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Review

Animals as Reservoir for Human Norovirus

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Abstract: Norovirus is the most common cause of non-bacterial gastroenteritis and is a burden worldwide. The increasing norovirus diversity is currently categorized into at least 10 genogroups which are further classified into more than 40 genotypes. In addition to humans, norovirus can infect a broad range of hosts including livestock, pets, and wild animals, e.g., marine mammals and bats. Little is known about norovirus infections in most non-human hosts, but the close genetic relatedness between some animal and human noroviruses coupled with lack of understanding where newly appearing human norovirus genotypes and variants are emerging from has led to the hypothesis that norovirus may not be host restricted and might be able to jump the species barrier. We have systematically reviewed the literature to describe the diversity, prevalence, and geographic distribution of noroviruses found in animals, and the pathology associated with infection. We further discuss the evidence that exists for or against interspecies transmission including surveillance data and data from in vitro and in vivo experiments.

Keywords: *Caliciviridae*; Norwalk; norovirus; host range; animal reservoir; pathogenesis; zoonosis; reverse zoonosis

1. Introduction

The majority of emerging infectious diseases that affect humans originate from animal reservoirs, predominantly wild life, including bats, rodents and birds. Norovirus is one of five genera of the family *Caliciviridae* and the most common non-bacterial cause of foodborne gastroenteritis worldwide. Noroviruses are currently categorized into at least seven genogroups (GI–GVII) that are further divided into more than 40 genotypes [1]. The virus contains three open reading frames (ORFs), ORF1 encoding the polyprotein that includes the viral polymerase, and ORF2 and ORF3 encoding the major- and minor capsid protein (VP1, VP2), respectively [2]. Recombination between ORF1 and ORF2 frequently occurs and therefore a dual nomenclature describing both the polymerase and capsid genotype is used [3–5]. Viruses from genogroups GI, GII and GIV are known to infect humans. Animal noroviruses including viruses found in pigs, dogs, and cats are closely related to human strains and cluster within GII (porcine norovirus) and GIV (feline and canine norovirus), respectively [1]. Noroviruses belonging to the other genogroups infect a broad range of hosts that includes livestock animals such as cows and sheep but also marine mammals and rodents. In the past years, an increasing number of metagenomic studies have led to the discovery of additional noroviruses in new animal hosts and it seems evident that we lack understanding of the full diversity of noroviruses and their host range [6,7]. Most human infections and outbreaks are caused by viruses belonging to GI and GII. The GII.4 genotype viruses have been particularly prevalent in the past two decades, and evolve through accumulation of mutations but also by recombination. Such recombinants and other new genotypes emerge regularly but the origin of these new viruses is not well understood [8]. This regular detection of novel strains and the reporting of human-like norovirus genotypes in stool samples of symptomatic and asymptomatic farm animals have sparked interest in the possible role of animals as potential zoonotic reservoir for these

emerging strains [9–12]. Antibodies directed against bovine and canine norovirus have been detected in humans suggesting some level of exposure of humans to animal norovirus [13–16]. For other viruses of the *Caliciviridae* family, interspecies transmission has been reported including some case reports of zoonotic events between marine mammals and humans (reviewed in [17]).

This systematic review summarizes the literature on the known animal reservoir for norovirus, the virus diversity, prevalence, and geographic distribution, as well as pathological findings associated with norovirus infections in animals. We will further discuss the existing evidence and probability of interspecies transmission including susceptibility of animals used as models in norovirus research. There are several reviews that focus exclusively on the role of mice in norovirus research [18–20]; therefore, we will discuss murine norovirus only in context of surveillance of wild animals. Molluscs are an important vehicle of foodborne norovirus transmission, but do not support norovirus replication and have been reviewed elsewhere [21,22].

2. Results

2.1. Search Output:

The search yielded 6702 papers of which a total of 182 were included in the review. An additional nine papers were later included (see methods).

2.2. Noroviruses in Domesticated and Wild Animals

Norovirus was first described from a gastroenteritis outbreak in 1968, which affected children in a school in Norwalk, Ohio, USA [23]. In 1972, the virus was visualized for the first time by immune electron microscopy revealing "small round structured viruses" (SRSV) of 27–35 nm in diameter, which was used as their first classification [24]. Viruses of similar morphology were soon described from stool samples of domestic calves and pigs, and sequencing confirmed the presence of viruses belonging to the same family as human noroviruses. To date, porcine noroviruses are genetically most similar to human norovirus; porcine noroviruses have been classified among a diverse range of human norovirus genotypes in GII as GII.11 (prototype SW918), GII.18 and GII.19 [10,25] and have been found in stools and intestinal content of pigs all over Europe, North and South America, and Asia (Figure 1A,B, Table 1).

In most countries, the overall detection rate of porcine norovirus in stool samples is low (0–16.6%) and outbreaks have not been reported, although there is evidence for symptomatic porcine norovirus infections. When specific-pathogen-free (SPF) piglets were inoculated with GII.11 or GII.18 positive fecal filtrate they showed mild to moderate diarrhea within 1 day post inoculation (dpi) and norovirus RNA was amplified from intestinal content as well as from sera [26,27]. The majority of surveillance studies have been screening healthy pigs from farms and slaughterhouses [9,10,25,28–44]. Asymptomatic finisher pigs most commonly tested positive, but porcine noroviruses have also been found in stools from asymptomatic pigs of other age categories as well as diarrheic piglets [26,34,45]. Virus circulation is thought to be widespread. A survey of pigs found antibodies to GII.11 virus like particles (VLPs) in 71% and 36% of pigs in the USA and Japan [46].

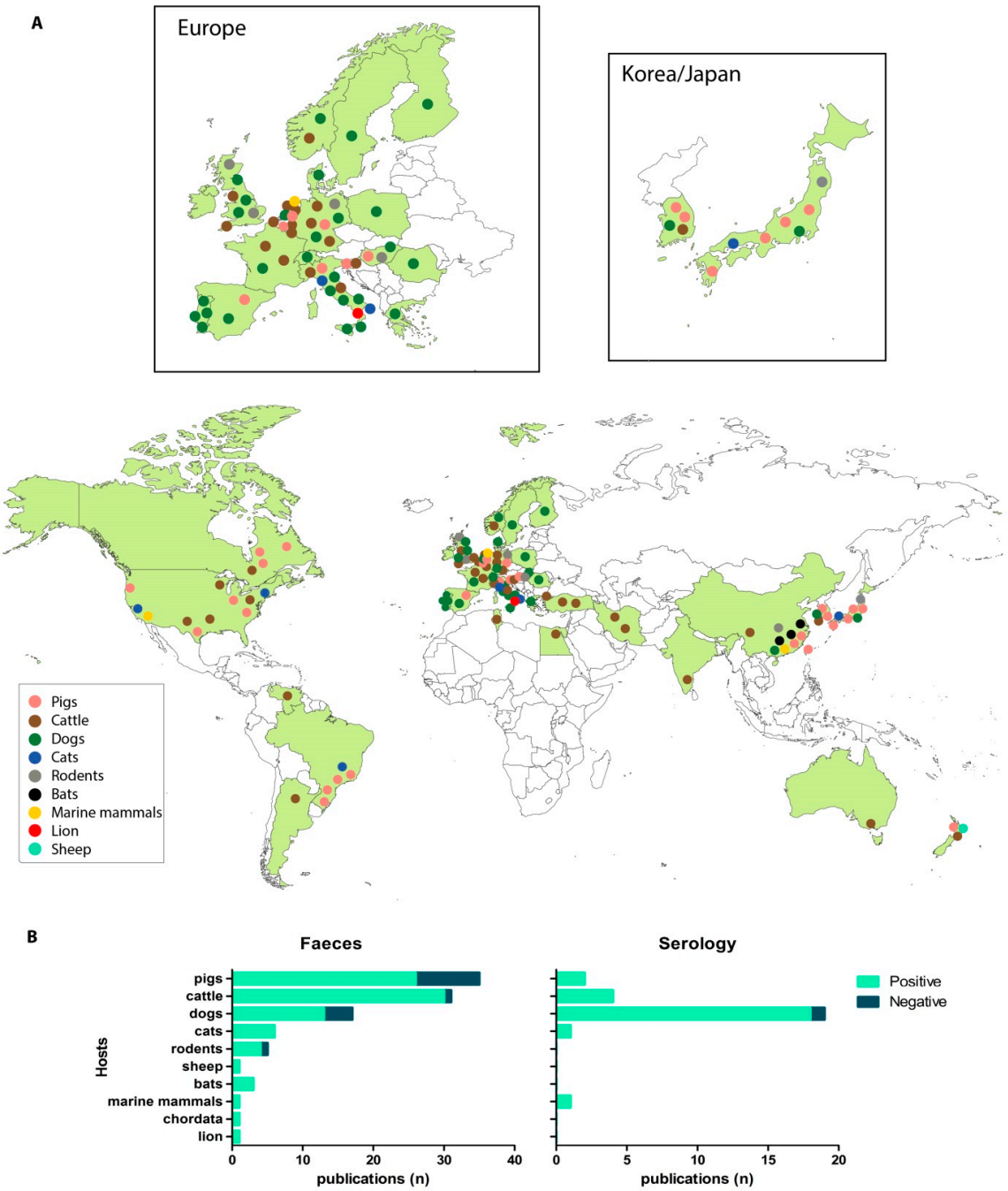

Figure 1. Studies describing the presence of animal norovirus across the world. (**A**) Countries in which animal norovirus have been detected are colored green. Each dot represents a study and location where animals have been found positive by either RT-PCR, real-time RT-PCR, or serology. The color indicates the host. (**B**) Number (n) of publications reporting positive versus negative surveillance results in different hosts for PCR results in feces and serology studies. Note that a paper that studied GVI.2 seropositivity in dogs in 14 European countries is listed as 14 studies in 1B [47]. Details of the studies are listed in Table 1 and Supplementary Table S1.

Table 1. Summary of studies detecting animal norovirus in animals, either in feces or by serology. Details of each study can found in Supplementary Table S1.

	Location	Host	Genotype	Prevalence in % (References)	
				Serology	Feces
The Americas	USA	Pigs	GII.18, GII.11, GII.19	71 [46]	0–19 [25,28,46,48]
		Cattle	GIII.1, GIII.2	100 [49]	29–72 [50–52]
		Cats	GIV.2		17–43 [53,54]
		Sea lion	GII/GIV		9 [55]
	Canada	Pigs	GII, GII.11, GII.18		2–85 [30–32]
		Cattle	GIII.2		1 [30]
	Venezuela	Pigs	all		0 [39]
		Cattle	GIII		0.7 [56]
	Argentina	Cattle	GIII.1, GIII.2		3 [57]
	Brazil	Pigs	GII.11, GII.18, GII.19		0–52 [44,58–61]
		Cats	GIV,2		3 [62]
Asia/New Zealand	China	Pigs	GII.11, GII.18, GII.19		0–17 [26,27,33,35]
		Cattle	GIII.1		11 [63]
		Bats	NA		3–4 [6,64]
	Taiwan	Pigs	GII.11		1.6 [34]
	Japan	Pigs	GII.11	36 [46]	0.4–15 [10,36,45]
		Dogs	GIV		2 [65]
		Cats	GIV.2		1.2 [65]
		Rodents	GV		0–14 [66]
	Korea	Pigs	GII.11, GII.18		0.5–2 [37,67]
		Dogs	Canine norovirus	16 [68]	3 [68]
		Cattle	GIII.1, GIII.2		9 [69]
	Iran	Cattle	GIII.1, GIII.2		18–40 [70,71]
	Turkey	Cattle	GIII.2		4–9 [72,73]
	India	Cattle	GIII.1		0.4 [74]
	New Zealand	Pigs	GII.11		9 [38]
		Cattle	GIII.1		54 [75]
		Sheep	GIII.3		24 [38]
Europe	Italy	Pigs	GII.11		0–0.5 [76,77]
		Cattle	GIII.1, GIII.2		11–21 [78,79]
		Dogs	GIV, GVI	5–60 [47,80,81]	2–5 [82,83]
		Lion	GIV.2		100 [84]
		Cats	GIV.2	16 [85]	3 [81]
	Spain	Pigs	all		12 [86]
		Dogs	GVI		8 [83]
	Portugal	Dogs	GIV, GVI	64 [47]	23–28 [87–89]
	Greece	Dogs	GIV.2		8 [90]
	France	Cattle	GIII.1, GIII.2		20–37 [91,92]
		Dogs	GVI.2	20 [47,83]	0 [83]
	Switzerland	Dogs	GVI.2	20 [47]	
	Germany	Pigs	GII.18		14 [41]
		Cattle	GIII.1, GIII.2	66–99 [93,94]	93 [95]
		Dogs	GIV, GVI.2	16 [47]	4 [83]
		Rodents	GV		10 [96]
	Netherlands	Pigs	GII.11		2 [9]
		Cattle	GIII.2	0–44 [9]	4 [97]
		Dogs	GVI.2	34 [47]	
		Porpoise	not classified yet	24 [98]	10 [98]
	Belgium	Pigs	GII.19		4.6 [99]
		Cattle	GIII.2	93 [100]	4–9 [80,100–102]
	UK	Cattle	GIII.1, GIII.2	66–98 [93,103]	11 [104]
		Dogs	GIV, GVI, GVII	45–48 [47,105,106]	0 [106]
		Rodents	GV		22–67 [107]
	Ireland	Pigs	none		0 [40]
		Dogs	none	0 [47]	
	Denmark	Dogs	GVI.2	20 [47]	
		Rodents	none		0 [108]
	Sweden	Dogs	GVI.2	40 [47]	

Table 1. *Cont.*

	Location	Host	Genotype	Prevalence in % (References)	
				Serology	Feces
Europe	**Norway**	Cattle Dogs	GIII.1, GIII.2 GVI.2	 32 [47]	50 [109]
	Finland	Dogs Rodents	GVI.2 none	70 [47]	0 [110] 0 [111]
	Poland	Dogs	GIV.2	32 [47]	
	Slovenia	Pigs Cattle	GII.11, GII.18 GIII.2		1.2 [42] 2 [42]
	Hungary	Pigs Dogs Rodents	GII.11 GVI GV	0 [47]	6 [112] 3 [113] 24–67 [114]
Africa	**Egypt**	Cattle	GIII.2		24 [115]
	Tunisia	Cattle	GIII.2		17 [116]
	South Africa	Pigs	none		0 [117]
	Ethiopia	Pigs	GII.1		0 [43]

The SRSV found in stool samples from cattle have subsequently been characterized as bovine norovirus GIII.1 (Jena agent) and GIII.2 (Newbury Agent 2), discovered in cattle in Germany and England, respectively [12,118]. Upon experimental inoculation with a GIII.1 or GIII.2 gnotobiotic calves develop diarrhea, shed virus for several days and seroconvert, although not in 100% of the cases [11,103,109,119–124]. Both genotypes are widely distributed among diarrheic and healthy cattle, juveniles, and adults, although GIII.2 viruses have been found more frequently than GIII.1. The majority of published surveys has tested diarrheic calves, in which bovine norovirus was frequently found [13,42,50,51,63,69,71,72,78,79,91,92,100,102,109,115,116]. One case–control study that investigated pathogens associated with calf diarrhea in the USA tested 444 samples of 1–2 week-old diarrheic and asymptomatic calves for a panel of 11 enteric pathogens (bacteria and viruses) using real-time RT-PCR with bovine norovirus specific probes. A prevalence of 44.7% was reported in diarrheic and 16.3% in healthy calves [50]. Less is known about bovine norovirus in adult cattle. One study compared prevalence of bovine norovirus RNA in pooled manure samples of 75 dairy farms with those of 43 veal calf farms. A high proportion (44%) from the veal calf farms was positive, but bovine norovirus RNA was not detected in samples from the dairy farms [9]. The prevalence of antibodies to GIII.1 or GIII.2 VLPs was >70%, independent of location (Table 1) and only very few studies failed to detect GIII viral RNA or antibodies (Figure 1B). A proposed third GIII genotype, GIII.3, was found in asymptomatic sheep in New Zealand [38].

While pigs and cows are the best studied non-human hosts—apart from mice—noroviruses have also been detected in stool samples from cats and dogs. Both animal species were shown to be infected by viruses belonging to genotype GIV.2, while dogs are also hosts of canine GVI and GVII strains. The first carnivore norovirus was documented in a captive lion cub (*Panthera leo*) in Italy that had died of severe hemorrhagic enteritis [84]. This new strain shared ~70% aa VP1 identity with the human GIV.1 sequence, which is only identified sporadically in the human population, but is more commonly detected in sewage samples [125]. One outbreak study documented the arrival of two diarrheic young dogs into a kennel in Lisbon [88]. Two days later, five young dogs housed in the same kennel developed diarrhea and the isolated GVI.2 sequences were identical to each other. Canine noroviruses sequences have since been detected in feces from healthy and sick dogs from kennels, shelters, and households in South America, Europe, and Asia (Figure 1, Table 1). To date, no infection studies have been conducted with canines and the pathology of noroviruses in dogs is therefore unclear. However, during a study in Portugal, canine norovirus RNA was found more often in the stool samples of symptomatic dogs compared to asymptomatic dogs (40% versus 9%), suggesting they play an important role as cause of disease [87,126]. In a Europe-wide study, an overall 4.4% prevalence was found for diarrheic dogs while none of the healthy animals tested positive [83]. A strong seasonal pattern was observed during a four year period of sampling dogs in Portugal, with the highest prevalence (36%) in winter and lowest

(7%) in autumn, similar to the seasonality observed for norovirus in humans [89,126]. A serological survey screening dogs from 14 different countries found variable prevalences of antibodies to GVI.2, ranging from 0% in Hungary and Ireland up to 60% in Portugal [47].

The first evidence for feline noroviruses was provided through an Italian study, where 16% of cats tested positive for GIV.2-specific antibodies, with the highest prevalence among stray cats (32%) [81]. Three years later, in 2012, a feline norovirus was discovered during a gastroenteritis outbreak in cats in a shelter in the USA [53]. The cats were negative for known feline parasites, but a full norovirus genome was recovered (JF781268). Similar viruses were later detected, mostly in diarrheic cats [54,62,65,85]. After inoculation of SPF cats with feline norovirus, the cats shed the virus up to 7 dpi, viral RNA was detected in sera of all cats, three of the four cats developed diarrhea and one started vomiting [127]. Another study using the same inoculum showed that cats developed IgG against recombinant VP1 protein identical to the strain used for the experimental infections [128].

Apart from domesticated animals, noroviruses have also been detected in wild animals, such as harbor porpoises (*Phocoena phocoena*) and californian sea lions (*Zalophus californianus*) [55,98]. Neither of these viruses could be assigned to an existing genogroup. Further investigation found 10% of harbor porpoise intestinal tissues RT-PCR positive and 24% of the animals seropositive for porpoise norovirus, suggesting that norovirus infections are common in these animals. With the recently increasing trend of metagenomic studies, additional norovirus have been identified. In a metagenomics analysis of bats intended to decipher the bat virome, a full norovirus genome was recovered from intestinal tissue of *Rhinolophus pusillus* bats captured in two Chinese provinces [6]. In one location the prevalence in fecal samples was as high as 20%. This strain belongs to a new genotype which shares highest sequence homology with GV norovirus (Figure 2) [129]. Subsequent studies have detected norovirus in two species of insectivorous bats in China, namely *Rhinolophus sinicus* and *Rhinolophus affinis* [64,130]. Most of the animal noroviruses have not been detected in animals other than the species were they were first identified in. Exceptions are the GV noroviruses, which are detected in mice and rats, and the canine/feline GIV and GVI noroviruses.

2.3. Is There Evidence for Cross Species Transmission?

Since the first norovirus has been detected from animals, the question has been raised whether norovirus can jump the species barrier. To date, there are no controlled outbreak studies during which both animals and humans have been sampled simultaneously. One calicivirus outbreak in a nursing home in 1983 in the UK was epidemiologically linked to a sick dog. While virus particles were found in the patients, no stool sample was available from the dog and only antibodies against the same virus could be detected [131].

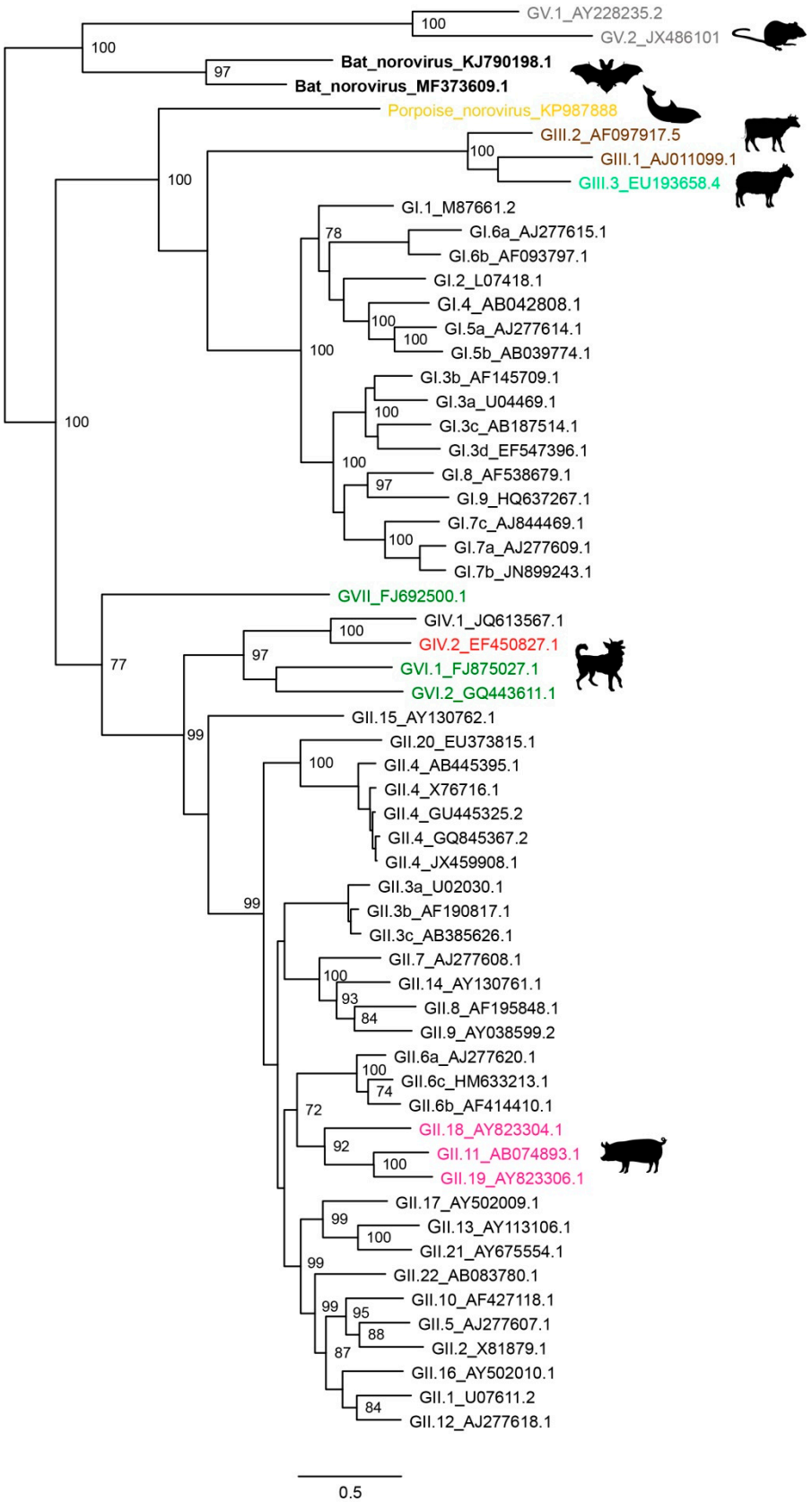

Figure 2. Maximum-likelihood tree of open reading frame 2 (ORF2). The tree was inferred by PhyML 3.0 software (http://www.atgc-montpellier.fr/phyml/) by using the general time reversible nucleotide substitution model. Bootstrap values >70 are shown. Scale bars indicate nucleotide substitutions per site. Animal noroviruses are colored with same color code as in Figure 1A.

2.3.1. Animal-to-Human Transmission

To date, no animal norovirus have been detected in human stool, but some serological evidence hints to possible transmission from animals to humans. This includes a handful of studies that reported seroprevalence against bovine [13,14,132] and canine [15,16] norovirus in humans. A Dutch study compared antibody titres against GIII.2 VLPs from 210 bovine or porcine veterinary specialists against age, sex, and residence matched controls with the aim to evaluate whether higher exposure to animals is reflected in increased titers against animal noroviruses [132]. More veterinarians had anti-GIII.2 IgG antibodies compared to the control group (28% versus 20%). Similarly, the seroprevalence of antibodies to canine GVI.2 VLPs was tested in a cohort of 373 veterinarians versus age, sex, and district matched controls. Of the veterinarians, 22.3% were seropositive for GVI.2 in comparison to 5.8% in the control group [15]. Anti-GIII antibodies were also detected in 26.7% of adult blood donors in Sweden [14] and in a birth cohort in India, which compared seroprevalence of mothers and their children [13]. However, the possible presence of cross-reactive antibodies needs to be considered in these studies: the GIII.2 response was in part correlated with GI.1 response, but not with the GII.4 response. The finding that some sera contained higher antibody titers against GIII.2 than human norovirus indicates that not all anti-GIII.2 response can be explained by cross-reactivity [132]. Importantly, no cross-reactivity between bovine GIII.2 and human GI.3, GII.1, GII.3, GII.4, GII.6 was detected when convalescent anti-GIII.2 sera of a gnotobiotic calf or specific anti-GIII.2 or GII.3 antibodies were used [14,121]. Cross-reactivity between GVI.2 and GII.4 was assessed by pre-incubating GVI.2 positive sera with GVI.2 VLPs before assessing their binding to GII.4 or GVI.2. Preincubation with GVI.2 blocked binding to GVI.2 VLPs but had no effect on sera binding to GII.4, suggesting that these two genotypes share no conserved epitopes [15]. In contrast, cross-reactivity was observed between more closely related human GIV.1 and canine GIV.2 noroviruses in an age stratified cohort of 535 people in Italy [16], where 28.2% of the sera reacted to both GIV.1 and GIV.2 VLPs and only 0.9% detected exclusively GIV.2 VLPs.

2.3.2. Human-to-Animal Transmission

Numerous studies have investigated the possibility of human norovirus transmission to animals by screening animal stool samples for human noroviruses or by investigating the seroprevalence against human norovirus strains (Figure 3, Supplementary Table S2). The closest to an outbreak study was one case-control study that included 92 dogs from Finnish households. The main inclusion criterion was that either the dog or a human in the household had suffered from vomiting or diarrhea [110]. Four dogs tested PCR positive and they all came from households in which at least two people suffered from severe gastroenteritis symptoms that had disappeared not longer than three days before the dog samples were taken. Based on a ~370 nt region two GII.4 variants and one GII.12 genotype were identified, of which one GII.4 was identical to the virus found in the owner's feces. The other strains were >98% nt identical to circulating human norovirus strains. Antibodies against GII.4 and GI.1 VLPs have been detected in dogs sampled in a European study and against GII.4 and GIV.1 in dogs in Italy [47,80]. Both studies found that sera from some animals reacted exclusively to the human strains but not to canine GVI.2 VLPs. Caddy et al. investigated the seroprevalence against human noroviruses (GI.1, GI.2, GI.3, GII.3, GII.4, GII.6, GII.12) in two dog populations; sera from dogs in a rehoming kennel in 1999–2001 and sera collected in 2012–2013 from a diagnostic lab. Overall, seropositivity against GI was very low, but 10.7–18.6% were seropositive against GII VLPs [106]. The majority of seropositive dogs had antibodies detecting GII.4 viruses which was the most prevalent human norovirus circulating during this time. Only weak cross-reactivity was observed with canine sera or polyclonal sera specific for GII.4 or GVI.1/GIV.2 [106]. Combined, these studies suggest that human noroviruses could infect dogs, although more work is needed to unravel potential cross-reactivity with non-human viruses, like GVI.2 [80].

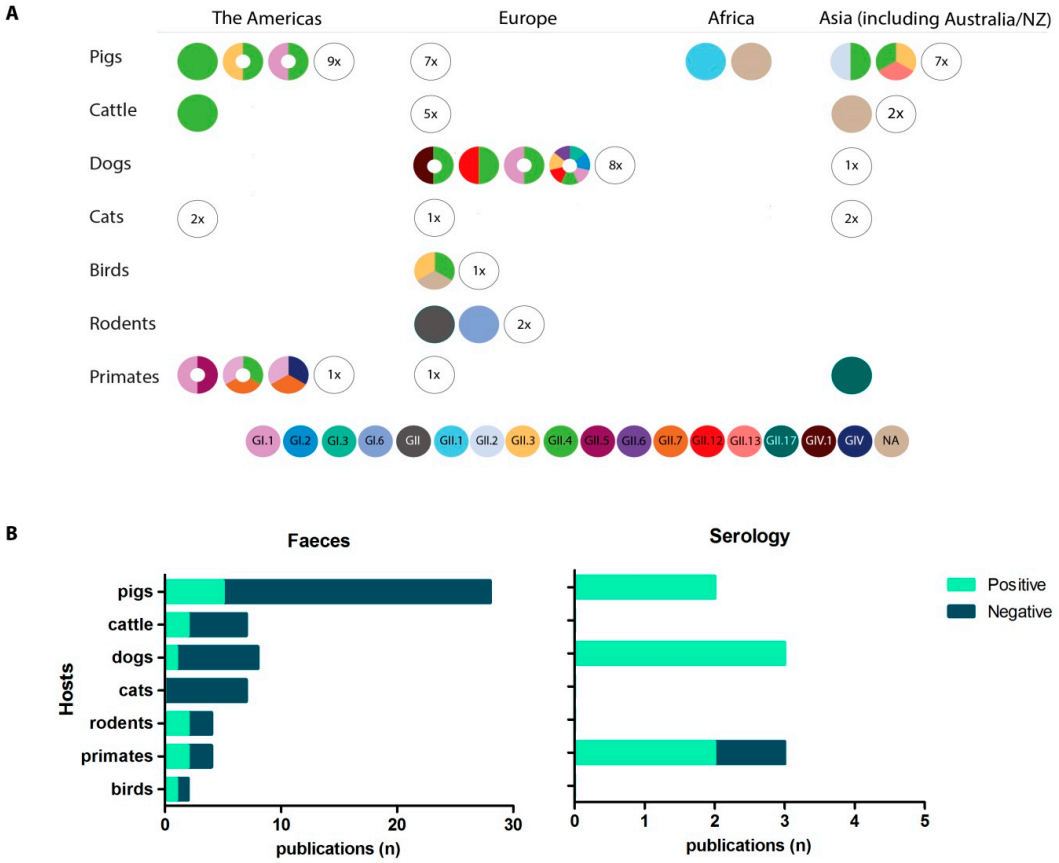

Figure 3. Human norovirus genogroups and genotypes detected in studies investigating human-to-animal transmission. (**A**) Studies that analyzed fecal samples for human norovirus sequences by RT-PCR, real-time RT-PCR or serological studies. Every circle represents one study and colors represent different norovirus strains identified through sequencing. Serological studies are marked with a central white circle, and colors here represent antigens used for the serological testing. Numbers in empty circles indicate the number of studies in which no evidence for human norovirus infection was found. NA stands for studies where the genogroup or genotype was not identified. (**B**) Number (n) of virological and serological studies of norovirus in different hosts, grouped according to results (positive versus negative). More details can be found in Supplementary Table S1. NZ = New Zealand.

Several surveys in pigs reported human norovirus in pig feces and two reported more than one genotype [30,34,36,43,117]. In a longitudinal study in Japan intestinal content of 20 apparently healthy 6 month-old pigs were screened each month with calicivirus-specific primers. Of these, 11/354 were positive for human GII without a seasonal pattern being recognized [36]. Based on partial capsid sequences these strains were classified as GII.4, GII.3 and one GII.13, all three genotypes that had been reported in outbreaks in humans during that season. Another study tested 530 fecal samples of asymptomatic pigs (<8 month) from six farms in Taiwan, 7% tested positive with RdRp-specific primers, while GII capsid specific primers resulted in 32% positive samples, 41% in winter and 26% in summer [34]. The GII.4 and GII.2 classified sequences were found in pigs of all age categories and from different farms. Sequences of GII.1 and GII.4 noroviruses have also been detected in feces of two healthy sows in Ethiopia and GII.4 in pig feces from two different farms in Canada [30,43].

Antibodies recognizing human norovirus have been detected in healthy household pigs in Nicaragua and US pigs with prevalences ranging from 52%–70% [46,133]. While those antibodies recognized VLPs of GI.1, GII.1, GII.3 and GII.4 they were not able to block their binding to pig mucin [133]. Cross-reactivity was also investigated and antibodies against GII.1 and GII.3 but not against GI genotypes cross reacted with porcine GII.11 [46]. The studies thus far raise the question if certain norovirus genotypes considered to be "human" noroviruses co-circulate among pigs. As these

observations are not consistent, this could be restricted to some regions where opportunity for contact of pigs with humans is higher.

During the 2014–2015 epidemic season, GII.17 was the dominant human norovirus genotype in some Asian countries [134,135]. 32 of 50 rhesus macaques on a Chinese farm tested positive using GII.17 specific primers and a whole GII.17 genome (KX356908) was recovered from one animal [136,137]. This GII.17 genotype was 99% identical to a human GII.17 recently detected in China [137]. Rectal swabs of juvenile rhesus macaques from a primate research center in the USA were screened by real-time RT-PCR for GI, GII, and GIV noroviruses; of the 500 samples, 8.2% were positive [138,139]. Sanger sequencing showed that the animals were positive for 30 GI.1 and eight GII.7 strains, and yielded two full ORFs of GI.1 and GII.7 sequences (KT943503–KT943505). Surprisingly, the GI.1 sequences were not only identical to each other but also to the prototype Norwalk virus described in 1968. The GII.7 sequences were 99–100% identical to each other and 95% identical to a human norovirus (KJ196295). Furthermore, antibodies against various human norovirus genotypes were detected in captive primates in the US; IgG against GI.1, GII.4, GII.5 and GII.7 VLPs were detected in mangabeys (85%), macaques (~60–65%), and chimpanzees (92%) [140,141].

Compared to surveillance in livestock animals only a few studies have investigated wild animals. Bird feces were collected during three winters (2009–2011) from fresh snow of a household waste dumping site in Finland and analyzed by GI and GII specific real-time RT-PCR [111]. Of the 115 avian feces tested, six were positive for GI and 25 for GII, albeit with high Ct values, the lowest being 36. Sequencing and typing was successful for four GII.4 (GII.4 2006a/b, 2009) and two GII.3 viruses, all at least 94% identical to known human strains. Based on cytrochrome c oxidase I sequencing, the positive feces could be assigned to gulls and crows. A human norovirus was found in the intestinal content of a dead Norway rat that had been trapped in the sewer system in Copenhagen; a ~4000 bp sequence was recovered and was typed as a GI.Pb-GI.6 strain [108]. The virus titer was calculated to be 5×10^7 genome copies/g feces and norovirus particles were detected in feces by immunogold electron microscopy [108].

2.3.3. Susceptibility of Animals to Human Norovirus Strains

In addition to finding human norovirus in animal stool samples, noroviruses have been found to cross the species barrier under experimental conditions. To date, seven animal models have been developed to study human norovirus infection; gnotobiotic calves and pigs, immunocompromised BALB/c Rag-$^{\gamma c}$-deficient mice, Yucatan miniature pig, and three non-human primates, namely chimpanzees, rhesus, and pigtail macaques (Table 2). In contrast, common marmosets, cotton top tamarin, immunocompromised ferrets, and cynomolgus macaques were not found to be susceptible to infection, although only a limited number of norovirus genotypes was tested [142,143]. All models support viral replication evident by viral shedding and seroconversion upon oral or intragastric inoculation with a high viral dose (10^4–10^6 genomes). Whereas pigs and calves developed diarrhea, both chimpanzees and rhesus macaques did not display any gastrointestinal symptoms. Virus replication was usually found to be restricted to sites of the small intestine. In mice, viral genomes could be amplified from various organs, and in minipiglets, low levels of the virus were additionally found in blood as well as in tonsils, spleen, and lymph nodes [144,145]. Pathological changes were detectable only in calves and pigs but not in primates. These changes included villous blunting, atrophy, and an increase in inflammatory cells in the lamina propria. Norovirus antigen was detected in the small intestine, varying between duodenum, jejunum, and ileum depending on the animal and the virus strain used for inoculation. Noteworthy, in pig as well as in chimpanzee experiments, animals were chosen based on their histo-blood group antigen (HBGA) and secretor status. In pigs, take of infection was strongly dependent on their HBGA phenotype and secretor status. HBGA type A+/H+ pigs were more readily infected than type A-/H- pigs [146]. However, while two culturing systems have been described for human norovirus [147,148], attempts to grow human norovirus in animal cell culture have not yet been successful [149,150].

Table 2. Summary of animal models for human norovirus.

	Gnotobiotic Calf [123]	**Gnotobiotic Pig [151–160]**	**Mini Piglet [145]**	**Rhesus Macaque [136,142,161]**	**Pigtail Macaque [162]**	**Chimpanzee [163,164]**	**Balb/c RAG/γc$^{-/-}$ Mouse [144]**
Virus	GII.4	GII.4, GII.12	GII.3	GI.1, GII.2, GII.4, GII.17	GII.3	GI.1	GII.4
Inoculation (route and virus quantity)	Oral 1.62×10^7 genomes	Oral/intranasal 10^4–10^{10} genomes	Intragastric 10^7 genomes	Oral/intragastric 10^5–10^6 genomes	Nasogastric, Quantity not clear	Intravenous/intragastric 4×10^6–4×10^8 genomes	Intraperitoneal 4×10^3–7×10^4 genomes
Shedding	3 days	2–16 days	7 days	1–19 days	Up to 21 days	2 days–17 weeks	No shedding [1]
Seroconversion	Yes	Yes	NA	Yes/no [2]	Yes	Yes	No
Pathology	Lesions, mild villous atrophy, enterocyte vacuolization in small intestine	Increase in inflammatory cells in LM, necrosis, shortening of villous tips	No damage	No damage	NA	No damage	No damage
Tropism (detection of viral antigen or genome)	Positive enterocytes in the ileum, cells in LM	Enterocytes and cells in LM of duodenum, jejunum, ileum. Spleen and MLN	Immune cells in the small/large intestine, tonsils, spleen, lymph nodes, MLN	NA	NA	Cells in LM of duodenum and jejunum	Macrophage-like cells in liver and spleen. Viral genomes detected in various tissue [3]
Disease	Diarrhea	Diarrhea	Diarrhea	Asymptomatic	Diarrhea	Asymptomatic	Asymptomatic
Viremia	Yes (low)	Yes	Yes	NA	NA	NA	NA

[1] When inoculated orally and intraperitoneal simultaneously, virus was shedded in feces. [2] Depending on study. [3] Stomach, small/large intestine, MSN, liver, spleen, kidney, heart lung, bone marrow. MSN = mesenteric lymph nodes, LM = lamina propria.

The best understood host factors influencing susceptibility to human norovirus infections are the HBGA, glycans that act as attachment factors for norovirus, and the host secretor status [165–170]. Alternative attachment factors, including sialic acids and heparan sulfate, have been proposed and it is likely that other cell surface molecules play a role in norovirus binding to the cell [171–174]. Virus attachment is a prerequisite for a cell's susceptibility to infection and studying a host's or population's HBGA distribution can imply putative target cells and susceptible populations, respectively; HBGA expression and distribution within a host can indicate virus cell tropism while their expression in different putative human and animal hosts can be an indicator for host range.

A host's HBGAs type is determined by the ABO- and Lewis blood group systems. ABO synthesis begins with the addition of fucose to a carbohydrate precursor on glycoprotein or glycolipid precursor structures by a α1-2 fucosyltransferase. This enzyme is expressed from two separate loci (*H* and *Se*) one expressed on red blood cell precursors, the other on epithelia cells of the gastrointestinal, respiratory, and reproductive tract. Individuals who have a non-functional fucosyltransferase 2 (*FUT2*) version express the H antigen only on their red blood cells but not in their gastrointestinal tract. The A and B antigen are subsequently added onto the H antigen by various other glycosyltransferases. Lewis antigens are sugar moieties, consisting of a precursor structure, or the A, B, H antigens to which an extra fucose group has been added. The *Se* locus also determines whether soluble forms of the ABH antigens are secreted into bodily fluids. Humans with an inactive *Se* gene are referred to as non-secretors since no ABH antigens are found in their saliva and mucus [175]. Noroviruses bind these HBGA in a strain dependent manner, thus leaving non-secretors non-susceptible to some norovirus strains. In pigs and primates, the HBGA phenotype seems to be important for infection with human norovirus as well. In animal studies the host's HBGA phenotype and virus strain used for inoculation can be selectively paired. Binding assays have been used as an alternative surrogate to study interaction between virus attachment factors (Figure 4, Supplementary Table S3).

Animal or human norovirus VLPs or purified virus can be tested with regards to their attachment to either animal or human saliva or tissue with known HBGA content. Canine and the newly discovered norovirus from bats appear to attach to HBGAs similar to human noroviruses [129,176]. Bovine GIII.2 and murine GV have been shown to be dependent on receptors that are not thought to be expressed in humans; GIII.2 strains do not bind the same sugar moieties as human norovirus but to a αGal 1–3 sugar (Gala3Galb4GlcNAcb-R) instead [177]. This epitope is expressed in all mammals with the exception of the *Hominidae* family. In line with this, GIII.2 particles bound strongly to bovine saliva but neither to human saliva nor duodenal tissue.

GV infection in mice was reported to depend on terminal sialic acids and glycoproteins on macrophages, in a strain dependent manner [178]. Recently, a proteinaceous receptor, CD300lf, was detected in mice, which is expressed on tuft cells that are present in small numbers in the intestine as well as on cells of the hematopoietic/myeloid lineage. However, the human CD300lf homologue does not function as receptor for human or murine norovirus [74,179]. For other noroviruses, including porcine and feline genotypes, no attachment factor or receptor is known.

Most of the susceptible hosts mentioned above, with the exception of several fish and bird species, contain a *FUT1* and *FUT2* gene. The lack of these genes can be potentially compensated for by another fucosyltransferase, or alternatively in these newly discovered animal norovirus, could attach to an alternative receptor [180].

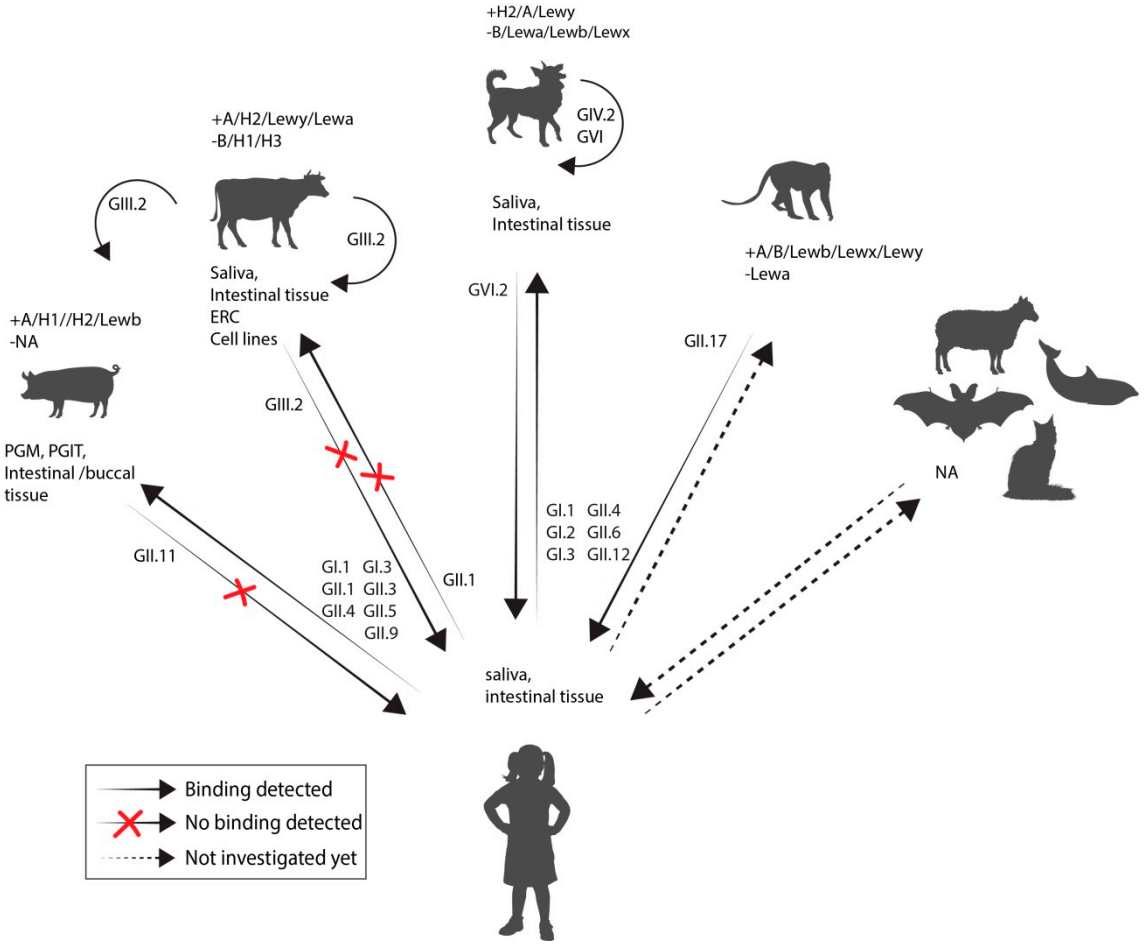

Figure 4. Results of binding studies with animal and human norovirus VLPs. The histo-blood group antigen (HBGA) phenotype is indicated with the presence (+) or absence (−) for different glycans. Arrows indicate direction in which attachment was tested and whether attachment was observed or not (red cross). Dotted arrows indicate that attachment has not been assessed yet. The half circular arrows indicate binding of animal norovirus to tissue/saliva of either the same or another animal species. Detailed information about the individual studies can be found in Supplementary Table S3.

3. Discussion and Conclusions

More than two thirds of emerging infectious diseases that affect humans originate from animal reservoirs, predominantly bats, rodents, birds, and other wildlife, and therefore, we sought to review evidence for interspecies transmission of noroviruses [181]. While most of our understanding about the norovirus animal reservoir stems from domestic animals, the recently increasing number of metagenomic studies, investigating the virome in a more unbiased way, have extended the norovirus host range by new species, while simultaneously complementing the knowledge about norovirus diversity. For many of these newly discovered viruses, we have little more information than a genome sequence and it remains to be determined if they indeed are host specific. Bats, wild rodents, and birds are known to frequently host pathogens that can cause disease, but have hardly been studied for evidence of norovirus infection.

Our review found more evidence for human noroviruses in animals than the reverse, suggesting that human norovirus could be a reverse zoonosis, with identification of human norovirus RNA in stool samples from pets, rodents, birds, pigs, and cattle. However, the question is what constitutes evidence for infection, as it can be argued that the detection of norovirus in feces indicates ingestion of norovirus contaminated material rather than an active infection. The molecular RNA detection methods can be sensitive enough to detect amounts as low as 10 virus genomes and such low virus levels could be

due to ingestion [182]. To establish that both species can serve as a host, detection of either replicating virus by increase in virus titer over time, a specific immune response, or detection of proteins that are only expressed upon infection is required. This has been shown experimentally in cattle, pigs, macaques, and chimpanzees, confirmed by seroconversion and virus shedding. Serological studies can also be used to confirm viral detection in field studies, thus increasing the window of detection, as antibodies persist much longer than virus shedding. However, serological assays have their draw backs: antibodies can potentially also be induced by exposure to the virus rather than infection and cross-reactivity has to be taken into consideration when analyzing the results. Cross-reactivity has been described primarily between strains within one genogroup and less between viruses from separate genogroups [183]. This is of importance when analyzing serology data against human and animal noroviruses that cluster in the same genogroups, such as porcine, feline, and canine noroviruses. Many serology studies reported some sera that contained antibodies only recognizing animal strains but not humans or vice versa, increasing the chance that these are specific antibody responses. Serology has the advantage of providing information about the prevalence of a pathogen in a certain host species without relying on samples to be taken during an active infection. It is therefore a good tool to screen potential hosts with regards to their risk of exposure. However, this data should be complemented by detection of viable virus from the host. Since culturing is difficult for norovirus, deep sequencing to detect viral genomes is for now the best alternative. Should human norovirus infect animals the question remains whether these interspecies transmissions are relevant for human infections; if once transmitted to animals, these strains can be re-introduced into humans. Furthermore, strains that only cause sporadic infection in humans, such as GIV noroviruses, could reside in an animal reservoir between outbreaks.

Evidence for transmission of animal norovirus to humans is sparse and solely based on serological evidence. If these transmissions occur they are likely to be rare events that could be difficult to detect if they are asymptomatic or sporadic infections. In addition surveillance is not developed to detect these viruses in human stool samples. Several papers reported differences in detection rate based on their choice of primers; protocols with GI or GII specific probes will potentially miss the animal noroviruses, while the generic calici- or norovirus primers that are often used for detection of human and animal noroviruses in animals might have lower sensitivity compared to more specific primers [34,53,77,89,99,139]. It is open to debate whether some viruses that are categorized as human norovirus today might have originated from an animal source; the origin of newly emerging recombinants, such as the GII.pe polymerase, is unknown and it is a possible scenario that these new recombinants are the result of a recombination event between an animal and a human norovirus. Recombination occurs primarily within genogroups and only three intergenogroup recombinants namely between GI.3–GII.4, GII(NA)–GVI, and feline GIV.2–GVI.1, have been identified [127,184,185]. Recombinants are also found within bovine, porcine, canine, and feline genotypes. The formation of human-animal norovirus recombinants is a possible scenario, especially for animal genotypes that cluster close together with human genotypes. Water, food sources, and filter feeding shellfish can harbor a variety of multiple human and animal genotypes and genogroups simultaneously thereby posing a possible source of co-infection in humans and animals [186–189]. Based on the current body of evidence it is too early to consider norovirus a zoonotic or reverse zoonotic pathogen. To increase chances of catching a transspecies transmission event more targeted surveillance would be needed; to include samples of animals and humans that are in close contact, ideally during an outbreak situation and with an unbiased detection method [15,131,132,190]. Unravelling norovirus reservoirs and movement between species will help us understand norovirus evolution and emergence.

4. Methods

4.1. Search Strategy

We searched the literature in the Embase, Medline Ovid, Web of science, and Google scholar databases, using the search strings shown below. Number of papers found is depicted in brackets.

4.1.1. embase.com (2903)

("Norovirus"/exp OR "norovirus infection"/exp OR (Norovirus* OR Norwalk OR "small round-structur*" OR srsv*):ab,ti) AND ([animals]/lim OR "reservoir"/exp OR (nonhuman/de NOT human/exp) OR "zoonosis"/de OR "disease model"/de OR (animal* OR reservoir* OR nonhuman* OR non-human* OR animal* OR rat OR rats OR mouse OR mice OR murine OR dog OR dogs OR canine OR cat OR cats OR feline OR rabbit OR cow OR cows OR bovine OR rodent* OR sheep OR ovine OR pig OR swine OR porcine OR veterinar* OR chick* OR baboon* OR nonhuman* OR primate* OR cattle* OR goose OR geese OR duck OR macaque* OR avian* OR bird* OR mammal* OR poultry OR bat OR porpoise* OR zoono* OR farm OR farms OR "disease model*"):ab,ti)

4.1.2. Medline Ovid (1550)

(Norovirus/OR (Norovirus* OR Norwalk OR small round-structur* OR srsv*).ab,ti.) AND ((exp animals/NOT exp humans/) OR Disease Reservoirs/OR Zoonoses/OR Models, Animal/OR Disease Models, Animal/OR (animal* OR reservoir* OR nonhuman* OR non-human* OR animal* OR rat OR rats OR mouse OR mice OR murine OR dog OR dogs OR canine OR cat OR cats OR feline OR rabbit OR cow OR cows OR bovine OR rodent* OR sheep OR ovine OR pig OR swine OR porcine OR veterinar* OR chick* OR baboon* OR nonhuman* OR primate* OR cattle* OR goose OR geese OR duck OR macaque* OR avian* OR bird* OR mammal* OR poultry OR bat OR porpoise* OR zoono* OR farm OR farms OR disease model*).ab,ti.)

4.1.3. Web of Science (2049)

TS = (((Norovirus* OR Norwalk OR "small round-structur*" OR srsv*)) AND ((animal* OR reservoir* OR nonhuman* OR non-human* OR animal* OR rat OR rats OR mouse OR mice OR murine OR dog OR dogs OR canine OR cat OR cats OR feline OR rabbit OR cow OR cows OR bovine OR rodent* OR sheep OR ovine OR pig OR swine OR porcine OR veterinar* OR chick* OR baboon* OR nonhuman* OR primate* OR cattle* OR goose OR geese OR duck OR macaque* OR avian* OR bird* OR mammal* OR poultry OR bat OR porpoise* OR zoono* OR farm OR farms OR "disease model*")))

4.1.4. Google Scholar (200)

Norovirus|Norovirusses|Norwalk|"smallround-structur"|srsv animal|animals|reservoir|nonhuman|zoonosis|zoonoses|"disease model"

4.2. Selection Criteria

Two independent reviewers screened titles and abstracts for their relevance. We included publications that mentioned norovirus in the title or abstract but we excluded papers about food (oyster) and waterborne outbreaks, food surveillance or food related experiments, and oyster/seafood surveillance. We excluded papers on murine noroviruses as models. Papers describing norovirus surveillance in wild mice and papers using mice as model for human norovirus were included (Figure 5).

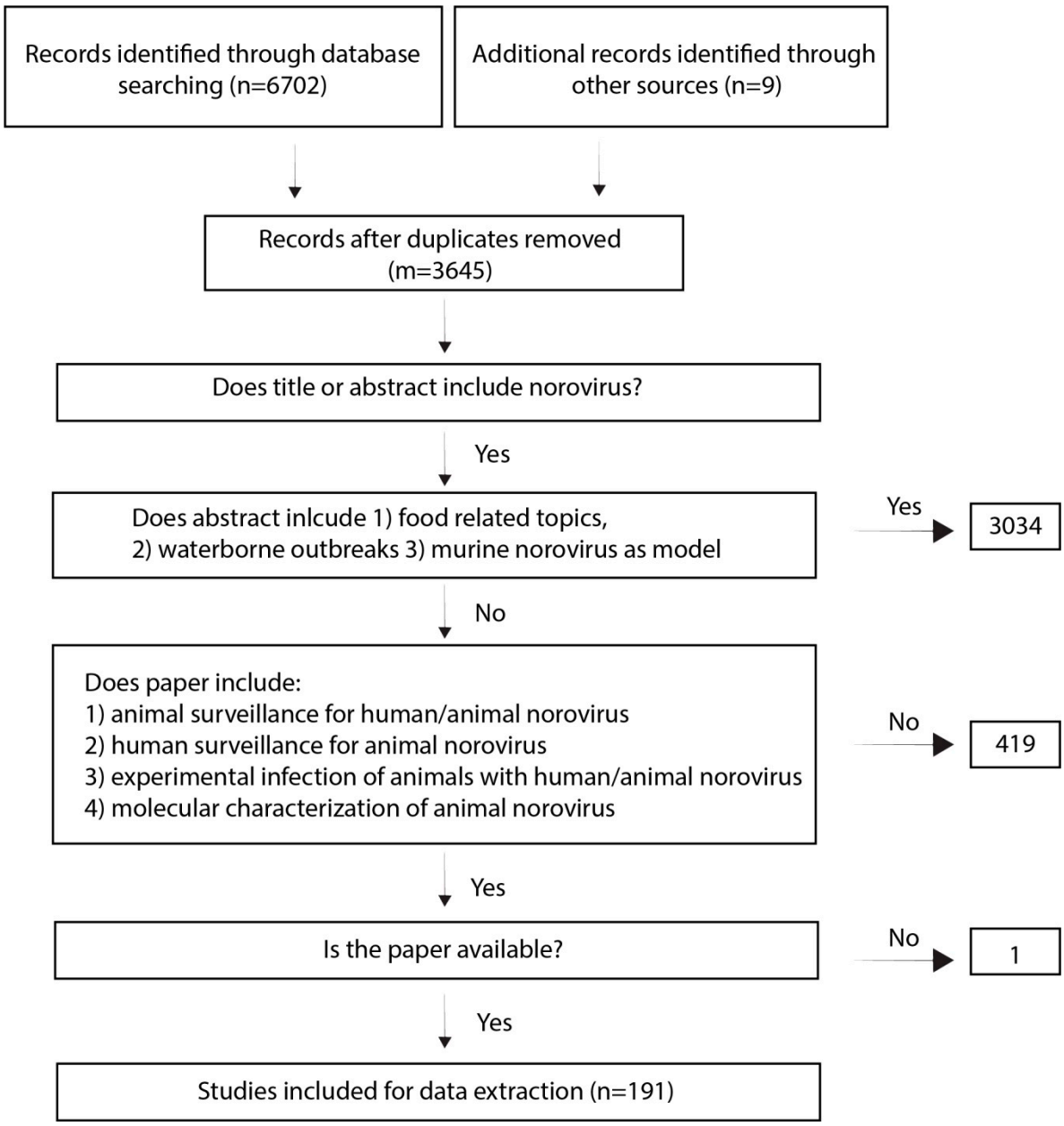

Figure 5. Inclusion and exclusion criteria for paper selection.

In a second round, we screened the papers for whether they described (1) animal surveillance studies to detect human or animal norovirus by PCR, sequencing or by serosurveillance including negative results; (2) experimental animal infections with human or animal norovirus; (3) human surveillance studies to detect animal norovirus by PCR, sequencing or by serosurveillance including negative results; (4) animal norovirus characterization including molecular assays and genome announcements.

4.3. Data Extraction

Of the remaining papers, the following data was extracted:

1. General description. Location (country, district, city), duration of study, date of study, species and number of tested animals and age of animals. For studies describing experimental infections of animals with human or animal noroviruses, the following information was collected if described in the paper:

2. Details on experimental infection methods. Regarding the experimental infection, the route of inoculation was documented since this may affect which subclasses of immunoglobulins are induced. In addition, genogroup/genotype of the virus inoculate, as well as amount used (number of genome copies) and the sample type collected (e.g., saliva, feces, sera) were registered. It was further recorded how virus replication was confirmed, which methods was used to detect virus (RT-PCR, real-time RT-PCR, antigen capturing ELISA, EM), how much was detected and at what time points.
3. Details on clinical picture; description of the health state of the animals; which symptoms (e.g., diarrhea, vomiting), as well as the duration of symptoms.
4. Pathology; pathological examination results.
5. Immunohistochemistry data was extracted to for information regarding the organ and cell tropism.
6. Host response was assessed by collecting serological data including method of antibody detection, type of immunoglobulins (Igs) tested (IgM, IgG, IgA), origin of Igs (saliva, sera, feces), the time period Igs were detected and if available whether they were blocking virus from binding to HBGAs. Since some animal noroviruses cluster close to human norovirus, information about cross-reactivity was also collected. Host factors such as HBGA, secretor and non-secretor status were of interest, since they are known to be important for susceptibility in humans, while in animals this link is less evident.

For surveillance studies additional data was collected regarding duration of surveillance, species, setting of the animals (farm, slaughterhouse, research facility, households, and the wild), and type of farm (if applicable; indoor/outdoor/free range). When virus shedding was detected by RT-PCR, it was noted which region of the genome was detected and whether the ORF1/ORF2 overlap was amplified. Furthermore, the similarity of new virus sequences with known sequences in the database was recorded. When sequences were available, they were re-typed with the Noronet typing tool.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4915/11/5/478/s1.

Author Contributions: Conceptualization, N.V., M.P.G.K. and M.d.G.; methodology, N.V., M.P.G.K. and M.d.G.; investigation, N.V. and M.d.G.; writing—original draft preparation, N.V. and M.d.G.; writing—review and editing, N.V., M.P.G.K. and M.d.G.; visualization, N.V. and M.d.G., supervision, M.P.G.K. and M.d.G.; project administration, N.V., M.P.G.K. and M.d.G.; funding acquisition, M.P.G.K.

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Conflicts of Interest: The authors declare no conflict of interest.

References

1. Vinje, J. Advances in Laboratory Methods for Detection and Typing of Norovirus. *J. Clin. Microbiol.* **2015**, *53*, 373–381. [CrossRef] [PubMed]
2. Throne, L.; Goodfellow, I. Norovirus gene expression and replication. *J. Gen. Virol.* **2014**, *95*, 278–291. [CrossRef] [PubMed]
3. Bull, R.A.; Tanaka, M.M.; White, P.A. Norovirus recombination. *J. Gen. Virol.* **2007**, *88*, 3347–3359. [CrossRef] [PubMed]
4. Bull, R.A.; Hansman, G.S.; Clancy, L.E.; Tanaka, M.M.; Rawlinson, W.D.; White, P.A. Norovirus Recombination in ORF1/ORF2 Overlap. *Emerg. Infect. Dis.* **2005**, *11*, 1079–1085. [CrossRef]
5. Kroneman, A.; Vega, E.; Vennema, H.; Vinjé, J.; White, P.A.; Hansman, G.; Green, K.; Martella, V.; Katayama, K.; Koopmans, M. Proposal for a unified norovirus nomenclature and genotyping. *Arch. Virol.* **2013**, *158*, 2059–2068. [CrossRef] [PubMed]
6. Hu, D.; Zhu, C.; Wang, Y.; Ai, L.; Yang, L.; Ye, F.; Ding, C.; Chen, J.; He, B.; Zhu, J.; et al. Virome analysis for identification of novel mammalian viruses in bats from Southeast China. *Sci. Rep.* **2017**, *7*, 10917. [CrossRef] [PubMed]

7. Shi, M.; Lin, X.D.; Chen, X.; Tian, J.H.; Chen, L.J.; Li, K.; Wang, W.; Eden, J.S.; Shen, J.J.; Liu, L.; et al. The evolutionary history of vertebrate RNA viruses. *Nature* **2018**, *556*, 197–202. [CrossRef] [PubMed]
8. Siebenga, J.J.; Vennema, H.; Zheng, D.P.; Vinjé, J.; Lee, B.E.; Pang, X.L.; Ho, E.C.M.; Lim, W.; Choudekar, A.; Broor, S.; et al. Norovirus illness is a global problem: Emergence and spread of norovirus GII. 4 variants, 2001–2007. *J. Infect. Dis.* **2009**, *200*, 802–812. [CrossRef]
9. Van Der Poel, W.H.M.; Vinjé, J.; Van Der Heide, R.; Herrera, M.I.; Vivo, A.; Koopmans, M.P.G. Norwalk-like calicivirus genes in farm animals. *Emerg. Infect. Dis.* **2000**, *6*, 36–41. [CrossRef]
10. Sugieda, M.; Nagaoka, H.; Kakishima, Y.; Ohshita, T.; Nakamura, S.; Nakajima, S. Detection of Norwalk-like virus genes in the caecum contents of pigs. Brief report. *Arch. Virol.* **1998**, *143*, 1215–1221. [CrossRef] [PubMed]
11. Dastjerdi, A.M.; Green, J.; Gallimore, C.I.; Brown, D.W.G.; Bridger, J.C. The bovine Newbury agent-2 is genetically more closely related to human SRSVs than to animal caliciviruses. *Virology* **1999**, *254*, 1–5. [CrossRef] [PubMed]
12. Liu, B.L.; Lambden, P.R.; Günther, H.; Otto, P.; Elschner, M.; Clarke, I.N. Molecular characterization of a bovine enteric calicivirus: Relationship to the Norwalk-like viruses. *J. Virol.* **1999**, *73*, 819–825.
13. Menon, V.K.; George, S.; Shanti, A.A.; Saravanabavan, A.; Samuel, P.; Ramani, S.; Estes, M.K.; Kang, G. Exposure to human and bovine noroviruses in a birth Cohort in southern India from 2002 to 2006. *J. Clin. Microbiol.* **2013**, *51*, 2391–2395. [CrossRef]
14. Vildevall, M.; Grahn, A.; Oliver, S.L.; Bridger, J.C.; Charpilienne, A.; Poncet, D.; Larson, G.; Svensson, L. Human antibody responses to bovine (newbury-2) norovirus (GIII.2) and association to histo-blood group antigens. *J. Med. Virol.* **2010**, *82*, 1241–1246. [CrossRef] [PubMed]
15. Mesquita, J.R.; Costantini, V.P.; Cannon, J.L.; Lin, S.C.; Nascimento, M.S.J.; Vinjé, J. Presence of Antibodies against Genogroup VI Norovirus in Humans. *Virol. J.* **2013**. [CrossRef]
16. Martino, B.D.; Di Profio, F.; Ceci, C.; Felice, E.D.; Green, K.Y.; Bok, K.; Grazia, S.D.; Giammanco, G.M.; Massirio, I.; Lorusso, E.; et al. Seroprevalence of norovirus genogroup IV antibodies among humans, Italy, 2010–2011. *Emerg. Infect. Dis.* **2014**, *20*, 1828–1832. [CrossRef] [PubMed]
17. Smith, A.W.; Skilling, D.E.; Cherry, N.; Mead, J.H.; Matson, D.O. Calicivirus emergence from ocean reservoirs: Zoonotic and interspecies movements. *Emerg. Infect. Dis.* **1998**, *4*, 13–20. [CrossRef] [PubMed]
18. Karst, S.M.; Wobus, C.E. Viruses in Rodent Colonies: Lessons Learned from Murine Noroviruses. *Annu. Rev. Virol.* **2015**, *2*, 525–548. [CrossRef]
19. Karst, S.M.; Wobus, C.E.; Goodfellow, I.G.; Green, K.Y.; Virgin, H.W. Advances in norovirus biology. *Cell Host Microbe* **2014**, *15*, 668–680. [CrossRef]
20. Baldridge, M.T.; Turula, H.; Wobus, C.E. Norovirus Regulation by Host and Microbe. *Trends Mol. Med.* **2016**, *22*, 1047–1059. [CrossRef] [PubMed]
21. Wang, J.; Deng, Z. Detection and forecasting of oyster norovirus outbreaks: Recent advances and future perspectives. *Mar. Environ. Res.* **2012**, *80*, 62–69. [CrossRef]
22. Hassard, F.; Harris, J.P.; Jones, D.L.; Sharp, J.H.; Taft, H.; LeVay, L.; McDonald, J.E.; Tuson, K.; Malham, S.K. Critical Review on the Public Health Impact of Norovirus Contamination in Shellfish and the Environment: A UK Perspective. *Food Environ. Virol.* **2017**, *9*, 123–141. [CrossRef] [PubMed]
23. Adler, J.L.; Zickl, R. Winter Vomiting Disease. *J. Infect. Dis.* **1969**, *119*, 668–673. [CrossRef] [PubMed]
24. Kapikian, A.Z. The Discovery of the 27-nm Norwalk Virus: An Historic Perspective. *J. Infect. Dis.* **2000**, *181* (Suppl. 2), S295–S302. [CrossRef] [PubMed]
25. Wang, Q.H.; Myung, G.H.; Cheetham, S.; Souza, M.; Funk, J.A.; Saif, L.J. Porcine noroviruses related to human noroviruses. *Emerg. Infect. Dis.* **2005**, *11*, 1874–1881. [CrossRef]
26. Shen, Q.; Zhang, W.; Yang, S.; Cui, L.; Hua, X. Complete genome sequence of a new-genotype porcine norovirus isolated from piglets with diarrhea. *J. Virol.* **2012**, *86*, 7015–7016. [CrossRef] [PubMed]
27. Shen, Q.; Zhang, W.; Yang, S.; Yang, Z.; Chen, Y.; Cui, L.; Zhu, J.; Hua, X. Recombinant porcine norovirus identified from piglet with diarrhea. *BMC Vet. Res.* **2012**, *8*, 155. [CrossRef]
28. Scheuer, K.A.; Oka, T.; Hoet, A.E.; Gebreyes, W.A.; Molla, B.Z.; Saif, L.J.; Wang, Q. Prevalence of porcine Noroviruses, molecular characterization of emerging porcine sapoviruses from finisher swine in the United States, and unified classification scheme for sapoviruses. *J. Clin. Microbiol.* **2013**, *51*, 2344–2353. [CrossRef]
29. Niendorf, S.; Klemm, U.; Marques, A.M.; Bock, C.T.; Höhne, M. Infection with the persistent murine norovirus strain MNV-S99 suppresses IFN-Beta release and activation of stat1 In vitro. *PLoS ONE* **2016**, *11*, e0156898. [CrossRef]

30. Mattison, K.; Shukla, A.; Cook, A.; Pollari, F.; Friendship, R.; Kelton, D.; Bidawid, S.; Farber, J.M. Human noroviruses in swine and cattle. *Emerg. Infect. Dis.* **2007**, *13*, 1184–1188. [CrossRef]
31. L'Homme, Y.; Sansregret, R.; Plante-Fortier, É.; Lamontagne, A.M.; Lacroix, G.; Ouardani, M.; Deschamps, J.; Simard, G.; Simard, C. Genetic diversity of porcine Norovirus and Sapovirus: Canada, 2005–2007. *Arch. Virol.* **2009**, *154*, 581–593. [CrossRef]
32. L'Homme, Y.; Sansregret, R.; Simard, C. Broad range RT-PCR assays targeting human noroviruses also detect swine noroviruses. *Food Microbiol.* **2009**, *26*, 552–555. [CrossRef]
33. Shen, Q.; Ren, R.; Zhang, W.; Yang, Z.; Yang, S.; Chen, Y.; Cui, L.; Hua, X. Prevalence of hepatitis E virus and porcine caliciviruses in pig farms of Guizhou province, China. *Hepat. Mon.* **2011**, *11*, 459–463.
34. Chao, D.Y.; Wei, J.Y.; Chang, W.F.; Wang, J.; Wang, L.C. Detection of Multiple Genotypes of Calicivirus Infection in Asymptomatic Swine in Taiwan. *Zoonoses Public Health* **2012**, *59*, 434–444. [CrossRef]
35. Shen, Q.; Zhang, W.; Yang, S.; Chen, Y.; Ning, H.; Shan, T.; Liu, J.; Yang, Z.; Cui, L.; Zhu, J.; et al. Molecular detection and prevalence of porcine caliciviruses in eastern China from 2008 to 2009. *Arch. Virol.* **2009**, *154*, 1625–1630. [CrossRef]
36. Nakamura, K.; Saga, Y.; Iwai, M.; Obara, M.; Horimoto, E.; Hasegawa, S.; Kurata, T.; Okumura, H.; Nagoshi, M.; Takizawa, T. Frequent detection of noroviruses and sapoviruses in swine and high genetic diversity of porcine sapovirus in Japan during fiscal year 2008. *J. Clin. Microbiol.* **2010**, *48*, 1215–1222. [CrossRef]
37. Song, Y.J.; Yu, J.N.; Nam, H.M.; Bak, H.R.; Lee, J.B.; Park, S.Y.; Song, C.S.; Seo, K.H.; Choi, I.S. Identification of genetic diversity of porcine Norovirus and Sapovirus in Korea. *Virus Genes* **2011**, *42*, 394–401. [CrossRef]
38. Wolf, S.; Williamson, W.; Hewitt, J.; Lin, S.; Rivera-Aban, M.; Ball, A.; Scholes, P.; Savill, M.; Greening, G.E. Molecular detection of norovirus in sheep and pigs in New Zealand farms. *Vet. Microbiol.* **2009**, *133*, 184–189. [CrossRef]
39. Martínez, M.A.; Alcalá, A.C.; Carruyo, G.; Botero, L.; Liprandi, F.; Ludert, J.E. Molecular detection of porcine enteric caliciviruses in Venezuelan farms. *Vet. Microbiol.* **2006**, *116*, 77–84. [CrossRef]
40. Collins, P.J.; Martella, V.; Buonavoglia, C.; O'Shea, H. Detection and characterization of porcine sapoviruses from asymptomatic animals in Irish farms. *Vet. Microbiol.* **2009**, *139*, 176–182. [CrossRef]
41. Machnowska, P.; Ellerbroek, L.; Johne, R. Detection and characterization of potentially zoonotic viruses in faeces of pigs at slaughter in Germany. *Vet. Microbiol.* **2014**, *168*, 60–68. [CrossRef]
42. Mijovski, J.Z.; Poljšak-Prijatelj, M.; Steyer, A.; Barlič-Maganja, D.; Koren, S. Detection and molecular characterisation of noroviruses and sapoviruses in asymptomatic swine and cattle in Slovenian farms. *Infect. Genet. Evol.* **2010**, *10*, 413–420. [CrossRef] [PubMed]
43. Sisay, Z.; Djikeng, A.; Berhe, N.; Belay, G.; Abegaz, W.E.; Wang, Q.H.; Saif, L.J. First detection and molecular characterization of sapoviruses and noroviruses with zoonotic potential in swine in Ethiopia. *Arch. Virol.* **2016**, *161*, 2739–2747. [CrossRef] [PubMed]
44. Silva, P.F.; Alfieri, A.F.; Barry, A.F.; de Arruda Leme, R.; Gardinali, N.R.; van der Poel, W.H.; Alfieri, A.A. High frequency of porcine norovirus infection in finisher units of Brazilian pig-production systems. *Trop. Anim. Health Prod.* **2015**, *47*, 237–241. [CrossRef]
45. Yin, Y.; Tohya, Y.; Ogawa, Y.; Numazawa, D.; Kato, K.; Akashi, H. Genetic analysis of calicivirus genomes detected in intestinal contents of piglets in Japan. *Arch. Virol.* **2006**, *151*, 1749–1759. [CrossRef]
46. Farkas, T.; Nakajima, S.; Sugieda, M.; Deng, X.; Zhong, W.; Jiang, X. Seroprevalence of noroviruses in swine. *J. Clin. Microbiol.* **2005**, *43*, 657–661. [CrossRef]
47. Mesquita, J.R.; Delgado, I.; Costantini, V.; Heenemann, K.; Vahlenkamp, T.W.; Vinjé, J.; Nascimento, M.S.J. Seroprevalence of canine norovirus in 14 European countries. *Clin. Vaccine Immunol.* **2014**, *21*, 898–900. [CrossRef] [PubMed]
48. Sisay, Z.; Wang, Q.; Oka, T.; Saif, L. Prevalence and molecular characterization of porcine enteric caliciviruses and first detection of porcine kobuviruses in US swine. *Arch. Virol.* **2013**, *158*, 1583–1588. [CrossRef]
49. Thomas, C.; Jung, K.; Han, M.G.; Hoet, A.; Scheuer, K.; Wang, Q.; Saif, L.J. Retrospective serosurveillance of bovine norovirus (GIII.2) and nebovirus in cattle from selected feedlots and a veal calf farm in 1999 to 2001 in the United States. *Arch. Virol.* **2014**, *159*, 83–90. [CrossRef] [PubMed]
50. Cho, Y.I.; Han, J.I.; Wang, C.; Cooper, V.; Schwartz, K.; Engelken, T.; Yoon, K.J. Case-control study of microbiological etiology associated with calf diarrhea. *Vet. Microbiol.* **2013**, *166*, 375–385. [CrossRef]

51. Wise, A.G.; Monroe, S.S.; Hanson, L.E.; Grooms, D.L.; Sockett, D.; Maes, R.K. Molecular characterization of noroviruses detected in diarrheic stools of Michigan and Wisconsin dairy calves: Circulation of two distinct subgroups. *Virus Res.* **2004**, *100*, 165–177. [CrossRef]
52. Smiley, J.R.; Hoet, A.E.; Tråvén, M.; Tsunemitsu, H.; Saif, L.J. Reverse transcription-PCR assays for detection of bovine enteric caliciviruses (BEC) and analysis of the genetic relationships among BEC and human caliciviruses. *J. Clin. Microbiol.* **2003**, *41*, 3089–3099. [CrossRef]
53. Pinto, P.; Wang, Q.; Chen, N.; Dubovi, E.J.; Daniels, J.B.; Millward, L.M.; Buonavoglia, C.; Martella, V.; Saif, L.J. Discovery and genomic characterization of noroviruses from a gastroenteritis outbreak in domestic cats in the us. *PLoS ONE* **2012**, *7*, e32739. [CrossRef]
54. Zhang, W.; Li, L.; Deng, X.; Kapusinszky, B.; Pesavento, P.A.; Delwart, E. Faecal virome of cats in an animal shelter. *J. Gen. Virol.* **2014**, *95*, 2553–2564. [CrossRef]
55. Li, L.; Shan, T.; Wang, C.; Côté, C.; Kolman, J.; Onions, D.; Gulland, F.M.D.; Delwart, E. The fecal viral flora of California sea lions. *J. Virol.* **2011**, *85*, 9909–9917. [CrossRef] [PubMed]
56. Alcalá, A.C.; Hidalgo, M.A.; Obando, C.; Vizzi, E.; Liprandi, F.; Ludert, J.E. Molecular identification of bovine enteric caliciviruses in Venezuela. *Acta Cient. Venez.* **2003**, *54*, 148–152. [PubMed]
57. Ferragut, F.; Vega, C.G.; Mauroy, A.; Conceição-Neto, N.; Zeller, M.; Heylen, E.; Uriarte, E.L.; Bilbao, G.; Bok, M.; Matthijnssens, J.; et al. Molecular detection of bovine Noroviruses in Argentinean dairy calves: Circulation of a tentative new genotype. *Infect. Genet. Evol.* **2016**, *40*, 144–150. [CrossRef]
58. Cunha, J.B.; de Mendonça, M.C.L.; Miagostovich, M.P.; Leite, J.P.G. First detection of porcine norovirus GII.18 in Latin America. *Res. Vet. Sci.* **2010**, *89*, 126–129. [CrossRef]
59. Cunha, J.B.; de Mendonça, M.C.L.; Miagostovich, M.P.; Leite, J.P.G. Genetic diversity of porcine enteric caliciviruses in pigs raised in Rio de Janeiro State, Brazil. *Arch. Virol.* **2010**, *155*, 1301–1305. [CrossRef]
60. Das Merces Hernandez, J.; Stangarlin, D.C.; Siqueira, J.A.M.; de Souza Oliveira, D.; Portal, T.M.; Barry, A.F.; Dias, F.A.; de Matos, J.C.S.; Mascarenhas, J.D.P.; Gabbay, Y.B. Genetic diversity of porcine sapoviruses in pigs from the Amazon region of Brazil. *Arch. Virol.* **2014**, *159*, 927–933. [CrossRef] [PubMed]
61. Almeida, P.R.; Lorenzetti, E.; Cruz, R.S.; Watanabe, T.T.; Zlotowski, P.; Alfieri, A.A.; Driemeier, D. Diarrhea caused by rotavirus A, B, and C in suckling piglets from southern Brazil: Molecular detection and histologic and immunohistochemical characterization. *J. Vet. Diagn. Investig.* **2018**. [CrossRef] [PubMed]
62. Castro, T.X.; Cubel Garcia, R.C.N.; Fumian, T.M.; Costa, E.M.; Mello, R.; White, P.A.; Leite, J.P.G. Detection and molecular characterization of caliciviruses (vesivirus and norovirus) in an outbreak of acute diarrhea in kittens from Brazil. *Vet. J.* **2015**, *206*, 115–117. [CrossRef]
63. Guo, Z.; He, Q.; Yue, H.; Zhang, B.; Tang, C. First detection of Nebovirus and Norovirus from cattle in China. *Arch. Virol.* **2018**, *163*, 475–478. [CrossRef] [PubMed]
64. Yang, L.; Wang, Q.; Xu, L.; Tu, C.; Huang, X.; He, B. Detection and Characterization of a Novel Norovirus in Bats, China. *Virol. Sin.* **2018**, *33*, 100–103. [CrossRef] [PubMed]
65. Soma, T.; Nakagomi, O.; Nakagomi, T.; Mochizuki, M. Detection of norovirus and sapovirus from diarrheic dogs and cats in Japan. *Microbiol. Immunol.* **2015**, *59*, 123–128. [CrossRef]
66. Tsunesumi, N.; Sato, G.; Iwasa, M.; Kabeya, H.; Maruyama, S.; Tohya, Y. Novel murine norovirus-like genes in wild rodents in Japan. *J. Vet. Med. Sci.* **2012**, *74*, 1221–1224. [CrossRef]
67. Keum, H.O.; Moon, H.J.; Park, S.J.; Kim, H.K.; Rho, S.M.; Park, B.K. Porcine noroviruses and sapoviruses on Korean swine farms. *Arch. Virol.* **2009**, *154*, 1765–1774. [CrossRef]
68. Lyoo, K.S.; Jung, M.C.; Yoon, S.W.; Kim, H.K.; Jeong, D.G. Identification of canine norovirus in dogs in South Korea. *BMC Vet. Res.* **2018**, *14*, 413. [CrossRef] [PubMed]
69. Park, S.I.; Jeong, C.; Kim, H.H.; Park, S.H.; Park, S.J.; Hyun, B.H.; Yang, D.K.; Kim, S.K.; Kang, M.I.; Cho, K.O. Molecular epidemiology of bovine noroviruses in South Korea. *Vet. Microbiol.* **2007**, *124*, 125–133. [CrossRef]
70. Pourasgari, F.; Kaplon, J.; Sanchooli, A.; Fremy, C.; Karimi-Naghlani, S.; Otarod, V.; Ambert-Balay, K.; Mojgani, N.; Pothier, P. Molecular prevalence of bovine noroviruses and neboviruses in newborn calves in Iran. *Arch. Virol.* **2018**. [CrossRef]
71. Mahzounieh, M.; Moghtadaei, E.; Zahraei Salehi, T. Detection of calicivirus genomes in calves using Ni/E3 primers in Shahrekord Area, Iran. *Pak. J. Biol. Sci.* **2006**, *9*, 227–230.
72. Yilmaz, H.; Turan, N.; Altan, E.; Bostan, K.; Yilmaz, A.; Helps, C.R.; Cho, K.O. First report on the phylogeny of bovine norovirus in Turkey. *Arch. Virol.* **2011**, *156*, 143–147. [CrossRef] [PubMed]

73. Thuran, T.; Irehan, B. Detection and molecular analysis of bovine enteric norovirus and nebovirus in Turkey. *J. Vet. Res.* **2018**, *62*, 129–135. [CrossRef] [PubMed]
74. Haga, K.; Fujimoto, A.; Takai-Todaka, R.; Miki, M.; Doan, Y.H.; Murakami, K.; Yokoyama, M.; Murata, K.; Nakanishi, A.; Katayama, K. Functional receptor molecules CD300lf and CD300ld within the CD300 family enable murine noroviruses to infect cells. *Proc. Natl. Acad. Sci. USA* **2016**, *113*, E6248–E6255. [CrossRef]
75. Wolf, S.; Williamson, W.M.; Hewitt, J.; Rivera-Aban, M.; Lin, S.; Ball, A.; Scholes, P.; Greening, G.E. Sensitive multiplex real-time reverse transcription-PCR assay for the detection of human and animal noroviruses in clinical and environmental samples. *Appl. Environ. Microbiol.* **2007**, *73*, 5464–5470. [CrossRef]
76. Monini, M.; Di Bartolo, I.; Ianiro, G.; Angeloni, G.; Magistrali, C.F.; Ostanello, F.; Ruggeri, F.M. Detection and molecular characterization of zoonotic viruses in swine fecal samples in Italian pig herds. *Arch. Virol.* **2015**, *160*, 2547–2556. [CrossRef]
77. Di Bartolo, I.; Tofani, S.; Angeloni, G.; Ponterio, E.; Ostanello, F.; Ruggeri, F.M. Detection and characterization of porcine caliciviruses in Italy. *Arch. Virol.* **2014**, *159*, 2479–2484. [CrossRef]
78. Di Martino, B.; Di Profio, F.; Di Felice, E.; Melegari, I.; Ceci, C.; Mauroy, A.; Thiry, E.; Martella, V.; Marsilio, F. Genetic heterogeneity of bovine noroviruses in Italy. *Arch. Virol.* **2014**, *159*, 2717–2722. [CrossRef]
79. Di Bartolo, I.; Ponterio, E.; Monini, M.; Ruggeri, F.M. A pilot survey of bovine norovirus in northern Italy. *Vet. Rec.* **2011**, *169*, 73. [CrossRef]
80. Di Martino, B.; Di Profio, F.; Melegari, I.; Sarchese, V.; Massirio, I.; Palermo, G.; Romito, G.; Lorusso, E.; Lanave, G.; Bodnar, L.; et al. Seroprevalence for norovirus genogroup II, IV and VI in dogs. *Vet. Microbiol.* **2017**, *203*, 68–72. [CrossRef]
81. Di Martino, B.; Marsilio, F.; Di Profio, F.; Lorusso, E.; Friedrich, K.G.; Buonavoglia, C.; Martella, V. Detection of antibodies against Norovirus genogroup GIV in carnivores. *Clin. Vaccine Immunol.* **2010**, *17*, 180–182. [CrossRef]
82. Martella, V.; Decaro, N.; Lorusso, E.; Radogna, A.; Moschidou, P.; Amorisco, F.; Lucente, M.S.; Desario, C.; Mari, V.; Elia, G.; et al. Genetic heterogeneity and recombination in canine noroviruses. *J. Virol.* **2009**, *83*, 11391–11396. [CrossRef]
83. Bodnar, L.; Lorusso, E.; Di Martino, B.; Catella, C.; Lanave, G.; Elia, G.; Bányai, K.; Buonavoglia, C.; Martella, V. Identification of a novel canine norovirus. *Infect. Genet. Evol.* **2017**, *52*, 75–81. [CrossRef]
84. Martella, V.; Campolo, M.; Lorusso, E.; Cavicchio, P.; Camero, M.; Bellacicco, A.L.; Decaro, N.; Elia, G.; Greco, G.; Corrente, M.; et al. Norovirus in captive lion cub (Panthera leo). *Emerg. Infect. Dis.* **2007**, *13*, 1071–1073. [CrossRef]
85. Di Martino, B.; Di Profio, F.; Melegari, I.; Sarchese, V.; Cafiero, M.A.; Robetto, S.; Aste, G.; Lanave, G.; Marsilio, F.; Martella, V. A novel feline norovirus in diarrheic cats. *Infect. Genet. Evol.* **2016**, *38*, 132–137. [CrossRef]
86. Halaihel, N.; Masía, R.M.; Fernández-Jiménez, M.; Ribes, J.M.; Montava, R.; De Blas, I.; Gironés, O.; Alonso, J.L.; Buesa, J. Enteric calicivirus and rotavirus infections in domestic pigs. *Epidemiol. Infect.* **2010**, *138*, 542–548. [CrossRef]
87. Mesquita, J.R.; Nascimento, M.S. Molecular epidemiology of canine norovirus in dogs from Portugal, 2007–2011. *BMC Vet. Res.* **2012**, *8*, 107. [CrossRef]
88. Mesquita, J.R.; Nascimento, M.S.J. Gastroenteritis outbreak associated with faecal shedding of canine norovirus in a portuguese kennel following introduction of imported dogs from russia. *Transbound. Emerg. Dis.* **2012**, *59*, 456–459. [CrossRef]
89. Mesquita, J.R.; Barclay, L.; Nascimento, M.S.J.; Vinjé, J. Novel norovirus in dogs with diarrhea. *Emerg. Infect. Dis.* **2010**, *16*, 980–982. [CrossRef]
90. Ntafis, V.; Xylouri, E.; Radogna, A.; Buonavoglia, C.; Martella, V. Outbreak of canine norovirus infection in young dogs. *J. Clin. Microbiol.* **2010**, *48*, 2605–2608. [CrossRef]
91. Kaplon, J.; Guenau, E.; Asdrubal, P.; Pothier, P.; Ambert-Balay, K. Possible novel Nebovirus genotype in cattle, France. *Emerg. Infect. Dis.* **2011**, *17*, 1120–1123. [CrossRef]
92. Kaplon, J.; Fremy, C.; Bernard, S.; Rehby, L.; Aho, S.; Pothier, P.; Ambert-Balay, K. Impact of rotavirus vaccine on rotavirus genotypes and caliciviruses circulating in French cattle. *Vaccine* **2013**, *31*, 2433–2440. [CrossRef]
93. Oliver, S.L.; Wood, E.; Asobayire, E.; Wathes, D.C.; Brickell, J.S.; Elschner, M.; Otto, P.; Lambden, P.R.; Clarke, I.N.; Bridger, J.C. Serotype 1 and 2 bovine noroviruses are endemic in cattle in the United Kingdom and Germany. *J. Clin. Microbiol.* **2007**, *45*, 3050–3052. [CrossRef] [PubMed]

94. Deng, Y.; Batten, C.A.; Liu, B.L.; Lambden, P.R.; Elschner, M.; Günther, H.; Otto, H.P.; Schnürch, P.; Eichhorn, W.; Herbst, W.; et al. Studies of epidemiology and seroprevalence of bovine Noroviruses in Germany. *J. Clin. Microbiol.* **2003**, *41*, 2300–2305. [CrossRef]
95. Ike, A.C.; Roth, B.N.; Böhm, R.; Pfitzner, A.J.; Marschang, R.E. Identification of bovine enteric Caliciviruses (BEC) from cattle in Baden-Württemberg. *DTW Dtsch Tierarztl Wochenschr* **2007**, *114*, 12–15.
96. Sachsenröder, J.; Braun, A.; Machnowska, P.; Ng, T.F.F.; Deng, X.; Guenther, S.; Bernstein, S.; Ulrich, R.G.; Delwart, E.; Johne, R. Metagenomic identification of novel enteric viruses in urban wild rats and genome characterization of a group A rotavirus. *J. Gen. Virol.* **2014**, *95*, 2734–2747. [CrossRef]
97. Van Der Poel, W.H.M.; Van Der Heide, R.; Verschoor, F.; Gelderblom, H.; Vinjé, J.; Koopmans, M.P.G. Epidemiology of Norwalk-like virus infections in cattle in The Netherlands. *Vet. Microbiol.* **2003**, *92*, 297–309. [CrossRef]
98. De Graaf, M.; Bodewes, R.; van Elk, C.E.; van de Bildt, M.; Getu, S.; Aron, G.I.; Verjans, G.M.G.M.; Osterhaus, A.D.M.E.; van den Brand, J.M.A.; Kuiken, T.; et al. Norovirus infection in harbor porpoises. *Emerg. Infect. Dis.* **2017**, *23*, 87–91. [CrossRef] [PubMed]
99. Mauroy, A.; Scipioni, A.; Mathijs, E.; Miry, C.; Ziant, D.; Thys, C.; Thiry, E. Noroviruses and sapoviruses in pigs in Belgium. *Arch. Virol.* **2008**, *153*, 1927–1931. [CrossRef]
100. Mauroy, A.; Scipioni, A.; Mathijs, E.; Saegerman, C.; Mast, J.; Bridger, J.C.; Ziant, D.; Thys, C.; Thiry, E. Epidemiological study of bovine norovirus infection by RT-PCR and a VLP-based antibody ELISA. *Vet. Microbiol.* **2009**, *137*, 243–251. [CrossRef]
101. Mauroy, A.; Scipioni, A.; Mathijs, E.; Ziant, D.; Daube, G.; Thirya, E. Complete genome sequence of a novel bovine norovirus: Evidence for slow genetic evolution in genogroup III genotype 2 noroviruses. *J. Virol.* **2012**, *86*, 12449–12450. [CrossRef]
102. Mauroy, A.; Scipioni, A.; Mathijs, E.; Thys, C.; Thiry, E. Molecular detection of kobuviruses and recombinant noroviruses in cattle in continental Europe. *Arch. Virol.* **2009**, *154*, 1841–1845. [CrossRef] [PubMed]
103. Woode, G.N.; Bridger, J.C. Isolation of small viruses resembling astroviruses and caliciviruses from acute enteritis of calves. *J. Med. Microbiol.* **1978**, *11*, 441–452. [CrossRef]
104. Milnes, A.S.; Binns, S.H.; Oliver, S.L.; Bridger, J.C. Retrospective study of noroviruses in samples of diarrhoea from cattle, using the Veterinary Laboratories Agency's Farmfile database. *Vet. Rec.* **2007**, *160*, 326–330. [CrossRef]
105. Caddy, S.; Emmott, E.; El-Attar, L.; Mitchell, J.; De Rougemont, A.; Brownlie, J.; Goodfellow, I. Serological evidence for multiple strains of canine norovirus in the UK dog population. *PLoS ONE* **2013**, *8*, e81596. [CrossRef] [PubMed]
106. Caddy, S.L.; De Rougemont, A.; Emmott, E.; El-Attar, L.; Mitchell, J.A.; Hollinshead, M.; Belliot, G.; Brownlie, J.; Le Pendu, J.; Goodfellow, I. Evidence for human norovirus infection of dogs in the United Kingdom. *J. Clin. Microbiol.* **2015**, *53*, 1873–1883. [CrossRef] [PubMed]
107. Smith, D.B.; McFadden, N.; Blundell, R.J.; Meredith, A.; Simmonds, P. Diversity of murine norovirus in wild-rodent populations: Species-specific associations suggest an ancient divergence. *J. Gen. Virol.* **2012**, *93*, X259–266. [CrossRef] [PubMed]
108. Wolf, S.; Reetz, J.; Johne, R.; Heiberg, A.C.; Petri, S.; Kanig, H.; Ulrich, R.G. The simultaneous occurrence of human norovirus and hepatitis E virus in a Norway rat (Rattus norvegicus). *Arch. Virol.* **2013**, *158*, 1575–1578. [CrossRef]
109. Jor, E.; Myrmel, M.; Jonassen, C.M. SYBR Green based real-time RT-PCR assay for detection and genotype prediction of bovine noroviruses and assessment of clinical significance in Norway. *J. Virol. Methods* **2010**, *169*, 1–7. [CrossRef]
110. Summa, M.; von Bonsdorff, C.H.; Maunula, L. Pet dogs-A transmission route for human noroviruses? *J. Clin. Virol.* **2012**, *53*, 244–247. [CrossRef] [PubMed]
111. Summa, M.; Henttonen, H.; Maunula, L. Human noroviruses in the faeces of wild birds and rodents-new potential transmission routes. *Zoonoses Public Health* **2018**. [CrossRef] [PubMed]
112. Reuter, G.; Bíró, H.; Szucs, G. Enteric caliciviruses in domestic pigs in Hungary. *Arch. Virol.* **2007**, *152*, 611–614. [CrossRef]
113. Mihalov-Kovács, E.; Marton, S.; Fehér, E.; Lengyel, G.; Jakab, F.; Tuboly, T.; Bányai, K. Enteric viral infections of sheltered dogs in Hungary. *Magy. Allatorv. Lapja* **2014**, *136*, 661–670.

114. Farkas, T.; Fey, B.; Keller, G.; Martella, V.; Egyed, L. Molecular detection of murine noroviruses in laboratory and wild mice. *Vet. Microbiol.* **2012**, *160*, 463–467. [CrossRef]
115. Mohamed, F.F.; Mansour, S.M.; El-Araby, I.E.; Mor, S.K.; Goyal, S.M. Molecular detection of enteric viruses from diarrheic calves in Egypt. *Arch. Virol.* **2017**, *162*, 129–137. [CrossRef] [PubMed]
116. Hassine-Zaafrane, M.; Kaplon, J.; Sdiri-Loulizi, K.; Aouni, Z.; Pothier, P.; Aouni, M.; Ambert-Balay, K. Molecular prevalence of bovine noroviruses and neboviruses detected in central-eastern Tunisia. *Arch. Virol.* **2012**, *157*, 1599–1604. [CrossRef] [PubMed]
117. Taku, O.; Iweriebor, B.C.; Nwodo, U.U.; Obi, L.C.; Okoh, A.I. Occurrence of Norovirus in pig faecal samples in the Eastern Cape, South Africa. *Asian Pac. J. Trop. Dis.* **2017**, *7*, 151–155. [CrossRef]
118. Günther, H.; Otto, P.; Heilmann, P. Diarrhea in young calves. 6. Determination of the pathogenicity of a bovine coronavirus and an unidentified icosahedral virus. *Arch. Exp. Vet.* **1984**, *38*, 781–792.
119. Jung, K.; Scheuer, K.A.; Zhang, Z.; Wang, Q.; Saif, L.J. Pathogenesis of GIII.2 bovine norovirus, CV186-OH/00/US strain in gnotobiotic calves. *Vet. Microbiol.* **2014**, *168*, 202–207. [CrossRef]
120. Otto, P.H.; Clarke, I.N.; Lambden, P.R.; Salim, O.; Reetz, J.; Liebler-Tenorio, E.M. Infection of calves with bovine norovirus GIII.1 strain Jena virus: An experimental model to study the pathogenesis of norovirus infection. *J. Virol.* **2011**, *85*, 12013–12021. [CrossRef] [PubMed]
121. Han, M.G.; Wang, Q.; Smiley, J.R.; Change, K.O.; Saif, L.J. Self-assembly of the recombinant capsid protein of a bovine norovirus (BoNV) into virus-like particles and evaluation of cross-reactivity of BoNV with human noroviruses. *J. Clin. Microbiol.* **2005**, *43*, 778–785. [CrossRef]
122. Han, M.G.; Cheetham, S.; Azevedo, M.; Thomas, C.; Saif, L.J. Immune responses to bovine norovirus-like particles with various adjuvants and analysis of protection in gnotobiotic calves. *Vaccine* **2006**, *24*, 317–326. [CrossRef]
123. Souza, M.; Azevedo, M.S.P.; Jung, K.; Cheetham, S.; Saif, L.J. Pathogenesis and immune responses in gnotobiotic calves after infection with the genogroup II.4-HS66 strain of human norovirus. *J. Virol.* **2008**, *82*, 1777–1786. [CrossRef]
124. Oliver, S.L.; Asobayire, E.; Charpilienne, A.; Cohen, J.; Bridger, J.C. Complete genomic characterization and antigenic relatedness of genogroup III, genotype 2 bovine noroviruses. *Arch. Virol.* **2007**, *152*, 257–272. [CrossRef] [PubMed]
125. La Rosa, G.; Iaconelli, M.; Pourshaban, M.; Fratini, M. Molecular detection and genetic diversity of norovirus genogroup IV: A yearlong monitoring of sewage throughout Italy. *Arch. Virol.* **2010**, *155*, 589–593. [CrossRef] [PubMed]
126. Van Beek, J.; de Graaf, M.; Al-Hello, H.; Allen, D.J.; Ambert-Balay, K.; Botteldoorn, N.; Brytting, M.; Buesa, J.; Cabrerizo, M.; Chan, M.; et al. NoroNet, Molecular surveillance of norovirus, 2005–2016: An epidemiological analysis of data collected from the NoroNet network. *Lancet Infect. Dis.* **2018**, *18*, 545–553. [CrossRef]
127. Takano, T.; Kusuhara, H.; Kuroishi, A.; Takashina, M.; Doki, T.; Nishinaka, T.; Hohdatsu, T. Molecular characterization and pathogenicity of a genogroup GVI feline norovirus. *Vet. Microbiol.* **2015**, *178*, 201–207. [CrossRef]
128. Takano, T.; Hiramatsu, K.; Matsuyama, M.; Mutoh, K.; Matsumoto, Y.; Fukushima, T.; Doki, T.; Kusuhara, H.; Hohdatsu, T. Viral shedding and clinical status of feline-norovirus-infected cats after reinfection with the same strain. *Arch. Virol.* **2018**, *163*, 1503–1510. [CrossRef] [PubMed]
129. Kocher, J.F.; Lindesmith, L.C.; Huynh, J.; Gates, J.E.; Debbink, K.; Beall, A.; Mallory, M.L.; Donaldson, E.F.; Barica, R.S. Bat Caliciviruses and Human Noroviruses Are Antigenically Similar and Have Overlapping Histo-Blood Group Antigen Binding Profile. *MBio* **2018**, *9*, e00869-18. [CrossRef]
130. Wu, Z.; Yang, L.; Ren, X.; He, G.; Zhang, J.; Yang, J.; Qian, Z.; Dong, J.; Sun, L.; Zhu, Y.; et al. Deciphering the bat virome catalog to better understand the ecological diversity of bat viruses and the bat origin of emerging infectious diseases. *ISME J.* **2016**, *10*, 609–620. [CrossRef]
131. Humphrey, T.J. An outbreak of calicivirus associated gastroenteritis in an elderly persons home. A possible zoonosis? *J. Hyg. (Lond)* **1984**, *93*, 293–299. [CrossRef] [PubMed]
132. Widdowson, M.A.; Rockx, B.; Schepp, R.; Van Der Poel, W.H.M.; Vinje, J.; Van Duynhoven, Y.T.; Koopmans, M.P. Detection of serum antibodies to bovine norovirus in veterinarians and the general population in The Netherlands. *J. Med. Virol.* **2005**, *76*, 119–128. [CrossRef] [PubMed]

133. Bucardo, F.; González, F.; Reyes, Y.; Blandón, P.; Saif, L.; Nordgren, J. Seroprevalence in Household Raised Pigs Indicate High Exposure to GII Noroviruses in Rural Nicaragua. *Zoonoses Public Health* **2016**, *63*, 600–607. [CrossRef] [PubMed]
134. Chan, M.C.W.; Hu, Y.; Chen, H.; Podkolzin, A.T.; Zaytseva, E.V.; Komano, J.; Sakon, N.; Poovorawan, Y.; Vongpunsawad, S.; Thanusuwannasak, T.; et al. Global Spread of Norovirus GII.17 Kawasaki 308, 2014–2016. *Emerg. Infect. Dis.* **2017**, *23*, 1350–1354. [CrossRef]
135. De Graaf, M.; van Beek, J.; Vennema, H.; Podkolzin, A.T.; Hewitt, J.; Bucardo, F.; Templeton, K.; Nordgren, J.; Reuter, G.; Lynch, M.; et al. Emergence of a novel GII.17 norovirus - End of the GII.4 era? *Euro Surveill* **2015**, *20*, 1–8. [CrossRef]
136. He, Z.; Liu, B.; Tao, Y.; Li, C.; Xia, M.; Zhong, W.; Jiang, X.; Liu, H.; Tan, M. Norovirus GII.17 natural infections in Rhesus monkeys, China. *Emerg. Infect. Dis.* **2017**, *23*, 316–319. [CrossRef]
137. Liu, B.; Tao, Y.; Li, C.; Li, X.; Liu, J.; He, Z.; Xia, M.; Jiang, X.; Tan, M.; Liu, H. Complete Genome Sequence of a GII.17 Norovirus Isolated from a Rhesus Monkey in China. *Genome Announc.* **2016**, *4*. [CrossRef] [PubMed]
138. Farkas, T.; Cross, R.W.; Hargitt, I.E.; Lerche, N.W.; Morrow, A.L.; Sestak, K. Genetic diversity and histo-blood group antigen interactions of rhesus enteric caliciviruses. *J. Virol.* **2010**, *84*, 8617–8625. [CrossRef] [PubMed]
139. Farkas, T. Natural norovirus infections in rhesus macaques. *Emerg. Infect. Dis.* **2016**, *22*, 1272–1274. [CrossRef]
140. Jiang, B.; McClure, H.M.; Fankhauser, R.L.; Monroe, S.S.; Glass, R.I. Prevalence of rotavirus and norovirus antibodies in non-human primates. *J. Med. Primatol.* **2004**, *33*, 30–33. [CrossRef] [PubMed]
141. Farkas, T.; Dofour, J.; Jiang, X.; Sestak, K. Detection of norovirus-, sapovirus- and rhesus enteric calicivirus-specific antibodies in captive juvenile macaques. *J. Gen. Virol.* **2010**, *91*, 734–738. [CrossRef]
142. Rockx, B.H.G.; Bogers, W.M.J.M.; Heeney, J.L.; van Amerongen, G.; Koopmans, M.P.G. Experimental norovirus infections in non-human primates. *J. Med. Virol.* **2005**, *75*, 313–320. [CrossRef]
143. De Graaf, M.; van Beek, J.; Koopmans, M.P.G. Human norovirus transmission and evolution in a changing world. *Nat. Rev. Microbiol.* **2016**, *14*, 421–433. [CrossRef]
144. Taube, S.; Kolawole, A.O.; Höhne, M.; Wilkinson, J.E.; Handley, S.A.; Perry, J.W.; Thackray, L.B.; Akkina, R.; Wobus, C.E. A mouse model for human norovirus. *mBio* **2013**, *4*. [CrossRef]
145. Seo, D.J.; Jung, D.; Jung, S.; Ha, S.K.; Ha, S.D.; Choi, I.S.; Myoung, J.; Choi, C. Experimental miniature piglet model for the infection of human norovirus GII. *J. Med. Virol.* **2018**, *90*, 655–662. [CrossRef]
146. Cheetham, S.; Souza, M.; McGregor, R.; Meulia, T.; Wang, Q.; Saif, L.J. Binding patterns of human norovirus-like particles to buccal and intestinal tissues of gnotobiotic pigs in relation to A/H histo-blood group antigen expression. *J. Virol.* **2007**, *81*, 3535–3544. [CrossRef]
147. Jones, M.K.; Watanabe, M.; Zhu, S.; Graves, C.L.; Keyes, L.R.; Grau, K.R.; Gonzalez-Hernandez, M.B.; Iovine, N.M.; Wobus, C.E.; Vinjé, J.; et al. Enteric bacteria promote human and mouse norovirus infection of B cells. *Science* **2014**, *346*, 755–759. [CrossRef] [PubMed]
148. Ettayebi, K.; Crawford, S.E.; Murakami, K.; Broughman, J.R.; Karandikar, U.; Tenge, V.R.; Neill, F.H.; Blutt, S.E.; Zeng, X.L.; Qu, L.; et al. Replication of human noroviruses in stem cell–derived human enteroids. *Science* **2016**, *353*, 1387–1392. [CrossRef] [PubMed]
149. Duizer, E.; Schwab, K.J.; Neill, F.H.; Atmar, R.L.; Koopmans, M.P.G.; Estes, M.K. Laboratory efforts to cultivate noroviruses. *J. Gen. Virol.* **2004**, *85*, 79–87. [CrossRef] [PubMed]
150. Oka, T.; Stoltzfus, G.T.; Zhu, C.; Jung, K.; Wang, Q.; Saif, L.J. Attempts to grow human noroviruses, a sapovirus, and a bovine norovirus in vitro. *PLoS ONE* **2018**, *13*, e0178157. [CrossRef] [PubMed]
151. Lou, F.; Ye, M.; Ma, Y.; Li, X.; DiCaprio, E.; Chen, H.; Krakowka, S.; Hughes, J.; Kingsley, D.; Li, J. A Gnotobiotic Pig Model for Determining Human Norovirus Inactivation by High-Pressure Processing. *Appl. Environ. Microbiol.* **2015**, *81*, 6679–6687. [CrossRef]
152. Bui, T.; Kocher, J.; Li, Y.; Wen, K.; Li, G.; Liu, F.; Yang, X.; Leroith, T.; Tan, M.; Xia, M.; et al. Median infectious dose of human norovirus GII.4 in gnotobiotic pigs is decreased by simvastatin treatment and increased by age. *J. Gen. Virol.* **2013**, *94*, 2005–2016. [CrossRef] [PubMed]
153. Kocher, J.; Bui, T.; Giri-Rachman, E.; Wen, K.; Li, G.; Yang, X.; Liu, F.; Tan, M.; Xia, M.; Zhong, W.; et al. Intranasal P particle vaccine provided partial cross-variant protection against human GII.4 Norovirus diarrhea in gnotobiotic pigs. *J. Virol.* **2014**, *8*, 9728–9743. [CrossRef]
154. Lei, S.; Ramesh, A.; Twitchell, E.; Wen, K.; Bui, T.; Weiss, M.; Yang, X.; Kocher, J.; Li, G.; Giri-Rachman, E.; et al. High protective efficacy of probiotics and rice bran against human norovirus infection and diarrhea in gnotobiotic pigs. *Front. Microbiol.* **2016**, *7*. [CrossRef] [PubMed]

155. Lei, S.; Ryu, J.; Wen, K.; Twitchell, E.; Bui, T.; Ramesh, A.; Weiss, M.; Li, G.; Samuel, H.; Clark-Deener, S.; et al. Increased and prolonged human norovirus infection in RAG2/IL2RG deficient gnotobiotic pigs with severe combined immunodeficiency. *Sci. Rep.* **2016**, *6*, 25222. [CrossRef]
156. Takanashi, S.; Wang, Q.; Chen, N.; Shen, Q.; Jung, K.; Zhang, Z.; Yokoyama, M.; Lindesmith, L.C.; Baric, R.S.; Saif, L.J. Characterization of emerging GII.g/GII.12 noroviruses from a gastroenteritis outbreak in the United States in 2010. *J. Clin. Microbiol.* **2011**, *49*, 3234–3244. [CrossRef] [PubMed]
157. Souza, M.; Cheetham, S.M.; Azevedo, M.S.P.; Costantini, V.; Saif, L.J. Cytokine and antibody responses in gnotobiotic pigs after infection with human norovirus genogroup II.4 (HS66 strain). *J. Virol.* **2007**, *81*, 9183–9192. [CrossRef] [PubMed]
158. Lei, S.; Samuel, H.; Twitchell, E.; Bui, T.; Ramesh, A.; Wen, K.; Weiss, M.; Li, G.; Yang, X.; Jiang, X.; et al. Enterobacter cloacae inhibits human norovirus infectivity in gnotobiotic pigs. *Sci. Rep.* **2016**, *6*, 25017. [CrossRef]
159. Cheetham, S.; Menira, S.; Meulia, T.; Grimes, S.; Han, M.G.; Saif, L.J. Pathogenesis of a genogroup II human norovirus in gnotobiotic pigs. *J. Virol.* **2006**, *80*, 10372–10381. [CrossRef] [PubMed]
160. Park, B.J.; Jung, S.T.; Choi, C.S.; Myoung, J.; Ahn, H.S.; Han, S.H.; Kim, Y.H.; Go, H.J.; Lee, J.B.; Park, S.Y.; et al. Pathogenesis of Human Norovirus Genogroup II Genotype 4 in PostWeaning Gnotobiotic Pigs. *J. Microbiol. Biotechnol.* **2018**, *28*, 2133–2140. [CrossRef]
161. Sestak, K.; Feely, S.; Fey, B.; Dufour, J.; Hargitt, E.; Alvarez, X.; Pahar, B.; Gregoricus, N.; Vinjé, J.; Farkas, T. Experimental inoculation of juvenile rhesus macaques with primate enteric caliciviruses. *PLoS ONE* **2012**, *7*. [CrossRef]
162. Subekti, D.S.; Tjaniadi, P.; Lesmana, M.; McArdle, J.; Iskandriati, D.; Budiarsa, I.N.; Walujo, P.; Suparto, I.H.; Winoto, I.; Campbell, J.R.; et al. Experimental infection of Macaca nemestrina with a Toronto Norwalk-like virus of epidemic viral gastroenteritis. *J. Med. Virol.* **2002**, *66*, 400–406. [CrossRef] [PubMed]
163. Bok, K.; Parra, G.I.; Mitra, T.; Abente, E.; Shaver, C.K.; Boon, D.; Engle, R.; Yu, C.; Kapikian, A.Z.; Sosnovtsev, S.V.; et al. Chimpanzees as an animal model for human norovirus infection and vaccine development. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 325–330. [CrossRef] [PubMed]
164. Wyatt, R.G.; Greenberg, H.B.; Dalgard, D.W.; Allen, W.P.; Sly, D.L.; Thornhill, T.S.; Chanock, R.M.; Kapikian, A.Z. Experimental infection of chimpanzees with the Norwalk agent of epidemic viral gastroenteritis. *J. Med. Virol.* **1978**, *2*, 89–96. [CrossRef] [PubMed]
165. Marionneau, S.; Cailleau-Thomas, A.; Rocher, J.; Le Moullac-Vaidye, B.; Ruvoën, N.; Monique, C.; Le Pendu, J. ABH and Lewis histo-blood group antigens, a model for the meaning of oligosaccharide diversity in the face of a changing world. *Biochimie* **2004**, *83*, 565–573. [CrossRef]
166. Huang, P.; Farkas, T.; Marionneau, S.; Zhong, W.; Ruvoën-Clouet, N.; Morrow, A.L.; Altaye, M.; Pickering, L.K.; Newburg, D.S.; LePendu, J.; et al. Noroviruses Bind to Human ABO, Lewis, and Secretor Histo–Blood Group Antigens: Identification of 4 Distinct Strain-Specific Patterns. *J. Infect. Dis.* **2002**, *188*, 19–31. [CrossRef]
167. Ming, T.; Jiang, X. Histo-blood group antigens: A common niche for norovirus and rotavirus. *Expert Rev. Mol. Med.* **2014**, *16*, e5.
168. Tan, M.; Jiang, X. Norovirus Gastroenteritis, Carbohydrate Receptors, and Animal Models. *PLoS Pathog.* **2010**, *6*, e1000983. [CrossRef] [PubMed]
169. Huang, P.; Farkas, T.; Zhong, W.; Tan, M.; Thornton, S.; Morrow, A.L.; Jiang, X. Norovirus and Histo-Blood Group Antigens: Demonstration of a Wide Spectrum of Strain Specificities and Classification of Two Major Binding Groups among Multiple Binding Patterns. *J. Virol.* **2005**, *79*, 6714–6722. [CrossRef]
170. Marionneau, S.; Ruvoën, N.; Le Moullac-Vaidye, B.; Clement, M.; Cailleau-Thomas, A.; Ruiz-Palacois, G.; Huang, P.; Jiang, X.; Le Pendu, J. Norwalk Virus Binds to Histo-Blood Group Antigens Present on Gastroduodenal Epithelial Cells of Secretor Individuals. *Gastroenterology* **2002**, *122*, 1967–1977. [CrossRef]
171. Tamura, M.; Natori, K.; Kobayashi, M.; Miyamura, T.; Takeda, N. Genogroup II Noroviruses Efficiently Bind to Heparan Sulfate Proteoglycan Associated with the Cellular Membrane. *J. Virol.* **2004**, *78*, 3817–3826. [CrossRef] [PubMed]
172. Rydell, G.E.; Nilsson, J.; Rodriguez-Diaz, J.; Ruvoen-Clouet, N.; Svensson, L.; Le Pendu, J.; Larson, G. Human noroviruses recognize sialyl Lewis x neoglycoprotein. *Glycobiology* **2009**, *19*, 309–320. [CrossRef] [PubMed]
173. Han, L.; Tan, M.; Xia, M.; Kitova, E.N.; Jiang, X.; Klassen, J.S. Gangliosides are ligands for human noroviruses. *J. Am. Chem. Soc.* **2014**, *136*, 12631–12637. [CrossRef] [PubMed]
174. Almand, E.A.; Moore, M.D.; Jaykus, L.A. Norovirus Binding to Ligands Beyond Histo-Blood Group Antigens. *Front. Microbiol.* **2017**, *8*, 2549. [CrossRef]

175. Olival, K.J.; Hosseini, P.R.; Zambrana-Torrelio, C.; Ross, N.; Bogich, T.L.; Daszak, P. Host and viral traits predict zoonotic spillover from mammals. *Nature* **2017**, *546*, 646–650. [CrossRef] [PubMed]
176. Caddy, S.; Breiman, A.; le Pendu, J.; Goodfellow, I. Genogroup IV and VI canine noroviruses interact with histo-blood group antigens. *J. Virol.* **2014**, *88*, 10377–10391. [CrossRef] [PubMed]
177. Zakhour, M.; Ruvoën-Clouet, N.; Charpilienne, A.; Langpap, B.; Poncet, D.; Peters, T.; Bovin, N.; Le Pendu, J. The αGal epitope of the histo-blood group antigen family is a ligand for bovine norovirus Newbury2 expected to prevent cross-species transmission. *PLoS Pathog.* **2009**, *5*, e1000504. [CrossRef]
178. Taube, S.; Perry, J.W.; McGreevy, E.; Yetming, K.; Perkins, C.; Henderson, K.; Wobus, C.E. Murine Noroviruses Bind Glycolipid and Glycoprotein Attachment Receptors in a Strain-Dependent Manner. *J. Virol.* **2012**, *86*, 5584–5593. [CrossRef]
179. Orchard, R.C.; Wilen, C.B.; Doench, J.G.; Baldridge, M.T.; McCune, B.T.; Lee, Y.C.J.; Lee, S.; Pruett-Miller, S.M.; Nelson, C.A.; Fremont, D.H.; et al. Discovery of a proteinaceous cellular receptor for a norovirus. *Science* **2016**, *353*, 933–936. [CrossRef]
180. Yamamoto, F.; Cid, E.; Yamamoto, M.; Saitou, N.; Bertranpetit, J.; Blancher, A. An integrative evolution theory of histo-blood group ABO and related genes. *Sci. Rep.* **2014**, *4*. [CrossRef]
181. Jones, K.E.; Daszak, P. Global trends in emerging infectious diseases. *Nature* **2008**, *451*, 990–994. [CrossRef] [PubMed]
182. Jothikumar, N.; Lowther, J.A.; Henshilwood, K.; Lees, D.N.; Hill, V.R.; Vinjé, J. Rapid and sensitive detection of noroviruses by using TaqMan-based one-step reverse transcription-PCR assays and application to naturally contaminated shellfish samples. *Appl. Environ. Microbiol.* **2005**, *71*, 1870–1875. [CrossRef] [PubMed]
183. Parra, G.I.; Bok, K.; Taylor, R.; Haynes, J.R.; Sosnovtsev, S.V.; Richardson, C.; Green, K.Y. Immunogenicity and specificity of norovirus Consensus GII.4 virus-like particles in monovalent and bivalent vaccine formulations. *Vaccine* **2012**, *30*, 3580–3586. [CrossRef] [PubMed]
184. Nayak, M.K.; Balasubramanian, G.B.; Sahoo, G.C.; Bhattacharya, R.; Vinje, J.; Kobayashi, N.; Sarkar, M.C.; Bhattacharya, M.K.; Krishnan, T. Detection of a novel intergenogroup recombinant Norovirus from Kolkata, India. *Virology* **2008**, *377*, 117–123. [CrossRef] [PubMed]
185. Tung, G.P.; Kaneshi, K.; Ueda, Y.; Nakaya, S.; Nishimura, S.; Yamamoto, A.; Sugita, K.; Takanashi, S.; Okitsu, S.; Ushijima, H. Genetic heterogeneity, evolution, and recombination in noroviruses. *J. Med. Virol.* **2007**, *79*, 1388–1400. [CrossRef]
186. Le Guyader, F.S.; Loisy, F.; Atmar, R.L.; Hutson, A.M.; Estes, M.K.; Ruvoën-Clouet, N.; Pommepuy, M.; Le Pendu, J. Norwalk virus-specific binding to oyster digestive tissues. *Emerg. Infect. Dis.* **2006**, *12*, 931–936. [CrossRef]
187. Le Guyader, F.S.; Bon, F.; DeMedici, D.; Parnaudeau, S.; Bertone, A.; Crudeli, S.; Doyle, A.; Zidane, M.; Suffredini, E.; Kohli, E.; et al. Detection of multiple noroviruses associated with an international gastroenteritis outbreak linked to oyster consumption. *J. Clin. Microbiol.* **2006**, *44*, 3878–3882. [CrossRef]
188. Le Guyader, F.S.; Atmar, R.L.; Le Pendu, J. Transmission of viruses through shellfish: When specific ligands come into play. *Curr. Opin. Virol.* **2012**, *2*, 103–110. [CrossRef] [PubMed]
189. Costantini, V.; Loisy, F.; Joens, L.; Le Guyader, F.S.; Saif, L.J. Human and animal enteric caliciviruses in oysters from different coastal regions of the United States. *Appl. Environ. Microbiol.* **2006**, *72*, 1800–1809. [CrossRef]
190. Becker-Dreps, S.; Cuthbertson, C.C.; Bucardo, F.; Vinje, J.; Paniagua, M.; Giebultowicz, S.; Espinoza, F.; Emch, M. Environmental factors associated with childhood norovirus diarrhoea in León, Nicaragua. *Epidemiol. Infect.* **2017**, *145*, 1597–1605. [CrossRef]

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