Hepatitis E virus genome detection in commercial pork livers and pork meat products in Germany

Srinivas Reddy Pallerla1,2 | Sonja Schembecker1 | Christian G. Meyer1,2,3 | Le Thi Kieu Linh1,2 | Reimar Johne4 | Heiner Wedemeyer5,6 | C.-Thomas Bock1,7 | Peter G. Kremsner1 | Thirumalaisamy P. Velavan1,2,3

1Institute of Tropical Medicine, University of Tübingen, Tübingen, Germany
2Vietnamese-German Center for Medical Research, VG-CARE, Hanoi, Vietnam
3Medical Faculty, Duy Tan University, Da Nang, Vietnam
4German Federal Institute for Risk Assessment, Berlin, Germany
5German Center for Infection Research, Partner Hannover, Braunschweig, Germany
6German Federal Institute for Risk Assessment, Berlin, Germany
7Division of Viral Gastroenteritis and Hepatitis Pathogens and Enteroviruses, Department of Infectious Diseases, Robert Koch Institute, Berlin, Germany

Correspondence
Thirumalaisamy P. Velavan, Institute of Tropical Medicine, University of Tübingen, Wilhelmstrasse 27, 72074 Tübingen, Germany.
Email: velavan@medizin.uni-tuebingen.de

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Abstract
The hepatitis E virus (HEV) is one of the most common causes of hepatitis worldwide. HEV is also widespread in many developed countries, where the number of infections is steadily increasing. In those countries, the virus is transmitted mainly through consumption of undercooked or raw food or through contact with animals. Especially, pigs serve as a main reservoir of HEV. Here, we investigated the prevalence of HEV RNA in pork livers and pork meat products to assess the actual risk of HEV infection through food consumption in Germany. A total of 131 pork products were collected from grocery stores and butcher shops between October 2019 and February 2020 and screened for HEV RNA using nested PCR and subsequent sequencing. Overall, 10% of the samples were positive for HEV, including pork livers (5%), spreadable liver sausages (13%) and liver pâté samples (15%). Sequence analyses indicated that the large majority of HEV strains belonged to subtype HEV-3c, representing the most frequent subtype in Germany. One sample belonged to subtype HEV-3f. Further sequence analysis revealed large sequence variation between the samples; however, most of the mutations identified were synonymous. Although infectivity of the virus was not tested, the results suggest a considerable risk of HEV infection through food consumption. Therefore, preventive measures should be taken according to a One Health approach.

Keywords
Europe, Germany, hepatitis E, meat, pork products, zoonosis
INTRODUCTION

The hepatitis E virus (HEV) is a frequent cause of viral hepatitis. In developing countries, it accounts for roughly 20 million infections with approximately 3.4 million symptomatic cases and 70,000 deaths per year. The majority of HEV infections is asymptomatic. Symptomatic disease and fatalities occur mostly among pregnant women, immunocompromised individuals and those predisposed to liver diseases, transplant recipients, HIV-infected individuals and cancer patients.

Eight genotypes (HEV-1 to HEV-8) of this RNA virus exist, and the most common genotypes infecting humans are HEV-1, HEV-2, HEV-3 and HEV-4. HEV-1 and HEV-2 are the most frequent genotypes in low-income countries, where they are mainly transmitted through contaminated water. In contrast, HEV-3 and HEV-4 are more prevalent in developed countries and are zoonotically transmitted through consumption of contaminated food or contact with infected animals. Due to their high diversity, HEV genomes are further divided into subtypes. HEV3, which occurs frequently in Europe, is divided into subtypes. HEV3, which occurs frequently in Europe, is divided into subtypes HEV-3a to HEV-3m.

Depending on the type of sausage, 3%-30% of sausages from France derived from pigs have been established. However, only a few HEV surveys were also conducted in Germany, the Netherlands and the United States, as wild and domestic pigs, deer, rabbits and others are main reservoirs of human pathogenic HEV. Individuals in contact with pigs such as farmers, personnel of the meat processing industry, butchers and meat retailers are at an increased risk of infection. HEV RNA has been detected in serum or faeces of pigs (1%-88%) in breeding facilities, indicating a significant risk of contaminated pork entering the food chain with the potential to be the source of human infections. HEV-3 is a zoonotic virus that infects many animal species such as wild and domestic pigs, deer, rabbits and others. Pigs are the main reservoirs of human pathogenic HEV. Individuals in contact with pigs such as farmers, personnel of the meat processing industry, butchers and meat retailers are at an increased risk of infection. HEV RNA has been detected in serum or faeces of pigs (1%-88%) in breeding facilities, indicating a significant risk of contaminated pork entering the food chain with the potential to be the source of human infections.

In fact, consumption of contaminated pork and related meat products is a major transmission route for HEV in developed countries. For instance in France, Figatellu, a customary type of sausage (Delikatess Leberwurst, Hausmacher Leberwurst, Gutsleberwurst, Pfälzer Leberwurst, Sahneleberwurst) and 40 samples of liver pâté and 10 pork sausages without liver (Braunschweiger Mettwurst, Zwiebelmettwurst, Schinken-Zwiebel-Mettwurst). The samples were stored at 4°C and processed within 24 hours.

2 MATERIALS AND METHODS

2.1 Sample collection

Pork liver and pork meat products (liver sausage, liver pâté and pork sausage) were purchased between October 2019 and February 2020 from various supermarkets and butcher shops in Tübingen, Reutlingen, Stuttgart and Dortmund (Germany). Samples were catalogued and provided with a unique sample ID. The list of samples and details is given in Table S1. A total of 131 samples were collected, including 41 pork livers, 40 spreadable liver sausages (Delikatess Leberwurst, Hausmacher Leberwurst, Gutsleberwurst, Pfälzer Leberwurst, Sahneleberwurst) and 40 samples of liver pâté and 10 pork sausages without liver (Braunschweiger Mettwurst, Zwiebelmettwurst, Schinken-Zwiebel-Mettwurst). The samples were stored at 4°C and processed within 24 hours.

2.2 RNA isolation and cDNA synthesis from pork meat products

RNA isolation procedures differed slightly for pork liver and pork meat samples as shown in the flow chart in Figure 1. RNA isolation from pork liver was performed according to a protocol previously provided, which was slightly modified. Briefly, approximately 100 mg of liver tissue was dissected with a surgical blade and 1 mL of TRizol™ (Thermo Fisher Scientific, Waltham, MA, USA) was added to the supernatant and centrifuged 12,000 μL nuclease-free water. Quality and quantity of RNA were determined.

The proportion of HEV RNA in pork liver and meat products such as liver sausage, liver pâté and pork sausage without liver sold in Germany. This and the comparison of the detected strains with human strains should provide evidence on the risk of HEV infection through consumption of pork-derived meat products.
2.3 | Screening of HEV using nested PCR for ORF1 and ORF 2 and DNA sequencing

The extracted RNA was quantified (Table S3), and 2 μg of total RNA was subsequently reverse-transcribed with the high-capacity cDNA reverse transcription kit (Thermo Fisher Scientific) and screened for HEV ORF1 and ORF2 by nested PCR. PCR assays were performed using ORF1 and ORF2 primers according to our in-house laboratory protocol described in Hoan et al.30 The ORF1 and ORF2 amplicons were visualized by agarose gel electrophoresis. All HEV-positive samples were re-run with the QIAxcel Advanced gel electrophoresis system (Qiagen, Hilden, Germany) according to the manufacturer’s protocol, including a positive internal control and a negative control. ORF1 and ORF2 amplicons were sequenced using the ABI 3130XL sequencer (Thermo Fisher Scientific) according to an in-house protocol.30

2.4 | HEV genotyping and phylogenetic analysis

The 13 ORF1 and 13 ORF2 sequences were generated on the basis of the forward and reverse sequences with BioEdit 7.2.5 (www.mbio.ncsu.edu/BioEdit/bioedit.html). All 26 sequences were submitted to the NCBI GenBank database (accession numbers for ORF1: MT497739 to MT497751 and for ORF2: MT497752 to MT497764). Phylogenetic analyses were performed using MEGA-X (version 10.1.7; www.megasoftware.net). The evolutionary distances were calculated using the maximum composite likelihood method considering nucleotide substitutions. The HEV reference genome sequences and the respective accession number details are provided in the Supplementary Files as retrieved from the NCBI GenBank database for phylogenetic analysis (Supplementary File).

3 | RESULTS

A total of 131 pork liver and pork meat product samples (41 pork livers, 40 spreadable liver sausages, 40 samples of liver pâté and 10
pork sausages) were collected (Table S1). The origin of these samples was determined by the producer’s barcode on the wrapping of each product or by asking the retailers. Ingredients of the products were indicated on their packaging. Table S1 provides all product details of the pork livers and composition of meat samples purchased in various supermarkets or butchers’ and retailers’ shops. The meat samples tested for HEV originated from different locations in Europe, as shown on the map in green circles or red coloured shapes in Figure 2. Most of the samples came from the west and south-west Germany. Only a few samples originated from other European countries (Poland, Austria, Belgium and the Netherlands).

In order to screen meat samples for HEV RNA, RNA was isolated using published protocols, which were only slightly modified. These modifications enabled more efficient homogenization of the various sample types and supported improvement of RNA quality (Table S2). A detailed flow chart of the RNA isolation procedure is given in Figure 1. Of the 131 pork livers and meat samples screened for HEV RNA, 13 (10%) were tested positive by nested ORF1 and ORF2 PCR assays (sample IDs: L29, L31, S02, S03, S24, S33, S34, P04, P10, P30, P31, P32, P38). All positive ORF1 and ORF2 products were visualized on QIAxcel Advanced gel electrophoresis (Qiagen, Hilden Germany) with fragment sizes of 300 and 450 bp for ORF1 and ORF2, respectively.

Only samples positive for both ORFs were considered true positives, as in a few cases either only ORF1 or ORF2 was amplified (Table 1). The 13 HEV RNA-positive samples consisted of two pork livers (5%), five liver sausages (13%) and six liver pâté samples (15%) (Table 1). A higher percentage of pork meat product samples was HEV-positive compared to pork livers. The 13 HEV-positive samples originated from eight locations in Germany and Belgium (Table S1 and Figure S2). The HEV-positive sampling locations were broadly distributed over the whole investigated area, without a specific pattern or a particular region affected. All HEV-positive meat products contained at least 20% pork liver. However, in two samples the exact content of pork meat and pork liver could not be traced.

ORF1 and ORF2 PCR amplicons of all 13 HEV-positive samples were sequenced to determine genotypes and diversity. Three samples (P04, S33 and S34) contained a mixture of sequences. The mixture of sequences with ambiguous nucleotides was annotated according to the International Union of Pure and Applied Chemistry (IUPAC) code in the nucleotide sequences. Phylogenetic analyses of the samples were performed using HEV ORF1 and HEV ORF2.
TABLE 1 Results of HEV RNA screening in pork livers and pork meat products

| HEV RNA screened (n) | ORF1- and ORF2-positive n (%) |
|----------------------|-------------------------------|
| Pork liver           | 41                            | 02 (5)                        |
| Pork meat products   |                               |                               |
| Liver sausage        | 40                            | 05 (13)                       |
| Liver pâté           | 40                            | 06 (15)                       |
| Pork sausage         | 10                            | 00 (0)                        |
| Total                | 131                           | 13 (10)                       |

reference sequences retrieved from NCBI. These reference sequences belong to the subtypes HEV-3a to HEV-3m and reported from several countries isolated from humans, wild boars and pigs. The phylogenetic analysis indicates that all HEV-positive samples belong to HEV-3c, except one HEV-3f sample (Figures 3 and 4). The HEV-3c samples represent Germany and Belgium origin, whereas the HEV-3f from Belgium origin. Next, in order to study nucleotide variation of the HEV-positive samples, we aligned our ORF1 and ORF2 sequences with HEV-3c reference sequence FJ705359.1. Significant sequence variation was observed among the samples (Figures S1 and S2). However, most of nucleotide variation does not translate to amino acid substitutions, as almost all mutations are synonymous (Figures S3 and S4). We found few unique amino acid substitutions compared to the reference sequences.33

4 | DISCUSSION

Increasing numbers of HEV infections are observed in Germany,4 which are most likely acquired through consumption of contaminated food.23,24,35,36 The aim of this study was to assess the actual prevalence of HEV-contaminated meat products in German supermarkets and butcher shops to estimate the risk of HEV exposure and infections.

For the detection of HEV in the food matrix, efficient homogenization is crucial to obtain RNA of high quality. Minor modifications of the previously published protocols26,30-32 efficiently supported homogenization of different sample types and helped to improve RNA quality (Table S2). In fact, quantity and quality of isolated RNA was much higher with FastPrep-24™ when increasing the homogenization cycles and adding additional chloroform steps to remove fat in the sausage and pâté samples (Figure 1).

A total of 10% of all samples tested were HEV RNA-positive. For livers, a detection rate of 5% was assessed, which corresponds to an earlier study in Germany with 4%37 and to another study from the Netherlands with 7%27 of porcine livers from grocery stores. For liver sausages, we determined a prevalence of 13%, which is comparable with the detection rate of 22% in a former study in Germany.26 While taking the source of HEV-positive meat products into account, no regional prevalence could be identified (Figure 2), suggesting that HEV is evenly distributed across Germany. Taking together, the results indicate that the prevalence of HEV in pork liver-containing food in Germany is still high, without large prevalence changes over the last decade.

The rate of HEV genome detection was much higher in pork meat products than in pork livers. This might be due to the fact that pork products used in this study could have a mixture of different meat sources, and this could apparently affect HEV RNA positivity rate. Nevertheless, false-negative results are equally possible, when the viral load is low. Although Szabo et al (2015) found that 20% of raw pork sausages without pork liver tested positive for HEV RNA, in our study, pork sausages did not test positive, possibly due to the small sample size of just 10 samples of pork sausage. Although extrahpatic replication has been observed in experimental infections,38-42 the detection of HEV in muscle is very rare.41,43-46

Pork products such as pork liver sausages and pork pâté are processed foods intended for consumption without further cooking, which are heated during food processing. Since HEV is a very stable virus, it must be inactivated by heating the products at 72°C for at least 20 minutes.57 Liver pâté is heated at about 150°C for at least one hour,48 which seems to be sufficient for HEV inactivation. Also, the spreadable liver sausages sold in Germany are usually heated in a water bath at temperatures up to 80°C26 and sometimes additionally smoked at about 80°C. In contrast, pork sausages without liver are usually raw sausages, which are not heated during food processing.48 Nevertheless, the consumption of pork sausages without liver still poses a significant risk in HEV transmission and absence of HEV cannot be excluded.

Only a few studies have been conducted so far to assess the prevalence of infectious HEV in pork liver and pork-derived meat products. The presence of infectious HEV particles in pig liver has been demonstrated previously.27,28 In a study from France, infectious HEV was identified in a sample of sausage containing raw pork liver.49 Determination of the viral load might further help in assessing the risk of HEV infection through consumption of contaminated food. The infectious dose of HEV required to infect humans has not been studied in detail and is currently only estimated from data obtained from immunocompromised patients (3.6 x 10⁴ IU).50 Infectious doses of HEV in retail meat products urgently need to be further assessed, when reliable methods for determination of HEV infectivity in meat products are available for such studies.51

Phylogenetic analyses of HEV strains using partial ORF1 sequences lead to similar phylogenetic trees compared to whole-genome analyses.52 The phylogenetic analyses revealed 12 of the investigated HEV subtypes belong to the HEV-3c clade for both ORF1 and ORF2. Also, one HEV subtype investigated was assigned to HEV-3f for both ORF1 and ORF2. HEV-3c sequences investigated in this study had a closer homology to other human and wild boar sequences from Germany and Europe, indicating a possible autochthonous transmission through pork-based food products. Several years ago, the main HEV genotypes in Europe were HEV-3e, HEV-3f and HEV-3g, but now the commonly circulating strains include HEV-3e and HEV-3f and HEV-3c, which largely has replaced HEV-3g.53 This
is also reflected in the present study, where, except one HEV-3f subtype, all subtypes were HEV-3c. In a recent study on chronically infected hepatitis E patients from Germany, HEV-3c was also predominant and HEV-3f was found only in a minor percentage of patients.  

Hepatitis E virus has high mutation rates, leading to a considerable number of genotypes and subtypes. High genetic diversity of both ORFs was also observed in this study (Figures S3 and S4). Despite the enormous variability in the nucleotide sequences, only few amino acid substitutions were seen compared to the reference sequences. Due to the few amino acid substitutions observed in this study, their impact can currently not be estimated and needs to be further investigated if identified in human infections. Mixtures of sequences were found in three meat products (P04, S33 and S34) (Figure S1 and S2), likely as a result of used meat originating from different pigs.

A major limitation of this study is the small sample size and the viral load was not quantified. However, when reliable methods for determination of HEV infectivity in retail meat products are available, this shall help determine infectious doses required to infect humans. An yet another limitation is that all commercial products investigated in the study are largely liver based. Therefore, to what extent sausages without liver represent a risk cannot be

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**FIGURE 3**  Phylogenetic relationship of HEV sequences from pork livers and pork meat products. The phylogenetic tree is based on the 308 bp ORF1 region of HEV. The tree is drawn to scale, as the evolutionary distances used to derive the phylogenetic tree. The sequences retrieved from the NCBI GenBank with accession number, country of origin and host. The HEV sequences of this study are in bold with GenBank accession numbers. Reconstruction of phylogenetic tree using neighbour-joining method with 1000 bootstrap iterations. Abbreviations: hum, human; pig, pig/swine; and wb, wild boar; for countries, see Supplementary File for more information.
In summary, HEV is widespread in pork products in Germany and may explain the high rate of human HEV infections, especially in high-risk groups and adults over 50 years of age. A comprehensive ‘One Health’ approach is needed, which may include preventive measures such as vaccination of animals and humans, especially pigs and occupationally exposed farmers as well as meat processing workers. Seroprevalence studies should also be carried out at regular intervals to assess infection rates and to initiate evidence-based preventive measures. In addition, it is recommended that pork liver and pork products be thoroughly cooked before consumption. It is also advisable for high-risk groups to avoid contact with animals that are reservoirs for HEV.

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AUTHOR CONTRIBUTIONS
TPV designed and supervised the study, contributed to the materials and wrote the manuscript. PGK, CTB and HW were involved in the study design and contributed to the study materials. SRP and SS performed the experimental procedures and wrote the first draft of the manuscript.
manuscript. LTKL performed all sequencing reactions and organized the laboratory materials. CGM and RJ revised the main draft. SRP and SS contributed equally to this work. All authors agreed with the results and conclusions.

ORCID
ThirumalaAisy V. Velavan https://orcid.org/0000-0002-9809-9883

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SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section.

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