm的二十面体球形颗粒[93]。水产动物双RNA病毒的代表株是能引起鲑科鱼类高致死率、传染性急性病的传染性胰脏坏死病毒IPNV。我国已有关于传染性胰腺坏死病病毒IPNV研究的报道主要集中在对该病毒的检测与诊断方面[94-96]。

疱疹病毒　已对鱼类疱疹病毒开展了细胞培养及不同毒株的分离鉴定[97-100]、组织病理[101]、分子及免疫诊断[102-103]、功能基因分析[104]等研究。

鱼类疱疹病毒被列入2016年由农业部渔业渔政管理局和全国水产技术推广总站编制发布的中国“国家水生动物疫病监测”名录。我们从自然发病、有典型鲫鳃出血病症状的鱼组织中，分离鉴定了一株鲫疱疹病毒(*Crucian carp* herpesvirus, CaHV)。组织病理及超微观察显示鲫的鳃和头肾是CaHV侵染和复制的主要靶器官，CaHV在鳃细胞中以出“芽”或通过细胞裂解方式群体释放。由于子代CaHV的这种释放方式相比通常以单颗粒出芽释放的病毒释放效率更高，对相邻细胞与整个组织的破坏力也更强，这就使鳃组织易发生急剧病变，鳃软骨组织溶融消失，部分鳃丝断裂、缺损或严重变形，直至整个鳃组织坏死和崩解[105]。虽同为鲤疱疹病毒属成员，但经与已知鲤疱疹病毒属(*Cyprinivirus*)其他成员，如鲤疱疹病毒(cyprinid herpesvirus，CyHV)不同株型(如：CyHV-1、CyHV-2、SY-C1和CyHV-3等)的基因组架构进行比较，虽然 CaHV与鱼蛙疱疹病毒科成员都含12个核心基因，也含共同保守基因或同源序列，但在基因组大小、基因组两端有无直接重复序列等方面却有显著差异[106-107]，显示鱼蛙疱疹病毒科(*Alloherpesviridae*)成员存在遗传多样性。对鱼类疱疹病毒的功能基因也开展了研究，鲫疱疹病毒 CaHV ORF31R (CaHV-31R)是能编码一个含跨膜结构域(248–270 aa)和RNase E/G 家族蛋白的典型结构域(40–182 aa)的蛋白质，而该蛋白质能与2种有单层膜结构的细胞器——内质网和高尔基体共定位[108]。证明CyHV-2非结构蛋白 ORF4 可参与病毒复制，因此可将其作为病毒感染周期中的指示蛋白之一[109]。此外，还从患病欧洲鳗鲡(*Anguilla anguilla*)中分离鉴定了疱疹病毒,认为疱疹病毒可能与鳗鲡“脱粘败血病”有关[110]。构建了锦鲤疱疹病毒(koi herpesvirus, KHV) ORF81蛋白和鲤病毒性春季病毒血症(SVCV) G蛋白重组乳酸杆菌疫苗，并用其诱导鲤科鱼类对KHV和SVCV感染产生保护性免疫作用[111]。

鲤疱疹病毒属(*Cyprinivirus*)、鮰疱疹病毒属(*Ictalurivirus*)、鲑疱疹病毒属(*Salmonivirus*)和蛙疱疹病毒属(*Batrachovirus*)都是鱼蛙疱疹病毒科(*Alloherpesviridae*)成员，该科于2005年创立，归于疱疹病毒目(*Herpesvirales*)。据国际病毒分类委员会(10th ICTV)分类报告，它们是以鱼和蛙等水生动物为宿主的疱疹病毒病原，基因组为双链DNA，病毒颗粒直径约150~200 nm，核衣壳T=16对称，外有被膜(tegument)和囊膜的球形颗粒。该属病毒对鱼类有高致病性、强传染性和呈全球分布等特点[112]。不同疱疹病毒毒株可引起宿主鱼出现不同病症。一般认为鲤疱疹病毒1型(cyprinid herpesvirus-1, CyHV-1)，可诱发锦鲤体表痘疮。鲤疱疹病毒2型(cyprinid herpesvirus-2, CyHV-2)可引起鲤等造血器官坏死及鱼鳃贫血。而鲤疱疹病毒3型(cyprinid herpesvirus-3, CyHV-3)，也称为锦鲤疱疹病毒(koi herpesvirus, KHV)，这类病毒则可引起锦鲤鳃溃疡[113]。疱疹病毒能感染生长在不同阶段的鱼，发病后的鱼群死亡率最高可达100% [114]。

1.2　两栖与爬行动物病毒

包括蛙病毒属(*Ranavirus*)成员在内的的虹彩病毒科 (*Iridoviridae*)成员，由于其不仅感染蛙[115]，还能跨种传播[116-118]。蛙病毒(Ranaviruses)能感染养殖和野生的各种低等脊椎动物，如引起无尾目的牛蛙、有尾目的大鲵(*Andrias davidianus*)、龟鳖目的中华鳖(*Pelodiscus sinensis*)等两栖爬行动物高致死率而受到关注。

两栖动物病毒 无尾两栖动物(蛙类)虹彩病毒：在1996年首次报道了沼泽绿牛蛙蛙病毒(*Rana grylio* virus, RGV)之后，测定了RGV基因组序列[119]，可编码106个ORFs，其中包括虹彩病毒家族26个核心基因。点阵分析显示RGV的基因组序列排列顺序仅与3个已测序的虹彩病毒共线性。2002年报道了虎纹蛙病毒(tiger frog virus, TFV)及其基因组结构[120]。在鉴定蛙病毒RGV一个新囊膜蛋白的基础上[121]，构建了重组蛙病毒并建立双荧光可控基因表达技术，运用于虹彩病毒基因功能研究[122-123]，以及蛙病毒与宿主相互作用的研究[124]。宿主细胞内的线粒体片段化，膜电势升高，揭示RGV感染引起细胞凋亡是由线粒体介导的[125]。蛙病毒RGV的囊膜蛋白53R可被miRNA 干扰，使病毒复制受到抑制[126]。从细胞病变显微形态、病毒滴度、细胞病变与不同感染时间的相关性等不同侧面，比较了3种水生动物细胞系对不同蛙病毒株的敏感性，表明大鲵胸腺细胞系(giant salamander spleen cell, GSTC)对2种蛙病毒都更敏感[127]。近期，已完成对沼泽绿牛蛙蛙病毒(RGV)和大鲵蛙病毒(*Andrias davidianus* ranavirus, ADRV)感染大鲵的15个转录组分析，经对128 533个可编码蛋白基因比较，阐明蛙病毒(RGV)在感染大鲵早期，有较强的病毒基因表达和较弱的宿主转录组应答反应能力，而大鲵蛙病毒(ADRV)在感染自然宿主早期，病毒基因表达较弱，但所引起的宿主转录组应答却较强[128]，这为深入分析蛙病毒跨种感染中与宿主的相互作用提供了新的数据和视角。

2015年，由 24位美、德、澳、中专家合作完成、出版了国际上首部蛙病毒英文专著*Ranaviruses: lethal pathogens of ectothermic vertebrates*[129]，其中2位是中国专家。

有尾两栖动物(大鲵)虹彩病毒：自2010年始，四川农业大学报道了对大鲵蛙病毒(Chinese giant salamander virus, CGSV)电镜观察及PCR检测的结果[130-131]，西北农林大学[132]、北京动植物检疫研究所和中国水科院长江所等单位分别报道了大鲵虹彩病毒(giant salamander iridovirus, GSIV)和(*Andrias davidianus* iridovirus, ADIV)的特性[133-134]、组织病理等[135]。

2013年，由中国科学院水生生物研究所报道了大鲵蛙病毒(ADRV)的全基因组序列，并开展了其他相关研究。与已知的两栖类蛙病毒RGV全基因组进行了比对和进化分析，绘制出大鲵与两栖类蛙病毒亚群基因组特征及架构变化图[136]。对正常大鲵和感染病毒大鲵的血清与黏液蛋白图谱进行了比较，证实了经病毒感染后大鲵血清和黏液蛋白组分会出现变化[137]。开展对大鲵蛙病毒基因功能的研究[138]，证实大鲵蛙病毒核心基因所编码的蛋白ADRV-96L具有腺苷三磷酸酶活性及促细胞增殖和生长的作用[139]。在新建大鲵胸腺细胞系(GSTC), 大鲵脾细胞系(GSSC)和大鲵肾细胞系(giant salamander kidney cell line, GSKC)3株细胞系的基础上，分别测试了这些细胞系对野生型及重组型大鲵蛙病毒(ADRV)的敏感性[140]。2014年由不同单位测定和报道了大鲵虹彩病毒毒株(ADIV 或ADRV-2；Chinese giant salamander iridovirus，CGSIV-HN1104，以及GSIV)的基因组序列[141]。

龟鳖病毒 我国龟鳖病毒病原的研究始于1996年，中国科学院水生生物研究所报道了中华鳖病毒(*Trionyx sinesis* virus, TSV)的分离、超微观察、结构多肽分析及对不同细胞感染性测定等研究[142]。观察到TSV宿主细胞会出现染色质高度凝集和边缘化、核碎裂并形成“凋亡小体”等凋亡性病变，同时也出现核膜崩解、线粒体膜膨大、胞膜破损、胞质液泡化等坏死性细胞超微病变[143]，制备中华鳖病毒抗体，建立TSV的血清学检测方法[144]。中山大学和厦门大学也进行相关研究[145]。2009年由中国科学院南海海洋研究所和遗传发育所、深圳动植物检疫局等合作报道了中华鳖虹彩病毒(soft-shelled turtle iridovirus, STIV)全基因组的序列 [146]。另通过中和试验与酶联免疫试验对龟疱疹病毒(*Testudo* herpesvirus)进行检测，检出阳性率分别为6%和11%[147]。最近由南京师大经对数十种鱼类、两栖和爬行动物基因组进行系统发育分析，认为内源性逆转录病毒(endogenous retroviruses, EVV)在有颌脊椎动物中普遍存在的现象[148]。

1.3 虾类病毒病

可检索到我国早期有关对虾病毒病的研究报道是在1991年，由中国科学院武汉病毒研究所借助电镜，从患病中国对虾组织中观察到一种球形病毒[149]。1995年，对虾病毒病研究的相关报道数量大增[150-155]，有涉及对虾病毒形态、对虾抗病力、组织病理等的报道。

海水虾线头病毒　研究最为详细的海水虾病毒是对虾白斑综合征病毒(white spot syndrome virus, WSSV)。起初，由于不同学者研究方法及侧重点不同，该病毒的名称不同，被称为白斑杆状病毒(white spot baculovirus, WSBV)、对虾白斑综合病(white spot syndrome virus, WSSV)、对虾杆状DNA病毒(penaeid rod-shaped DNA virus, PRDV)、中国对虾杆状病毒病(*Penaeus chinensis* baculovirus, PCBV)等。通常认为，对虾白斑综合征病毒WSSV为含有囊膜、无包涵体的杆状双链DNA病毒，呈椭圆形，囊膜内主要由杆状的核衣壳和核衣壳内致密的髓核组成。属于线头病毒科(*Nimaviridae*)白斑病毒属(*Whispovirus*)中唯一成员。WSSV 的基因组大小约为300 kb，预测编码约180 种蛋白[156]。

2001年报道从中国大陆分离到对虾白斑杆状病毒(white spot bacilliform virus, WSBV)基因组的全序列(AF332093)[157]。结合cDNA 芯片与抑制差减杂交(suppression subtractive hybridization, SSH)技术，以克氏原螯虾(*Procambarus clarkii*)作为对虾白斑综合征病毒WSSV的增殖模型，测试WSSV病毒表达基因和螯虾免疫相关基因，显示感染后对虾体内的蛋白酶抑制物表达水平会上升[158]，并查明病毒基因在虾组织中的分布及对WSSV复制的作用[159]。证实中国对虾四跨膜蛋白超家族成员Tetraspanins 可能介导WSSV的感染[160]。经高通量测序和转录组分析获取对虾一批重要免疫相关基因和蛋白质[161]。从免疫识别、体液免疫、细胞免疫和免疫稳态维持等方面，阐述对虾抵御病原的先天性免疫调控体系框架及对虾白斑综合征病毒(WSSV)的致病性[162]。开展了对虾病毒基因克隆与分子诊断、病毒免疫、病毒基因功能等研究[163-166]。对来自不同地区WSSV的特定基因序列进行分析比较，显示WSSV序列中的缺失、重复单元数目，以及单核苷酸多态性(single nucleotide polymorphisms, SNPs)差异显著[167]，涉及在对虾抗病毒WSSV免疫反应中，miRNA与siRNA的鉴定、miRNA调控细胞吞噬及细胞凋亡机制等内容[168-170]。

淡水虾病毒　已证实淡水养殖的克氏原螯虾俗称小龙虾，能被对虾白斑综合征病毒(WSSV)侵染[171-172]。对人工感染克氏原螯虾血细胞和肝胰腺的转录组测试分析，获得一批与克氏原螯虾先天免疫系统相关的基因[173]。对克氏原螯虾组织切片进行观察，结果也显示感染虾的肝胰腺、肠、肌肉、鳃组织出现不同程度病变[174]。

已从自然发病的克氏原螯虾的组织中鉴定了克氏原螯虾病毒(*Procambarus clarkii* virus, PCV)。完整的PCV病毒颗粒两端呈钝圆、有尾附器和囊膜；核衣壳有垂直于纵轴的约14个节(图 1)，显示PCV有线头病毒科成员的超微形态特征。超薄切片电镜观察显示，在自然感染的小龙虾肝胰腺组织、肠和鳃细胞中分布大量的病毒颗粒。并已测定了PCV全基因组序列(MH663976)，正在分析中。

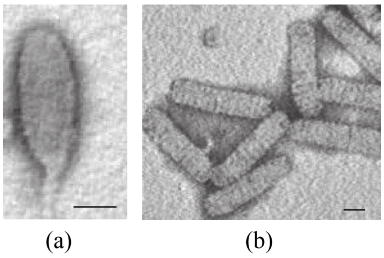

图 1　负染的克氏原螯虾病毒电镜图

(a) 完整病毒颗粒；(b) 病毒核衣壳. 标尺=100 nm (李涛和张奇亚提供)

Fig. 1　Electron micrograph of negatively stained PCV

(a) the intact virion particle; (b) virus nucleocapsid particles. Bar=100 nm. (provided by Li T & Zhang QY)

另外，从患病的红螯光壳螯虾(*Cherax quadricarinatus*)的组织中检出了红螯光壳螯虾虹彩病毒(*Cherax quadricarinatus* iridovirus, CQIV)。经人工感染实验，证实红螯光壳螯虾、克氏原螯虾和凡纳滨对虾(*Litopenaeus vannamei*)对红螯光壳螯虾虹彩病毒(CQIV)敏感[175]。

1.4　蟹及贝类病毒

从1987年在患蚌瘟病的三角帆蚌(*Hyriopsis cumingii*)组织中分离到嵌砂样病毒开始，我国开展了贝类病毒研究[176]。观察到形态多样、具有囊膜突起、内嵌有砂样颗粒及分节段单链RNA组成的三角帆蚌瘟病病毒(*Hyriopsis cumingii* plague virus，HcPV)[177]。研究表明，急性病毒性坏死性病毒(acute viral necrobiotic virus, AVNV)感染可使栉孔扇贝(*Chlamys farreri*)外套膜、鳃、胃、肾等器官出现严重病变，为该病毒是导致栉孔扇贝大量死亡的病毒病原提供了直接证据[178-179]。利用耗氧率、氨氮排泄率、超氧化物

歧化酶等基因表达，及以血浆超氧化物歧化酶活性和碱性磷酸酶活性为指标，对栉孔扇贝对急性病毒性坏死性病毒(AVNV)感染应答进行评估，结果显示，病毒感染能引起宿主扇贝的多种生理和免疫反应，同时水温升高与病毒感染栉孔扇贝引起的死亡率相关[180]。

自20世纪90年代末以来，鉴定了蟹病毒，包括蟹的小核糖核酸病毒、疱疹病毒、呼肠孤病毒等[181-182]。测定了锯缘青蟹(*scylla serrata*)双顺反子病毒(mud crab dicistrovirus, MCDV)的基因组，显示其为单分子线性正义ssRNA[183]

2 小结与展望

水产养殖动物正面临新发和再发病毒病增多、流行区域广、传播速度快、死亡率高、危害大等严峻挑战。虽自从德、俄、加等国学者提出鱼类淋巴囊肿和鱼痘是由病毒病原引起、确认在德国发生的虹鳟肾和肝坏死病是病毒性败血症 (viral hemorrhagic septicemia, VHS)[184-185] 之后40年，20世纪70年代后期，中国水产病毒学研究才开启并迅速崛起。对包括不同淡海水鱼类病毒、虾蟹贝等无脊椎水产动物病毒、鳖蛙等两栖爬行动物病毒都进行了研究和报道。不仅将有关科研成果撰写汇编成论著与教科书[186-192]，介绍常见水产动物疾病的病原、流行情况、病症、病理、诊断及防控方法，涉及水产动物病毒的形态与结构、病毒的分类、病毒的增殖及病毒致病机理等方面，拓展了水产病毒学知识，也在相关专业期刊中留下中国水产病毒学研究的历史印记[193-200]。

近年，借助各种新技术新方法，对水产动物病毒研究也更加深入。如抗病鱼类品种分子模块筛选[201]、量子点对草鱼呼肠孤病毒入侵单粒示踪[202]，利用基因敲除或RNA干扰技术，研究水产无脊椎动物的抗病毒免疫机制[203-204]，甚至还从更大尺度上探讨了包括水产动物病毒在内的各种水生病毒的多样性、进化贡献及生态作用[205]，使人们能以更开阔的视野探寻水产动物病毒学研究的发展趋势。由此预测：① 基于对病原本质特征的认识，可以研发高效、精准、实用的水产动物病毒病检测诊断技术方法，构建预警预报体系；② 由不当用药治疗向疾病预防为主的方向转变，防患于未然；③ 强化水产动物抗病毒免疫机制研究，加速研发安全高效的免疫综合防控新技术，包括疫苗免疫与生态防控并举；④ 提升公众参与意识，并采纳高新技术，消除环境中有害因素，阻断、避免或减少病毒病的传播；⑤ 测评养殖水产动物健康阈值(control threshold)及遗传特性，筛选和运用抗病分子标记，从源头做起，构建智能生态健康水产养殖体系，加速水产养殖方式的变革[206]。预期这些水产动物抗病毒病健康养殖的路径，将会成为中国水产动物病毒学发展的必然趋势。在已初步形成富有特色的中国水产病毒病研究主题、水产病毒病诊断预警与综合防控体系，讲述中国水产养殖成功精彩故事[207]的基础上，研究者们正积极致力于抗病良种选育，注重过程预警预报与病害控制，坚持健康养殖及保水渔业研究，以期为中国乃至世界水产养殖的健康发展奠定基础。

最后，在此感谢读者、编辑、审稿专家，以及几十年来为推动我国水产动物病毒学发展付出辛勤汗水和努力劳动的人们。但限于文稿篇幅与作者的视野，难免有遗漏或差错，敬请见谅与斧正。

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A brief review of aquatic animal virology researches in China

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Abstract: This review briefly introduced representative research results on the aquatic animal virology in China during the past several decades, including fish viruses, shrimp viruses, amphibian and reptile viruses and so on. Moreover, current trends in development of aquatic animal virology were further discussed. It can help to improve comprehensive understanding of the current state and development of the aquatic animal virology studies.

Key words: aquatic animal virology; fish viruses; shrimp viruses; amphibian and reptile viruses; disease diagnosis and prevention

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