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obstacle of HBV cure 3 Short Title: cccDNA
quantification harmonization 4 5**

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3 **1 Quantification of the Hepatitis B Virus cccDNA: Evidence-based guidelines for**
4 **2 monitoring the key obstacle of HBV cure**

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6 **3 Short Title: cccDNA quantification harmonization**
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9 Lena Allweiss^{1,2}, Barbara Testoni^{3,4}, Mei Yu⁵, Julie Lucifora^{3,4}, Chunkyu Ko^{6*}, Bingqian Qu^{7**},
10 Marc Lütgehetmann^{8,2}, Haitao Guo^{9,10}, Stephan Urban^{7,2}, Simon P. Fletcher⁵, Ulrike Protzer^{6,2},
11 Massimo Levrero^{3,4}, Fabien Zoulim^{3,4}, Maura Dandri^{1,2}
12

13 1. I. Medical Clinic and Polyclinic, University Medical Center Hamburg-Eppendorf, Hamburg,
14 Germany

15 2. German Center for Infection Research (DZIF), Germany

16 3. Cancer Research Center of Lyon, INSERM U1052, Lyon University, Hospices de Lyon,
17 Lyon, France

18 4. ANRS HBV Cure Task Force

19 5. Gilead Sciences, Foster City, California, United States of America

20 6. Institute of Virology, Technical University of Munich, Munich, Germany

21 * Current affiliation: Infectious Diseases Therapeutic Research Center, Therapeutics &
22 Biotechnology Division, Korea Research Institute of Chemical Technology (KRICT), 34114
23 Daejeon, Republic of Korea

24 7. Department of Infectious Diseases, Molecular Virology, University Hospital Heidelberg,
25 Germany

26 ** Current affiliation: Division of Veterinary Medicine, Paul Ehrlich Institute, Germany

27 8. Institute of Medical Microbiology, Virology and Hygiene, University Medical Center
28 Hamburg-Eppendorf Hamburg, Germany

29 9. Indiana University School of Medicine, Indianapolis, Indiana, United States of America

30 10. Current affiliation: Department of Microbiology and Molecular Genetics, Cancer Virology
31 Program, UPMC Hillman Cancer Center, University of Pittsburgh School of Medicine,
32 Pittsburgh, United State of America
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45 Abbreviations: cccDNA, covalently closed circular DNA; CHB, chronic hepatitis B; HBB,
46 hemoglobin subunit beta; HCl, hydrochloric acid; KCl, potassium chloride; Lam, Lamivudine;
47 ND2, mitochondrially encoded NADH: ubiquinone oxidoreductase core subunit 2; NTCP,
48 sodium-taurocholate co-transporting polypeptide; PCR, polymerase chain reaction; pf-rcDNA,
49 protein-free relaxed circular DNA; PSD, plasmid-safe ATP-dependent DNase; RI, replicative
50 intermediates; SB, Southern blot; SDS, sodium dodecyl sulfate; siRNA, small interfering RNA.
51

52 Corresponding authors: Dr. rer. nat. Maura Dandri
53 I. Department of Internal Medicine, Center for Internal Medicine
54 University Medical Center Hamburg-Eppendorf
55 Martinistr. 52, 20246 Hamburg, Germany
56 Tel.: +49 40 741052949, Fax: + 49 40 741057232
57 E-mail: m.dandri@uke.de
58
59

60 Prof. Dr. Fabien Zoulim
61

1
2
3 52 INSERM U1052, CNRS UMR-5286,
4 53 Cancer Research Center of Lyon (CRCL)
5 54 151 Cours Albert Thomas, 69424 Lyon, France
6 55 Tel.: +33 472681970, Fax: +33 472681971.
7 56 E-mail: fabien.zoulim@inserm.fr
8 57

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75 Abstract

76 **Objectives:** A major goal of curative hepatitis B virus (HBV) treatments is the reduction or
77 inactivation of intrahepatic viral covalently closed circular DNA (cccDNA). Hence, precise
78 cccDNA quantification is essential in preclinical and clinical studies. Southern blot (SB) permits
79 cccDNA visualization but lacks sensitivity and is very laborious. Quantitative PCR (qPCR) has
80 no such limitations but inaccurate quantification due to co-detection of viral replicative
81 intermediates (RI) can occur. The use of different samples, preservation conditions, DNA
82 extraction, nuclease digestion methods and qPCR strategies has hindered standardization.
83 Within the ICE-HBV consortium, available and novel protocols for cccDNA isolation and qPCR
84 quantification in liver tissues and cell cultures were compared in six laboratories to develop
85 evidence-based guidance for best practices. **Design:** Reference material (HBV-infected
86 humanized mouse livers and HepG2-NTCP cells) was exchanged for cross-validation. Each
87 group compared different DNA extraction methods (Hirt extraction, total DNA extraction with
88 or without proteinase K treatment (+PK/-PK) and nuclease digestion protocols (plasmid-safe
89 ATP-dependent DNase (PSD), T5 exonuclease, exonucleases I/III). Samples were analyzed
90 by qPCR and SB. **Results:** Hirt and -PK extraction reduced coexisting RI forms. However,
91 both cccDNA and the protein-free relaxed circular HBV DNA (pf-rcDNA) form were detected
92 by qPCR. T5 and Exo I/III nucleases efficiently removed all RI forms. In contrast, PSD did not
93 digest pf-rcDNA, but was less prone to induce cccDNA over-digestion. In stabilized tissues
94 (e.g. Allprotect), nucleases had detrimental effects on cccDNA. **Conclusions:** We present
95 here a comprehensive evidence-based guidance for optimizing, controlling and validating
96 cccDNA measurements using available qPCR assays.

97
98 **Keywords:** HBV, chronic hepatitis B, minichromosome, humanized mice, human liver chimeric
99 mice, HepG2-NTCP, Southern blot, qPCR, liver biopsies, plasmid-safe ATP-dependent
100 DNase, T5 exonuclease, exonuclease I, exonuclease III.

102 Summary box:

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104 **What is already known on this topic?** Persistence of the HBV genome, the covalently closed
105 circular DNA (cccDNA), in the liver is a major obstacle for developing HBV cure strategies and
106 its accurate quantification is essential in preclinical and clinical studies. However, cccDNA
107 quantification by PCR lacks standardization and is technically challenging due to the
108 heterogeneous population of HBV DNA molecules present in infected cells.

109 **What this study adds?** Distinct cccDNA extraction and quantification protocols were cross
110 validated using infected tissues and cell cultures. We provide experimental evidence that
111 coexistence of certain HBV DNA forms and potential cccDNA over-digestion due to sample
112 preservation conditions and nuclease treatment still challenges PCR-based quantification of
113 cccDNA. The results support recommendations for optimizing, controlling and validating
114 cccDNA measurements according to the sample type.

115 **How this study might affect research, practice or policy?** This work presents an evidence-
116 based guidance for best practices to quantify cccDNA by qPCR. Information provided will
117 assist the HBV cure research programs aiming at assessing the impact of therapies on the
118 HBV reservoir in preclinical studies and clinical trials.

119

120 Introduction

121 The hepatitis B virus (HBV) is the cause of chronic hepatitis B (CHB) and despite the availability
122 of effective prophylactic vaccines and treatments that efficiently suppress viral replication, HBV
123 puts 296 million carriers at risk of developing liver cirrhosis and hepatocellular carcinoma
124 (HCC)¹. Thus, there is a strong need to develop therapies with the potential to cure CHB. The
125 unique HBV replication strategy, however, makes viral eradication challenging². Knowledge
126 and precise monitoring of the different viral components present in infected cells and in the
127 circulation is paramount for the development and assessment of novel therapeutic strategies.

128 HBV is an enveloped virus harboring a small (3.2 kb) partially double-stranded relaxed circular
129 DNA (rcDNA) genome which specifically infects human hepatocytes. Upon infection, the
130 rcDNA is repaired by cellular enzymes to generate a double-stranded episomal DNA genome,
131 the covalently closed circular DNA (cccDNA)^{3,4} (**Supplementary figure 1**). By associating with
132 histone and non-histone proteins, the cccDNA forms a stable minichromosome within the cell
133 nuclei that serves as transcriptional template for all viral transcripts. Nucleoside analogs (NAs)
134 and interferon alpha are the only approved treatments for CHB but are mainly suppressive as
135 they do not clear cccDNA from the liver. Because of the central role of the cccDNA in HBV
136 persistence, the elimination of this molecule constitutes the ultimate goal of curative
137 treatments⁵. Such a goal may be very difficult to achieve and current investigational
138 approaches rather aim at achieving a functional cure, which is defined as the loss of HBsAg
139 and undetectable HBV DNA in serum². Examples of currently explored curative strategies
140 include, among others, the use of capsid assembly modulators (CAMs) and entry inhibitors,
141 which can also prevent cccDNA formation and intrahepatic amplification of the cccDNA pool⁶,
142 degradation of HBV transcripts using siRNA technologies, immune-mediated clearance and
143 silencing of cccDNA molecules, or its inactivation by gene editing⁷. Assessment of the impact
144 of novel therapies on cccDNA load and activity is therefore of utmost importance. Moreover,
145 our understanding of cccDNA biology in preclinical models and patient biopsies is still limited.
146 Because of the paucity of biopsy material, non-invasive biomarkers (e.g. HBcrAg, HBV RNA),
147 are increasingly studied as surrogate cccDNA markers⁸. However, for the primary validation of
148 these biomarkers, proper cccDNA quantification is needed.

149 A major limitation in HBV research and its translation into the clinic is the lack of standardized
150 PCR-based methods allowing specific cccDNA quantification in HBV-infected samples. The
151 main challenge is the reliable detection of cccDNA by quantitative PCR in the presence of high
152 excess of rcDNA coming from virus input or coexisting replicative intermediates (RI), which are
153 identical in sequence to the cccDNA (**Supplementary figure 1**). To gain specificity, PCR
154 approaches use primers spanning the cohesive ends region of the rcDNA to preferentially
155 detect the cccDNA (**Supplementary figure 2A**). Unfortunately, this approach is not completely
156 specific since it still detects certain amounts of the highly abundant RI leading to an over-
157 estimation of cccDNA amounts^{9,10}. Only when HBV replication is low (e.g., during NA
158 treatment), cccDNA quantification by PCR appears precise^{11,12}. Therefore, cccDNA
159 measurements in samples with high viral productivity or between samples with and without
160 treatment remain challenging and reducing the levels of RI is mandatory.

161 To reduce the levels of HBV RI prior to PCR, various nucleases and DNA extraction methods
162 have been proposed, although their efficacy and specificity in engaging distinct HBV DNA
163 forms in different experimental settings vary substantially. The conventional Hirt method
164 employs sodium dodecyl sulfate lysis and high salt precipitation of high-molecular-weight
165 cellular chromatin and protein-bound DNA¹³ thereby enriching the recovery of protein-free DNA

166 molecules and facilitating the removal of rcDNA, which is covalently linked to the viral
167 polymerase. Southern blot (SB) after Hirt DNA extraction allows visualization of different HBV
168 DNA molecules including cccDNA¹⁴. However, this methodology necessitates large amounts
169 of nucleic acids and therefore lacks sensitivity; it is not suitable for liver biopsy analysis or high-
170 throughput assays and doesn't allow precise quantification.

171 The nucleases commonly used display slightly different substrate specificities but share the
172 common characteristic of sparing closed circular double-stranded DNA (dsDNA) from
173 digestion^{11,15-18}. Apart from employing different nucleases, the use of different DNA extraction
174 procedures, qPCR conditions and normalization increases variability and hinders reliable
175 comparative analyses among laboratories. We therefore attempted to harmonize cccDNA
176 quantification processes by comparing the most used and newer protocols through cross-
177 validation experiments. Based on the results obtained, we propose recommendations of best
178 practice for controlling and validating cccDNA measurements also according to the sample
179 type.

180

181 **Material and Methods**

182 For generation, infection, treatment and viral characterization of human liver chimeric mouse,
183 as well as infection of HepG2-NTCP cell culture samples, nuclease digestion and qPCR
184 measurements see supplementary material.

185 **Preparation of liver tissue and cell samples.** Liver specimens removed at the time of
186 sacrifice were snap-frozen in 2-methylbutane and stored at -80°C until further use. Every lab
187 received three frozen liver pieces (approximately 13mg each) from one highly infected,
188 untreated uPA/SCID/beige/IL2RG^{-/-} (USG) mouse. The tissue pieces were homogenized
189 separately in 300µl 10mM Tris-HCl (pH 7.5)/10mM EDTA (pH 8.0) buffer using disposable
190 homogenizers (Biomasher II, DWK Life Sciences, Wertheim, Germany), then pooled and
191 distributed equally among the three DNA extractions. HBV-infected HepG2-NTCP cells were
192 pooled before being divided and shipped to the four participating labs. Every lab received a
193 frozen cell pellet of approximately 1x10⁷ cells, which upon arrival was dissolved in 900µl 10mM
194 Tris-HCl/10mM EDTA buffer and distributed equally for the three DNA extractions. Since all
195 samples were pooled and divided equally across the DNA extractions, the results could be
196 compared with each other directly without the need for additional normalization to cellular DNA.

197 **DNA extraction procedures.** Total cellular DNA was isolated with the MasterPure Complete
198 DNA and RNA Purification Kit (Epicentre, available through Lucigen, Middleton, WI, USA) as
199 recommended by the manufacturer^{12,19}. The total DNA extraction with proteinase K treatment
200 (+PK) and the one without proteinase K (-PK) were performed identically, except for the
201 proteinase K digestion step, which was omitted in the -PK extraction. Briefly, the samples were
202 split up in several microtubes (according to the manufacturer's instructions, 7x10⁵ cells or
203 4.4mg tissue per 300µl lysis buffer) and 10mM Tris-HCl/10mM EDTA buffer was added for a
204 final volume of 300µl each. One volume of double concentrated TCL buffer (Lucigen) was
205 added to lyse the cells. Subsequently, RNA digestion was performed with 2µl RNase A
206 (Lucigen) for 30min at 37°C. For the +PK extraction, 2µl of PK (Lucigen) was added and
207 incubated for 1h at 56°C. After the addition of 300µl of MPC buffer (Lucigen), the samples were
208 mixed and incubated on ice for 5min, followed by 10min high speed centrifugation to pellet the
209 protein. DNA was recovered from the supernatant through isopropanol precipitation, dissolved
210 in 10mM Tris-HCl/1mM EDTA buffer and the DNA from one extraction and sample was pooled

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3 211 again. The DNA content was determined by fluorometry (Qubit™, Invitrogen) or
4 212 spectrophotometry (NanoDrop™, Thermo Fisher Scientific, Waltham, Massachusetts, USA).
5 213 A detailed version of this protocol can be found on the ICE-HBV protocol database ([https://ice-
6 214 hbv.org/protocol/a-modified-kit-based-hbv-protein-free-dna-extraction-from-liver-tissues-and-
7 215 cell-cultures-for-hbv-cccDNA-southern-blot-and-qPCR/](https://ice-hbv.org/protocol/a-modified-kit-based-hbv-protein-free-dna-extraction-from-liver-tissues-and-cell-cultures-for-hbv-cccDNA-southern-blot-and-qPCR/)). For a comparison of different lysis
8 216 buffers, the protocol was repeated also using RLT buffer from the RNeasy Mini kit (Qiagen,
9 217 Hilden, Germany). Some mouse liver tissues were immersed in Allprotect Tissue Reagent
10 218 (Qiagen) as recommended by the manufacturer and stored at -20°C for several months.

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13 219 One third of the liver homogenate and cell suspension was subjected to DNA extraction
14 220 according to Hirt¹³. Briefly, the samples were further diluted in 10mM Tris-HCl/10mM EDTA
15 221 buffer to a final volume of 3ml. Cell lysis was achieved by adding SDS (final concentration
16 222 0.6%) and 30min of incubation at room temperature with slow agitation. After adding KCl (final
17 223 concentration 0.5M), the lysates were incubated at 4°C overnight, then centrifuged for 30 min
18 224 at 4°C and 14,500g. DNA from the supernatant was extracted twice with phenol and once with
19 225 phenol/chloroform/isoamyl alcohol (25:24:1) followed by an overnight ethanol precipitation.
20 226 The DNA was pelleted by centrifugation, washed in 70% ethanol and dissolved in 10mM Tris-
21 227 HCl/1mM EDTA buffer.

22 228 **Southern blot analyses** were performed as previously described^{19,20}. A detailed version of
23 229 this protocol can be found on the ICE-HBV protocol database ([https://ice-hbv.org/protocol/a-
24 230 sensitive-and-rapid-southern-blot-assay-based-on-branched-dna-technology-for-the-
25 231 detection-of-hbv-dna-in-cell-culture-and-liver-tissue-samples/](https://ice-hbv.org/protocol/a-sensitive-and-rapid-southern-blot-assay-based-on-branched-dna-technology-for-the-detection-of-hbv-dna-in-cell-culture-and-liver-tissue-samples/)) and as supplementary.

26 232

27 233 **Results**

28 234 **Comparison of cccDNA extraction protocols in HBV-infected liver tissues**

29 235 Currently available and novel protocols for cccDNA extraction and quantification were collected
30 236 and cross-validated according to the scheme depicted in **Figure 1A**. Frozen liver tissues from
31 237 HBV-infected humanized mice were used as reference material (**Supplementary Fig.3**). We
32 238 compared total DNA extraction methods that either included (+PK) or excluded (-PK) the
33 239 proteinase K digestion step, as well as the classical Hirt DNA extraction (Hirt) that does not
34 240 include PK digestion¹³. Omission of the PK should facilitate the removal of covalently protein-
35 241 bound HBV DNA and was investigated here as potential alternative to Hirt extraction. A
36 242 previously published cccDNA-selective PCR strategy²¹ based on selective primers and a
37 243 Taqman™ probe detecting all HBV genotypes except G (**Supplementary table 1**), and not
38 244 cross-reacting with human or murine genomic sequences, or HBV DNA integrations¹², was
39 245 chosen for cross-validation using improved PCR conditions (for details see **Supplementary**
40 246 **Fig.2A-C**). The specificity for cccDNA detection was assessed on serial dilutions of serum-
41 247 derived rcDNA and on mixtures of an HBV plasmid (as cccDNA surrogate) and increasing
42 248 amounts of serum-derived rcDNA (**Supplementary Fig.2D and E**). These analyses indicated
43 249 that serum rcDNA can be amplified in a false-positive manner despite using cccDNA-selective
44 250 PCR primers and probes when rcDNA levels exceed cccDNA levels by more than 250-fold.
45 251 Under such circumstances, measured cccDNA levels increase and a precise cccDNA
46 252 quantification is not possible without including strategies reducing rcDNA levels.

47 253 To evaluate the three distinct DNA extraction methods in different labs, we first analyzed the
48 254 liver of a highly viremic mouse. Hirt and -PK extractions resulted in reduced HBV RI levels on
49 255 the SB (**Fig.1B**) compared to the +PK extraction. The classical pattern of a “slow-migrating

band” around 3.5kb (known to contain protein-free (pf) relaxed circular DNA or deproteinated (dp)-rcDNA) and a “fast-migrating band” at 2.1kb (supercoiled cccDNA) was observed both after Hirt and -PK extraction procedures. The high amount of RI in the +PK extracts, however, prevented the visualization of distinct bands. Of note, using the highly sensitive bDNA detection method, a substantial smear was still present in -PK and Hirt extracted DNA, which was absent in samples from an uninfected mouse (see example in **Supplementary Fig.8C**), pointing out that those signals were HBV-specific. In line with the SB, qPCR measurements in all labs showed lower amounts of total HBV DNA (1.6log and 1.3log reduction) and cccDNA (0.5log and 0.4log) in Hirt and -PK extractions, respectively (**Fig.1C**), as compared to +PK samples. The reduction of protein-bound replicative intermediates clearly improved the selectivity of cccDNA quantification by PCR (**Fig.1C**) across all labs (**Fig.1D**).

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268 **Normalization of cccDNA counts to cellular levels**

269 For all downstream cross-validation experiments, the same amount of liver tissue or cell number was used to facilitate comparison between labs and settings. In every-day practice, 270 however, viral DNA counts have to be normalized to cell number to account for differences in 271 the amount of input material or human hepatocyte levels when analyzing chimeric livers. 272 Accordingly, we determined the recovery of genomic DNA (gDNA) and mitochondrial DNA 273 (mtDNA) (**Supplementary Fig.4A-C**). Although supernatants from a classical Hirt extraction 274 are known to harbor reduced levels of high molecular weight nucleic acids, genomic DNA was 275 consistently extracted in our Hirt preparation, albeit with a trend towards a slightly reduced 276 recovery of these DNA species in both Hirt and -PK conditions compared to the +PK extraction. 277 However, this trend was similar across analyses, indicating that viral DNA could be normalized 278 to gDNA or mtDNA derived from the same extraction. Moreover, a head-to-head comparison 279 of distinct lysis buffers revealed that the TCL lysis buffer (Lucigen) led to three-fold lower gDNA 280 levels compared to RLT lysis buffer (Qiagen), although these buffers did not affect mtDNA 281 recovery (**Supplementary Fig.4D-F**). Such differential enrichment of gDNA will skew the 282 normalization of viral DNA to target cells and has to be considered in the normalization 283 strategy. A modified Hirt procedure using alkaline extraction^{22,23}, which was tested on liver 284 tissue and cell culture samples in two labs, showed low but still quantifiable genomic DNA 285 recovery compared to the original Hirt (**Supplementary Fig 5**). By enriching only supercoiled 286 DNA species, this method also depleted all HBV DNA species except for the “fast-migrating 287 band”.

289

290 **Comparison of different nucleases and digestion conditions in chimeric liver tissues**

291 We next tested different nucleases and conditions to compare their efficacy. Based on existing 292 protocols commonly used in different laboratories, T5 exonuclease was used in two settings, 293 one being stronger (“T5”: 10U, 45min), the other one being gentler (“T5 low”: 5U, 30 min) 294 because over-digestion of cccDNA had sporadically been observed within this consortium and 295 gentler digestion conditions were anticipated to reduce this effect. PSD was employed in a 296 classical setting (“PSD”: 10U, 6h in 20µl total volume) and in a setting using more units in a 297 higher volume (“PSD high”: 30U, 2h in 200µl total volume) based on experiences in tissue- 298 derived samples. The Exo I/III combination was tested using one setting (20U ExoI, 25U ExoIII, 299 2h). All nuclease treatments reduced total HBV DNA to varying degrees (**Fig.2A**). However, 300 considerable variations were observed among labs. Using the classical +PK DNA extracts,

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3 301 “PSD low” conditions were unable to effectively digest total HBV DNA. This was most likely
4 302 caused by an inhibition of the enzyme by contaminants present in the extracts or inappropriate
5 303 pH values, since “PSD high” or the use of column-purified +PK DNA for the “PSD low” condition
6 304 remedied this issue (data not shown).

7
8 305 When using cccDNA selective primers, we observed a considerable reduction of cccDNA
9 306 counts after nuclease treatments even in Hirt and -PK DNA extracts, indicating that residual
10 307 HBV RI were still detected following these extractions in this highly infected sample (9×10^8
11 308 HBV DNA GE/ml) (**Fig.2B**). Analysis of the human mitochondrial gene ND2 as a cellular
12 309 surrogate marker for episomal DNA (**Fig.2C**), revealed that mtDNA levels were also lower after
13 310 nuclease digestion albeit to a lesser degree, indicating that the reduced detection of cccDNA
14 311 was not only due to improved primer specificity but partially due to cccDNA loss. Although
15 312 considerable variations were observed among labs, median cccDNA levels were 3.3-fold lower
16 313 after T5 or Exo I/III treatments compared to PSD treatments across all DNA extracts and labs.
17 314 To shed light on the reasons for these differences, we performed a head-to-head comparison
18 315 of qPCR and SB analyses using the same undigested and digested samples (**Fig.2D**). Both
19 316 methods proved that all nuclease digestions reduced HBV DNA copy numbers (qPCR) and
20 317 the typical smear present on the SB. However, PSD did not digest the “slow-migrating” band
21 318 where pf-rcDNA is generally found, while T5 and Exo I/III digested all HBV DNA forms except
22 319 for the cccDNA-containing “fast-migrating” band. Furthermore, cccDNA bands displayed very
23 320 similar densities after exonuclease- or PSD-based treatment within the same extraction,
24 321 indicating that the higher cccDNA PCR counts observed after PSD digestion is due to a co-
25 322 measurement of molecules present in the “slow-migrating” band.

31 323

32 324 **cccDNA and pf-rcDNA are detected by qPCR with the same efficiency**

33 325 To assess whether the HBV DNA species present in the “slow-migrating” band could be
34 326 recognized by the cccDNA PCR with the same efficiency as the cccDNA itself, we performed
35 327 preparative agarose gel electrophoresis, excised and analyzed by PCR the different HBV DNA
36 328 bands individually. Liver samples were analyzed from one untreated HBV-infected mouse and
37 329 two Lamivudine (Lam)-treated mice (six and 12 weeks, respectively; **Supplementary Fig.3B**),
38 330 which were expected to have lower levels of interfering RI. DNA extracted with the -PK method
39 331 was subjected to SB and qPCR after “PSD high” and “T5” digestion. The characteristic smear
40 332 on SB composed of HBV RI in highly infected samples (**Fig.3A**) and total HBV DNA copies by
41 333 PCR (**Fig.3B**) were reduced in Lam-treated mice, thus enabling specific cccDNA
42 334 measurements by qPCR before and after PSD digestion (**Fig.3B**). However, T5 treatment
43 335 removed the “slow-migrating” band, leading to 4-fold lower cccDNA PCR measurements than
44 336 PSD treatment, while the density of the faster migrating cccDNA bands remained the same
45 337 regardless of the nuclease digestion (**Fig.3A**). Interestingly, cccDNA levels appeared to
46 338 decrease in a time-dependent fashion in Lam-treated mice compared to the untreated mouse.

47 339 Identical samples were used for the preparative agarose gel, where slow- and fast-migrating
48 340 bands were excised separately and analyzed by qPCR for total HBV DNA and cccDNA
49 341 (**Supplementary Fig.6**). The cccDNA band was detected by both PCR assays in a very similar
50 342 fashion and the ratio of total HBV DNA to cccDNA copies was identical across all mice and
51 343 treatments except for the untreated, undigested sample (**Fig.3C**). This observation confirmed
52 344 that the “fast-migrating” band, solely composed of cccDNA, was detected by both PCR assays.
53 345 Interestingly, the same pattern was observed also when the “slow-migrating” band was
54 346 analyzed, indicating that the DNA species present in this band served as similarly efficient

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3 347 templates for the cccDNA PCR as cccDNA itself. The slightly higher ratios in the untreated,
4 348 undigested sample were likely due to the co-detection of HBV RI, presenting a visible smear
5 349 only in this sample. Taken together, the higher cccDNA PCR counts determined in samples
6 350 retaining the slow-migrating band strongly indicate that pf-rcDNA is an efficient template for
7 351 the cccDNA PCR. The precise composition of this band, however, needs further investigations.
8 352 Of note, a potential intermediate for cccDNA formation, the closed minus-strand rcDNA (CM-
9 353 rcDNA), may also be present in that “slow-migrating” band¹⁷. Nicking of the cccDNA (occurring
10 354 during active transcription⁷ or accidentally during the extraction process) would result in the
11 355 loss of supercoiling and nicked cccDNA would migrate together with pf-rcDNA (see below and
12 356 **Supplementary Fig.8C**). Thus, quantification strategies aiming at detecting cccDNA
13 357 contained in the “fast-migrating” band should include T5 or ExoI/III nucleases, whereas PSD
14 358 treatment will guarantee inclusion of potentially damaged, nicked cccDNA.

15 359

20 360 **Comparison of cccDNA extraction and quantification protocols in HepG2-NTCP cells**

21 361 Following the same criteria and protocols used for liver tissues, we comparatively assessed
22 362 the impact of distinct DNA extraction methods on HBV DNA levels in HBV-infected HepG2-
23 363 NTCP cells. Total HBV DNA qPCR measurements indicated that Hirt and -PK extractions
24 364 substantially removed protein-bound HBV DNA forms by 1.7 and 1.5 logs, respectively
25 365 (**Fig.4A**). Accordingly, cccDNA counts were reduced by median 0.9 and 0.8 logs compared to
26 366 +PK extractions indicating improved selectivity for cccDNA (**Fig.4A and B**). We next applied
27 367 different nuclease digestion conditions to all three DNA extraction method (**Fig.4C-F**). In +PK
28 368 extracts, the removal of RI reduced cccDNA counts by PCR. In both Hirt and -PK DNA,
29 369 however, no further substantial cccDNA decline was observed after nuclease digestion,
30 370 suggesting that HBV RI had been sufficiently removed through the extraction process allowing
31 371 for precise cccDNA quantification. The minor reduction of cccDNA levels after all nuclease
32 372 treatments was mirrored in ND2 measurements indicating a general small loss of circular DNA
33 373 molecules (**Fig.4E**). The SB in **Figure 4F** reproduced the characteristic HBV DNA pattern
34 374 similar to liver tissues albeit with less RI-derived smear. Nevertheless, in Hirt and -PK DNA
35 375 extracts, cccDNA levels determined by PCR were 1.5-fold lower after T5 and ExoI/III compared
36 376 to PSD-based methods. Again, the “slow-migrating” band visualized by SB was degraded only
37 377 after exonuclease-based treatments.

38 378 Another factor that can influence cccDNA measurements is the presence of the inoculum,
39 379 which contains high amounts of HBV particles that can persist in culture. To assess the impact
40 380 of input virus on cccDNA quantification, we infected HepG2-NTCP cells with a high-titer
41 381 HepAD38-derived inoculum (MOI 4000) and followed them up for 9 days in the absence or
42 382 presence of the entry inhibitor Bulevirtide (BLV)²⁴. The inoculum contained high levels of pf-
43 383 rcDNA, which persisted until day 9 in BLV-treated cells where the establishment of a productive
44 384 infection was precluded (**Supplementary Fig.7A**). This contaminant could be removed
45 385 through “T5” treatment, resulting in approx. 2-fold lower cccDNA levels detected by qPCR
46 386 (**Supplementary Fig.7B**). Of note, using this highly sensitive bDNA technology, several T5-
47 387 resistant HBV DNA species were detected by SB. Interestingly, these forms are not visible
48 388 under alkaline Hirt extraction conditions (**Supplementary Fig.5B**).

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50 390 **Impact of DNA quality and storage conditions on cccDNA quantification**

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3 391 Nuclease treatment bears some risks and should be employed with caution. First, we observed
4 392 high variations in terms of digestion efficiency between labs and even between replicates within
5 393 one lab (data not shown). Second, excessive digestion conditions can lead to over-digestion
6 394 of cccDNA. Third, the quality of the extracted DNA is of utmost importance since nicking of the
7 395 cccDNA will make it a template for T5 ExoIII, but not for PSD, while all enzymes (except ExoI)
8 396 will act on damaged cccDNA containing double strand breaks. Examples and explanations for
9 397 risks associated with nuclease treatments can be found in the supplementary results and
10 398 **Supplementary Fig.8.**

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13 399 Another factor that can influence the quality of extracted DNA derives from the storage
14 400 conditions. In this study we used freshly frozen, cryopreserved samples; however,
15 401 cryopreservation of liver biopsies is rarely feasible in clinical studies. Instead, tissue
16 402 preservatives are used. To mimic these conditions, cryopreserved small liver pieces from two
17 403 HBV-infected untreated humanized mice and two siRNA-treated mice¹⁹ were moved to
18 404 Allprotect, a common tissue preservative from Qiagen, and stored at -20°C for several months
19 405 before being extracted with -PK protocols and digested with “PSD high” or “T5” (**Fig.5A**).
20 406 Compared to the matched fresh frozen samples analyzed in parallel, the Allprotect-stored
21 407 samples showed an overall higher reduction of cccDNA levels after nuclease digestion by
22 408 qPCR, with PSD reaching approximately 1log and T5 2log reductions. For comparison, the
23 409 cccDNA quantified in freshly frozen liver tissue from siRNA-treated mice were not reduced by
24 410 PSD treatment indicating sufficiently low HBV DNA levels for specific cccDNA quantification in
25 411 this setting. Accordingly, the reduction of mtDNA was even more pronounced than the drop in
26 412 cccDNA following Allprotect storage, while mtDNA levels decreased only modestly in DNA
27 413 from freshly frozen tissue (**Fig.5B**). This data hints at a general DNA damage involving both
28 414 nicking and double strand breaks and warrants extreme caution when using nuclease digestion
29 415 in Allprotect-stored samples.

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36 417 **Discussion and recommendations for cccDNA quantification**

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38 418 To improve our knowledge on cccDNA biology, validate serological biomarkers and assess the
39 419 impact of new therapies on cccDNA levels and activity, reliable and standardized quantitative
40 420 cccDNA assays are paramount. To achieve this goal in a more reliable manner than previously
41 421 possible, it is critical to compare protocols and perform cross-validation experiments across
42 422 laboratories. The results of this concerted effort provide novel information to guide researchers
43 423 and clinical trial investigators in designing and performing protocols to accurately quantify
44 424 cccDNA.

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47 425 The comparative analysis of parallel qPCR and SB results was a strength of our study design
48 426 and allowed us to understand how each method influences the outcome and to identify the
49 427 most critical points. In **figure 6**, we summarized the methodologies that were validated within
50 428 our consortium and the observations relevant to cccDNA quantification. Because all protocols
51 429 must be adapted to the sample type, infection level and treatment, there is not one protocol
52 430 that suits all needs. Instead, we provide guidance and general recommendations, which are
53 431 summarized in **table 1**.

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57 432 Through the comparison of three DNA extraction methods, we could show that not only the
58 433 Hirt procedure, but also the omission of the proteinase K digestion step from a commercial kit
59 434 for fast nucleic acid purification led to efficient reduction of HBV DNA RI, thus improving the
60 435 selectivity of cccDNA PCR measurements. However, -PK or Hirt-based extractions^{13,22,23} might

not be sufficient for specific quantification in highly replicative settings and nuclease treatment will still be needed. Therefore, we recommend performing both a DNA extraction that reduces RI and virions, a nuclease treatment to further reduce non-cccDNA species and a PCR design spanning the cohesive ends region of the rcDNA. The use of such a cccDNA-selective PCR is further supported by the fact that none of the extraction methods tested (-PK, Hirt, alkaline Hirt) was able to guarantee a complete depletion of genomic DNA, which could represent a source of integrated HBV sequences. All nucleases used here reduced RI amounts to various degrees, even when -PK or Hirt DNA extraction procedures had already lowered HBV RI levels. Nevertheless, all nucleases showed specific strengths and weaknesses. PSD did not perform well in +PK-extracted liver DNA, possibly due to impurities present in these extracts, whereas T5 and Exo I/III exonucleases performed similarly well although high concentrations and incubation times bear the risk of cccDNA over-digestion. Additionally, the efficiency of the tested nucleases varied both among labs and even within a given lab. The reasons for these variations are unclear, but could depend on small handling differences, input DNA variations and presence of sample impurities. Moreover, we showed that tissue preservatives are particularly prone to damaging the cccDNA. Consequently, nucleases induced strong reduction of cccDNA PCR levels in Allprotect-stored samples. Since patient liver biopsies are often stored in Allprotect or similar tissue preservatives, omission of nuclease digestions should be considered. Ideally, liver biopsy samples should be fresh-frozen and cryopreserved. Thus, digestion conditions have to be carefully titrated to avoid unspecific side activities potentially leading to cccDNA digestion or to insufficient digestion of other HBV DNA forms. Since it is laborious to determine whether a nuclease treatment is needed for every sample and condition, we recommend including it for fresh and fresh frozen samples.

Additionally, we observed that PSD did not digest the “slow-migrating” band, although this treatment removed most RI from -PK and Hirt samples. Furthermore, we demonstrated that without nuclease treatment, the pf-rcDNA is still present even in the setting of low replication levels and that this “slow-migrating” band is detected by the cccDNA-selective PCR. We therefore recommend using exonuclease-based treatment when detection of this band is not wanted. The precise composition of this “slow-migrating” band detected by SB is not entirely known but it appears to contain a mixture of molecules, which underwent removal of the covalently attached HBV polymerase but that still are unrepaired or at different phases of the repair process, such as DP-rcDNA or CM-rcDNA^{3,4}. Fully repaired HBV DNA molecules that are not yet covalently closed and supercoiled (immature cccDNA) will also appear within this band^{3,4}. In cell culture experiments, a prominent part of the “slow-migrating” band might consist of input virus. Since it is unclear which factors and circumstances (infection status or treatments) may affect the conversion of rcDNA to cccDNA, the intensity of the “slow-migrating” band may also vary between samples and experimental settings. Additionally, the choice of the extraction method will influence the detected population of HBV DNA molecules. In the side-by-side comparison of the original Hirt with a modified alkaline Hirt known to preferentially extract supercoiled DNA, the “slow-migrating” bands – potentially resulting from circular HBV DNA with different degrees of supercoiling – appeared lost (**Supplementary Fig.5**). Thus, further studies are needed to assess the biological meaning of such differences and cccDNA quantification strategies including the “slow-migrating” band are justified.

For in vitro infection studies, we recommend employing exonuclease-based treatments (T5 or Exo I/III) to remove the non-cccDNA species present in the inoculum. This contaminant was present as a prominent “slow-migrating” band on SB and persisted until day 9 post infection of HepG2-NTCP cells despite the use of an entry inhibitor (Bulevirtide), known to abrogate the establishment of productive HBV infection²⁴. Although the example shown here used an

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3 484 extremely high MOI (4000), T5 exonuclease efficiently reduced this contaminant in Hirt-
4 485 extracted samples allowing specific cccDNA measurements by qPCR. Thus, it is advisable to
5 486 include an entry inhibitor control in cell culture to rule out interferences due to input HBV DNA.

7 487 Because cccDNA that contains nicks or double strand breaks will become a template for
8 488 nucleases and migrate together with pf-rcDNA on SB, it is of utmost importance to assess the
9 489 quality of the DNA in every extract. We recommend using mitochondrial DNA – an episomal
11 490 dsDNA – as a surrogate for cccDNA and to quantify a mitochondrial gene by PCR in every
12 491 sample before and after nuclease digestion. Based on our experience, a reduction of less than
13 492 1log indicates sufficiently intact DNA, while more than 1log reduction indicates damaged DNA.
14 493 Over-digestion of mtDNA after exonuclease-based but not PSD-based digestions, indicates
15 494 that the DNA contains single-strand nicks. Consequently, cccDNA will also be nicked and
16 495 reduced after exonuclease treatment. PCR assessment of mtDNA levels will indicate the
17 496 quality of the DNA in the sample and after the extraction.

20 497 We acknowledge that the present methods to quantify cccDNA are not optimal yet and
21 498 encourage the optimization or development of new methods for both DNA extraction and
22 499 cccDNA quantification²⁵. Ideally, improved PCR-based methods should have higher specificity
23 500 for cccDNA in the presence of contaminating HBV DNA species and should be robust,
24 501 sensitive and suitable for all virus isolates. A milestone will be reached when novel procedures
25 502 allow to avoid the use of nucleases. The implementation of digital PCR (dPCR) instead of
26 503 qPCR has allowed a significant increase in sensitivity and brought the major advantage of
27 504 absolute quantification without PCR standards, thus limiting the variability thereof^{12,26}.
28 505 However, the limited specificity for cccDNA in a complex mixture of sequence-identical HBV
29 506 DNA species remains even when using dPCR. Novel methodologies to visualize cccDNA in
30 507 infected cells are being developed and can complement quantitative analyses and serve to
31 508 corroborate PCR and SB results²⁷. Additionally, more research is needed to ascertain the
32 509 nature of all HBV DNA forms, their role in the life-cycle of HBV and how they are influenced by
33 510 various manipulations.

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4	1. Reduce HBV RI and rcDNA through means of the DNA extraction
5	<ul style="list-style-type: none"> • Extract DNA using Hirt or -PK method to lower RI and rcDNA contained in HBV capsids. This procedure will facilitate specific cccDNA quantification together with nuclease treatments and cccDNA-selective PCR measurements.
6	<ul style="list-style-type: none"> • PSD digestion has been shown to work more reliably after -PK or Hirt DNA extractions than after +PK extraction. Exonuclease-based methods are less frail, but low RI and rcDNA content is preferred in any case.
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11	2. Further reduce HBV RI and virions through nuclease digestion
12	<ul style="list-style-type: none"> • Perform nuclease digestion to further reduce non-cccDNA species.
13	<ul style="list-style-type: none"> • To exclusively measure the cccDNA, exonuclease-based treatments should be used. To quantify both cccDNA and species contained in the “slow-migrating” band, the use of PSD is recommended.
14	<ul style="list-style-type: none"> • The “slow-migrating” band contains nicked cccDNA, caused mostly by technical damage. Exonuclease digestion may thus result in a loss of these cccDNA forms and lower cccDNA levels detected by PCR.
15	<ul style="list-style-type: none"> • The digestion conditions should be carefully titrated for every new sample type and extraction protocol (by PCR analysis of total HBV DNA and cccDNA in the undigested and digested sample and a direct comparison by SB) and monitored routinely (PCR analysis of total HBV DNA and cccDNA in undigested and digested samples).
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25	3. Assess the quality of the extracted DNA
26	<ul style="list-style-type: none"> • Use mitochondrial DNA as a surrogate for cccDNA (circular dsDNA). A mitochondrial gene should be quantified in every sample before and after nuclease digestion.
27	<ul style="list-style-type: none"> • A reduction of <1Log10 after nuclease digestion indicates intact DNA; a reduction of >1Log10 indicates damaged DNA (DNA extract should be discarded).
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32	4. Determine the optimal normalization strategy
33	<ul style="list-style-type: none"> • Check for differential enrichment of genomic and mitochondrial DNA during the DNA extraction process to choose the optimal normalization strategy.
34	<ul style="list-style-type: none"> • The total amount of recovered DNA can also be used for normalization. In human chimeric mice, cccDNA numbers need to be normalized to the amounts of human hepatocytes present in every liver specimen.
35	<ul style="list-style-type: none"> • Control whether the treatments you want to test affect cell viability or mitochondria levels. Mitochondria count may vary between patients and samples.
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40	5. Report all methodological details for cccDNA quantification in publications
41	<ul style="list-style-type: none"> • To allow independent assessment of the data, all methodological details should be reported including the DNA extraction method, nuclease digestion, qPCR conditions and normalization strategy.
42	<ul style="list-style-type: none"> • Employ only one optimized method in a particular study for cccDNA extraction, nuclease digestion, and qPCR quantification.
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47	6. Considerations for the establishment of new assays
48	<ul style="list-style-type: none"> • For novel PCR assays, determine the degree of specificity towards cccDNA by measuring total HBV DNA and cccDNA in the untreated sample and calculate the ratio of total HBV DNA to cccDNA copy numbers. A ratio <100:1 is recommended. Copy numbers and not CT values should be used for comparison to avoid biases due to different sensitivities of PCR assays. Note that specificity ratios might also vary between types of samples and thus, falling below this ratio does not guarantee specific measurements in any case.
49	<ul style="list-style-type: none"> • Novel DNA extraction methods should assess the enrichment of cccDNA in comparison to RI and rcDNA. The optimal ratio of input sample and buffer volume has to be determined empirically. The extraction efficiency can be controlled by spiking the sample with known copy numbers of an unrelated supercoiled plasmid DNA.
50	<ul style="list-style-type: none"> • Assess the specificity to detect cccDNA in every new method including DNA extraction, nuclease digestions, PCR assays or other novel methodologies.
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- Confirm the results by performing Southern blotting.

512 **Table 1:** Recommendations for cccDNA quantification

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Confidential: For Review Only

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3 514 **Acknowledgements**

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5 515 We are grateful to Elena S. Kim, Soujuan Wang, Romina Bester, Chloé Saint Jean, Laura
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12 520 **References**

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3 589 **Figure legends**

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5 590 **Figure 1: The effect of different DNA extraction methods on cccDNA quantification by**
6 591 **qPCR and SB in HBV-infected USG mouse liver tissue.** (A) Schematic presentation of the
7 592 experimental design used for the cross-validation. (B) SB analysis on nondigested DNA
8 593 extracts using HBV DNA probes in three of the labs. (C) qPCR measurements of total HBV
9 594 DNA and cccDNA in the DNA extracts. Bars depict the median and range across all four labs.
10 595 (D) qPCR measurements of cccDNA shown separately for every lab, relative to the amount in
11 596 the +PK DNA extractions. Bars depict the mean of duplicate measurements. Hirt, Hirt DNA
12 597 extraction, which does not include a proteinase K digestion; +PK, total DNA extraction with
13 598 proteinase K digestion; -PK, total DNA extraction without proteinase K digestion; SB, Southern
14 599 blot.

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17 600 **Figure 2: The effect of nuclease digestions on different DNA extracts in HBV-infected**
18 601 **USG mouse liver tissue.** The bar graphs depict qPCR measurements of total HBV DNA (A)
19 602 and cccDNA (B) in all DNA extracts and labs without nuclease digestion (hatched bars) or after
20 603 the indicated nuclease treatments. The bars depict the median and range of the values from
21 604 three labs. Every lab performed the nuclease digestion in duplicates. The values (copies/PCR)
22 605 after nuclease treatment were first normalized to the nondigested value in the respective DNA
23 606 extract, then all values derived from Hirt or -PK DNA extracts were normalized to the +PK
24 607 extract. (C) qPCR of mtDNA DNA via the mitochondrial gene ND2, depicted as arbitrary units
25 608 normalized to the nondigested values in the respective DNA extract. (D) SB analysis in one of
26 609 the labs using a second stably HBV-infected and untreated USG mouse and all three DNA
27 610 extracts and four nuclease digestion conditions using HBV DNA probes (top panel) and
28 611 densitometric analysis of the cccDNA band (lower panel). The "X" denotes a sample that could
29 612 not be quantified because of high background staining. The samples were run on two separate
30 613 blots but identical amounts of nondigested DNA, with the help of which densitometry was
31 614 normalized between blots. ND2, mitochondrially encoded NADH:ubiquinone oxidoreductase
32 615 core subunit 2.

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36 616 **Figure 3: The pf-rcDNA is detected with the same efficiency as cccDNA by cccDNA-**
37 617 **selective qPCR but is removed through T5 exonuclease treatment.** Parallel SB (A) and
38 618 qPCR (B) analysis in three stably HBV-infected USG mice (after six or 12 weeks of Lamivudine
39 619 treatment, or untreated). Liver DNA was extracted with the -PK, digested with nucleases or left
40 620 undigested before analysis. (A) SB using HBV DNA probes (top panel) and densitometric
41 621 analysis of the pf-rcDNA (middle panel) and cccDNA band (lower panel). DNA amounts were
42 622 normalized to ND2 via qPCR with human-specific primers before digestion to ensure loading
43 623 of equal amounts of DNA derived from human cells. (B) qPCR measurements of total HBV
44 624 DNA (grey bars) and cccDNA (checked bars) normalized to human hepatocytes via human
45 625 HBB counts in the nondigested DNA extract. The cccDNA copy numbers/cell are depicted
46 626 above each bar. (C) Preparative agarose gel using the same samples as in (A) and identical
47 627 settings for the gel electrophoresis. The upper and lower bands were excised separately, DNA
48 628 was extracted and used for qPCR analysis (total HBV DNA and cccDNA). The ratio of total
49 629 HBV DNA copies to cccDNA copies was calculated for all samples derived from the upper SB
50 630 band (top) and the lower band (bottom), respectively. Lam, Lamivudine; NT, non-treated.

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54 631 **Figure 4: The effect of different DNA extraction methods and nuclease digestions on**
55 632 **cccDNA quantification by qPCR and SB in HBV-infected HepG2-NTCP cells.** (A-F) Frozen
56 633 cell pellets harvested at day nine post infection were shipped to the participating labs. (A)
57 634 qPCR measurements of total HBV DNA and cccDNA in the undigested DNA extracts. Bars
58 635 depict the median and range across all four labs. (B) PCR measurements of cccDNA shown
59 636 separately for every lab and relative to the amount in the +PK DNA extractions. Bars depict
60 637 the mean of duplicate measurements. (C, D) qPCR measurements of total HBV DNA (C) and
638 cccDNA (D) in all DNA extracts and labs either without nuclease digestion (hatched bars) or

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3 639 after the indicated nuclease treatments (performed in duplicates). The bars depict the median
4 640 and range of the values from three labs. The values (copies/PCR) after nuclease treatment
5 641 were first normalized to the nondigested value in the respective DNA extract, then all values
6 642 derived from Hirt or -PK DNA extracts were normalized to the +PK extract. (E) qPCR of mtDNA
7 643 DNA via the mitochondrial gene ND2, depicted as arbitrary units normalized to the nondigested
8 644 values in the respective DNA extract. (F) SB using HBV DNA probes (top panel) and
9 645 densitometric analysis of the cccDNA band (lower panel). The "X" denotes a sample that could
10 646 not be quantified because of high background staining. The samples were run on two separate
11 647 blots with identical amounts of nondigested DNA, with the help of which densitometry was
12 648 normalized between blots.

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15 649 **Figure 5: Nuclease treatment bears the risk of over-digesting cccDNA in Allprotect-**
16 650 **stored samples.** Comparison of nuclease digestion in fresh frozen liver tissue or liver tissue
17 651 preserved in Allprotect. Liver DNA was extracted using the -PK method from 2 untreated HBV-
18 652 infected mice and 2 mice treated with siRNA targeting all HBV transcripts for 6 weeks. DNA
19 653 was digested with PSD or T5 exonuclease and subjected to qPCR for cccDNA (A) and ND2
20 654 (B). Every dot depicts a single mouse, bars the median. siRNA, small interfering RNA.

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23 655 **Figure 6: Schematic presentation of the main findings of the study.** The flow chart
24 656 summarizes the experimental flow for cccDNA quantification and highlights optimal and
25 657 suboptimal results for both qPCR and SB, including the major caveats.

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1. I. Medical Clinic and Polyclinic, University Medical Center Hamburg-Eppendorf, Hamburg, Germany

2. German Center for Infection Research (DZIF), Germany

3. Cancer Research Center of Lyon, INSERM U1052, Lyon University, Hospices de Lyon, Lyon, France

4. ANRS HBV Cure Task Force

5. Gilead Sciences, Foster City, California, United States of America

6. Institute of Virology, Technical University of Munich, Munich, Germany

* Current affiliation: Infectious Diseases Therapeutic Research Center, Therapeutics & Biotechnology Division, Korea Research Institute of Chemical Technology (KRICT), 34114 Daejeon, Republic of Korea

7. Department of Infectious Diseases, Molecular Virology, University Hospital Heidelberg, Germany

** Current affiliation: Division of Veterinary Medicine, Paul Ehrlich Institute, Germany

8. Institute of Medical Microbiology, Virology and Hygiene, University Medical Center Hamburg-Eppendorf Hamburg, Germany

9. Indiana University School of Medicine, Indianapolis, Indiana, United States of America

10. Current affiliation: Department of Microbiology and Molecular Genetics, Cancer Virology Program, UPMC Hillman Cancer Center, University of Pittsburgh School of Medicine, Pittsburgh, United State of America

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Abbreviations: cccDNA, covalently closed circular DNA; CHB, chronic hepatitis B; HBB, hemoglobin subunit beta; HCl, hydrochloric acid; KCl, potassium chloride; Lam, Lamivudine; ND2, mitochondrially encoded NADH: ubiquinone oxidoreductase core subunit 2; NTCP, sodium-taurocholate co-transporting polypeptide; PCR, polymerase chain reaction; pf-rcDNA, protein-free relaxed circular DNA; PSD, plasmid-safe ATP-dependent DNase; RI, replicative intermediates; SB, Southern blot; SDS, sodium dodecyl sulfate; siRNA, small interfering RNA.

Corresponding authors: Dr. rer. nat. Maura Dandri
I. Department of Internal Medicine, Center for Internal Medicine
University Medical Center Hamburg-Eppendorf
Martinistr. 52, 20246 Hamburg, Germany
Tel.: +49 40 741052949, Fax: + 49 40 741057232
E-mail: m.dandri@uke.de

Prof. Dr. Fabien Zoulim

1
2
3 52 INSERM U1052, CNRS UMR-5286,
4 53 Cancer Research Center of Lyon (CRCL)
5 54 151 Cours Albert Thomas, 69424 Lyon, France
6 55 Tel.: +33 472681970, Fax: +33 472681971.
7 56 E-mail: fabien.zoulim@inserm.fr
8 57

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19 68 samples. LA generated liver tissue samples. LA, BT, MY, CK and BQ performed cross-
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75 Abstract

76 **Objectives:** A major goal of curative hepatitis B virus (HBV) treatments is the reduction or
77 inactivation of intrahepatic viral covalently closed circular DNA (cccDNA). Hence, precise
78 cccDNA quantification is essential in preclinical and clinical studies. Southern blot (SB) permits
79 cccDNA visualization but lacks sensitivity and is very laborious. Quantitative PCR (qPCR) has
80 no such limitations but inaccurate quantification due to co-detection of viral replicative
81 intermediates (RI) can occur. The use of different samples, preservation conditions, DNA
82 extraction, nuclease digestion methods and qPCR strategies has hindered standardization.
83 Within the ICE-HBV consortium, available and novel protocols for cccDNA isolation and qPCR
84 quantification in liver tissues and cell cultures were compared in six laboratories to develop
85 evidence-based guidance for best practices. **Design:** Reference material (HBV-infected
86 humanized mouse livers and HepG2-NTCP cells) was exchanged for cross-validation. Each
87 group compared different DNA extraction methods (Hirt extraction, total DNA extraction with
88 or without proteinase K treatment (+PK/-PK) and nuclease digestion protocols (plasmid-safe
89 ATP-dependent DNase (PSD), T5 exonuclease, exonucleases I/III). Samples were analyzed
90 by qPCR and SB. **Results:** Hirt and -PK extraction reduced coexisting RI forms. However,
91 both cccDNA and the protein-free relaxed circular HBV DNA (pf-rcDNA) form were detected
92 by qPCR. T5 and Exo I/III nucleases efficiently removed all RI forms. In contrast, PSD did not
93 digest pf-rcDNA, but was less prone to induce cccDNA over-digestion. In stabilized tissues
94 (e.g. Allprotect), nucleases had detrimental effects on cccDNA. **Conclusions:** We present
95 here a comprehensive evidence-based guidance for optimizing, controlling and validating
96 cccDNA measurements using available qPCR assays.

97
98 **Keywords:** HBV, chronic hepatitis B, minichromosome, humanized mice, human liver chimeric
99 mice, HepG2-NTCP, Southern blot, qPCR, liver biopsies, plasmid-safe ATP-dependent
100 DNase, T5 exonuclease, exonuclease I, exonuclease III.

102 Summary box:

103
104 **What is already known on this topic?** Persistence of the HBV genome, the covalently closed
105 circular DNA (cccDNA), in the liver is a major obstacle for developing HBV cure strategies and
106 its accurate quantification is essential in preclinical and clinical studies. However, cccDNA
107 quantification by PCR lacks standardization and is technically challenging due to the
108 heterogeneous population of HBV DNA molecules present in infected cells.

109 **What this study adds?** Distinct cccDNA extraction and quantification protocols were cross
110 validated using infected tissues and cell cultures. We provide experimental evidence that
111 coexistence of certain HBV DNA forms and potential cccDNA over-digestion due to sample
112 preservation conditions and nuclease treatment still challenges PCR-based quantification of
113 cccDNA. The results support recommendations for optimizing, controlling and validating
114 cccDNA measurements according to the sample type.

115 **How this study may affect research, practice or policy?** This work presents an evidence-
116 based guidance for best practices to quantify cccDNA by qPCR. Information provided will
117 assist the HBV cure research programs aiming at assessing the impact of therapies on the
118 HBV reservoir in preclinical studies and clinical trials.

119

120 Introduction

121 The hepatitis B virus (HBV) is the cause of chronic hepatitis B (CHB) and despite the availability
122 of effective prophylactic vaccines and treatments that efficiently suppress viral replication, HBV
123 puts 296 million carriers at risk of developing liver cirrhosis and hepatocellular carcinoma
124 (HCC)¹. Thus, there is a strong need to develop therapies with the potential to cure CHB. The
125 unique HBV replication strategy, however, makes viral eradication challenging². Knowledge
126 and precise monitoring of the different viral components present in infected cells and in the
127 circulation is paramount for the development and assessment of novel therapeutic strategies.

128 HBV is an enveloped virus harboring a small (3.2 kb) partially double-stranded relaxed circular
129 DNA (rcDNA) genome which specifically infects human hepatocytes. Upon infection, the
130 rcDNA is repaired by cellular enzymes to generate a double-stranded episomal DNA genome,
131 the covalently closed circular DNA (cccDNA)^{3,4} (**Supplementary figure 1**). By associating with
132 histone and non-histone proteins, the cccDNA forms a stable minichromosome within the cell
133 nuclei that serves as transcriptional template for all viral transcripts. Nucleoside analogs (NAs)
134 and interferon alpha are the only approved treatments for CHB but are mainly suppressive as
135 they do not clear cccDNA from the liver. Because of the central role of the cccDNA in HBV
136 persistence, the elimination of this molecule constitutes the ultimate goal of curative
137 treatments⁵. Such a goal may be very difficult to achieve and current investigational
138 approaches rather aim at achieving a functional cure, which is defined as the loss of HBsAg
139 and undetectable HBV DNA in serum². Examples of currently explored curative strategies
140 include, among others, the use of capsid assembly modulators (CAMs) and entry inhibitors,
141 which can also prevent cccDNA formation and intrahepatic amplification of the cccDNA pool⁶,
142 degradation of HBV transcripts using siRNA technologies, immune-mediated clearance and
143 silencing of cccDNA molecules, or its inactivation by gene editing⁷. Assessment of the impact
144 of novel therapies on cccDNA load and activity is therefore of utmost importance. Moreover,
145 our understanding of cccDNA biology in preclinical models and patient biopsies is still limited.
146 Because of the paucity of biopsy material, non-invasive biomarkers (e.g. HBcrAg, HBV RNA),
147 are increasingly studied as surrogate cccDNA markers⁸. However, for the primary validation of
148 these biomarkers, proper cccDNA quantification is needed.

149 A major limitation in HBV research and its translation into the clinic is the lack of standardized
150 PCR-based methods allowing specific cccDNA quantification in HBV-infected samples. The
151 main challenge is the reliable detection of cccDNA by quantitative PCR in the presence of high
152 excess of rcDNA coming from virus input or coexisting replicative intermediates (RI), which are
153 identical in sequence to the cccDNA (**Supplementary figure 1**). To gain specificity, PCR
154 approaches use primers spanning the cohesive ends region of the rcDNA to preferentially
155 detect the cccDNA (**Supplementary figure 2A**). Unfortunately, this approach is not completely
156 specific since it still detects certain amounts of the highly abundant RI leading to an over-
157 estimation of cccDNA amounts^{9,10}. Only when HBV replication is low (e.g., during NA
158 treatment), cccDNA quantification by PCR appears precise^{11,12}. Therefore, cccDNA
159 measurements in samples with high viral productivity or between samples with and without
160 treatment remain challenging and reducing the levels of RI is mandatory.

161 To reduce the levels of HBV RI prior to PCR, various nucleases and DNA extraction methods
162 have been proposed, although their efficacy and specificity in engaging distinct HBV DNA
163 forms in different experimental settings vary substantially. The conventional Hirt method
164 employs sodium dodecyl sulfate lysis and high salt precipitation of high-molecular-weight
165 cellular chromatin and protein-bound DNA¹³ thereby enriching the recovery of protein-free DNA

166 molecules and facilitating the removal of rcDNA, which is covalently linked to the viral
167 polymerase. Southern blot (SB) after Hirt DNA extraction allows visualization of different HBV
168 DNA molecules including cccDNA¹⁴. However, this methodology necessitates large amounts
169 of nucleic acids and therefore lacks sensitivity; it is not suitable for liver biopsy analysis or high-
170 throughput assays and doesn't allow precise quantification.

171 The nucleases commonly used display slightly different substrate specificities but share the
172 common characteristic of sparing closed circular double-stranded DNA (dsDNA) from
173 digestion^{11,15-18}. Apart from employing different nucleases, the use of different DNA extraction
174 procedures, qPCR conditions and normalization increases variability and hinders reliable
175 comparative analyses among laboratories. We therefore attempted to harmonize cccDNA
176 quantification processes by comparing the most used and newer protocols through cross-
177 validation experiments. Based on the results obtained, we propose recommendations of best
178 practice for controlling and validating cccDNA measurements also according to the sample
179 type.

180

181 **Material and Methods**

182 For generation, infection, treatment and viral characterization of human liver chimeric mouse,
183 as well as infection ~~and preparation of liver tissues and of~~ HepG2-NTCP cell culture samples,
184 nuclease digestion and qPCR measurements see supplementary material.

185 **Preparation of liver tissue and cell samples.** Liver specimens removed at the time of
186 sacrifice were snap-frozen in 2-methylbutane and stored at -80°C until further use. Every lab
187 received three frozen liver pieces (approximately 13mg each) from one highly infected,
188 untreated uPA/SCID/beige/IL2RG^{-/-} (USG) mouse. The tissue pieces were homogenized
189 separately in 300µl 10mM Tris-HCl (pH 7.5)/10mM EDTA (pH 8.0) buffer using disposable
190 homogenizers (Biomasher II, DWK Life Sciences, Wertheim, Germany), then pooled and
191 distributed equally among the three DNA extractions. HBV-infected HepG2-NTCP cells were
192 pooled before being divided and shipped to the four participating labs. Every lab received a
193 frozen cell pellet of approximately 1x10⁷ cells, which upon arrival was dissolved in 900µl 10mM
194 Tris-HCl/10mM EDTA buffer and distributed equally for the three DNA extractions. Since all
195 samples were pooled and divided equally across the DNA extractions, the results could be
196 compared with each other directly without the need for additional normalization to cellular DNA.

197 **DNA extraction procedures.** Total cellular DNA was isolated with the MasterPure Complete
198 DNA and RNA Purification Kit (Epicentre, available through Lucigen, Middleton, WI, USA) as
199 recommended by the manufacturer^{12,19}. The total DNA extraction with proteinase K treatment
200 (+PK) and the one without proteinase K (-PK) were performed identically, except for the
201 proteinase K digestion step, which was omitted in the -PK extraction. Briefly, the samples were
202 split up in several microtubes (according to the manufacturer's instructions, 7x10⁵ cells or
203 4.4mg tissue per 300µl lysis buffer) and 10mM Tris-HCl/10mM EDTA buffer was added for a
204 final volume of 300µl each. One volume of double concentrated TCL buffer (Lucigen) was
205 added to lyse the cells. Subsequently, RNA digestion was performed with 2µl RNase A
206 (Lucigen) for 30min at 37°C. For the +PK extraction, 2µl of PK (Lucigen) was added and
207 incubated for 1h at 56°C. After the addition of 300µl of MPC buffer (Lucigen), the samples were
208 mixed and incubated on ice for 5min, followed by 10min high speed centrifugation to pellet the
209 protein. DNA was recovered from the supernatant through isopropanol precipitation, dissolved
210 in 10mM Tris-HCl/1mM EDTA buffer and the DNA from one extraction and sample was pooled

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3 211 again. The DNA content was determined by fluorometry (Qubit™, Invitrogen) or
4 212 spectrophotometry (NanoDrop™, Thermo Fisher Scientific, Waltham, Massachusetts, USA).
5 213 A detailed version of this protocol can be found on the ICE-HBV protocol database ([https://ice-
6 214 hbv.org/protocol/a-modified-kit-based-hbv-protein-free-dna-extraction-from-liver-tissues-and-
7 215 cell-cultures-for-hbv-cccDNA-southern-blot-and-qPCR/](https://ice-hbv.org/protocol/a-modified-kit-based-hbv-protein-free-dna-extraction-from-liver-tissues-and-cell-cultures-for-hbv-cccDNA-southern-blot-and-qPCR/)). For a comparison of different lysis
8 216 buffers, the protocol was repeated also using RLT buffer from the RNeasy Mini kit (Qiagen,
9 217 Hilden, Germany). Some mouse liver tissues were immersed in Allprotect Tissue Reagent
10 218 (Qiagen) as recommended by the manufacturer and stored at -20°C for several months.

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12
13 219 One third of the liver homogenate and cell suspension was subjected to DNA extraction
14 220 according to Hirt¹³. Briefly, the samples were further diluted in 10mM Tris-HCl/10mM EDTA
15 221 buffer to a final volume of 3ml. Cell lysis was achieved by adding SDS (final concentration
16 222 0.6%) and 30min of incubation at room temperature with slow agitation. After adding KCl (final
17 223 concentration 0.5M), the lysates were incubated at 4°C overnight, then centrifuged for 30 min
18 224 at 4°C and 14,500g. DNA from the supernatant was extracted twice with phenol and once with
19 225 phenol/chloroform/isoamyl alcohol (25:24:1) followed by an overnight ethanol precipitation.
20 226 The DNA was pelleted by centrifugation, washed in 70% ethanol and dissolved in 10mM Tris-
21 227 HCl/1mM EDTA buffer.

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25 228 **Southern blot analyses** were performed as previously described^{19,20}. A detailed version of
26 229 this protocol can be found on the ICE-HBV protocol database ([https://ice-hbv.org/protocol/a-
27 230 sensitive-and-rapid-southern-blot-assay-based-on-branched-dna-technology-for-the-
28 231 detection-of-hbv-dna-in-cell-culture-and-liver-tissue-samples/](https://ice-hbv.org/protocol/a-sensitive-and-rapid-southern-blot-assay-based-on-branched-dna-technology-for-the-detection-of-hbv-dna-in-cell-culture-and-liver-tissue-samples/)) and as supplementary.

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30 232

31 233 **Results**

32 234 **Comparison of cccDNA extraction protocols in HBV-infected liver tissues**

33
34 235 Currently available and novel protocols for cccDNA extraction and quantification were collected
35 236 and cross-validated according to the scheme depicted in **Figure 1A**. Frozen liver tissues from
36 237 HBV-infected humanized mice were used as reference material (**Supplementary Fig.3**). We
37 238 compared total DNA extraction methods that either included (+PK) or excluded (-PK) the
38 239 proteinase K digestion step, as well as the classical Hirt DNA extraction (Hirt) that does not
39 240 include PK digestion¹³. Omission of the PK should facilitate the removal of covalently protein-
40 241 bound HBV DNA and was investigated here as potential alternative to Hirt extraction. A
41 242 previously published cccDNA-selective PCR strategy²¹ based on selective primers and a
42 243 Taqman™ probe detecting all HBV genotypes except G (**Supplementary table 1**), and not
43 244 cross-reacting with human or murine genomic sequences, or HBV DNA integrations¹², was
44 245 chosen for cross-validation using improved PCR conditions (for details see **Supplementary**
45 246 **Fig.2A-C**). The specificity for cccDNA detection was assessed on serial dilutions of serum-
46 247 derived rcDNA and on mixtures of an HBV plasmid (as cccDNA surrogate) and increasing
47 248 amounts of serum-derived rcDNA (**Supplementary Fig.2D and E**). These analyses indicated
48 249 that serum rcDNA can be amplified in a false-positive manner despite using cccDNA-selective
49 250 PCR primers and probes when rcDNA levels exceed cccDNA levels by more than 250-fold.
50 251 Under such circumstances, measured cccDNA levels increase and a precise cccDNA
51 252 quantification is not possible without including strategies reducing rcDNA levels.

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53
54 253 To evaluate the three distinct DNA extraction methods in different labs, we first analyzed the
55 254 liver of a highly viremic mouse. Hirt and -PK extractions resulted in reduced HBV RI levels on
56 255 the SB (**Fig.1B**) compared to the +PK extraction. The classical pattern of a “slow-migrating

band” around 3.5kb (known to contain protein-free (pf) relaxed circular DNA or deproteinated (dp)-rcDNA) and a “fast-migrating band” at 2.1kb (supercoiled cccDNA) was observed both after Hirt and -PK extraction procedures. The high amount of RI in the +PK extracts, however, prevented the visualization of distinct bands. Of note, using the highly sensitive bDNA detection method, a substantial smear was still present in -PK and Hirt extracted DNA, which was absent in samples from an uninfected mouse (see example in **Supplementary Fig.8C**), pointing out that those signals were HBV-specific. In line with the SB, qPCR measurements in all labs showed lower amounts of total HBV DNA (1.6log and 1.3log reduction) and cccDNA (0.5log and 0.4log) in Hirt and -PK extractions, respectively (**Fig.1C**), as compared to +PK samples. The reduction of protein-bound replicative intermediates clearly improved the selectivity of cccDNA quantification by PCR (**Fig.1C**) across all labs (**Fig.1D**).

267

268 **Normalization of cccDNA counts to cellular levels**

269 For all downstream cross-validation experiments, the same amount of liver tissue or cell
270 number was used to facilitate comparison between labs and settings. In every-day practice,
271 however, viral DNA counts have to be normalized to cell number to account for differences in
272 the amount of input material or human hepatocyte levels when analyzing chimeric livers.
273 Accordingly, we determined the recovery of genomic DNA (gDNA) and mitochondrial DNA
274 (mtDNA) that were recovered (**Supplementary Fig.4A-C**). Although supernatants from a
275 classical Hirt extraction are known to harbor reduced levels of high molecular weight nucleic
276 acids, genomic DNA was consistently extracted in our Hirt preparation, albeit with a trend
277 towards a slightly reduced recovery of these DNA species in both Hirt and -PK conditions
278 compared to the +PK extraction. However, this trend was similar across analyses, indicating
279 that viral DNA could be normalized to gDNA or mtDNA derived from the same extraction.
280 Moreover, a head-to-head comparison of distinct lysis buffers revealed that the TCL lysis buffer
281 (Lucigen) led to three-fold lower gDNA levels compared to RLT lysis buffer (Qiagen), although
282 these buffers did not affect mtDNA recovery (**Supplementary Fig.4D-F**). Such differential
283 enrichment of gDNA will skew the normalization of viral DNA to target cells and has to be
284 considered in the normalization strategy. A modified Hirt procedure using alkaline
285 extraction^{22,23}, which was tested on liver tissue and cell culture samples in two labs, showed
286 low but still quantifiable genomic DNA recovery compared to the original Hirt (**Supplementary**
287 **Fig 5**). By enriching only supercoiled DNA species, this method also depleted all HBV DNA
288 species except for the “fast-migrating band”.

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290 **Comparison of different nucleases and digestion conditions in chimeric liver tissues**

291 We next tested different nucleases and conditions to compare their efficacy. Based on existing
292 protocols commonly used in different laboratories, T5 exonuclease was used in two settings,
293 one being stronger (“T5”: 10U, 45min), the other one being gentler (“T5 low”: 5U, 30 min)
294 because over-digestion of cccDNA had sporadically been observed within this consortium and
295 gentler digestion conditions were anticipated to reduce this effect. PSD was employed in a
296 classical setting (“PSD”: 10U, 6h in 20µl total volume) and in a setting using more units in a
297 higher volume (“PSD high”: 30U, 2h in 200µl total volume) based on experiences in tissue-
298 derived samples. The Exo I/III combination was tested using one setting (20U ExoI, 25U ExoIII,
299 2h). All nuclease treatments reduced total HBV DNA to varying degrees (**Fig.2A**). However,
300 considerable variations were observed among labs. Using the classical +PK DNA extracts,

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3 301 “PSD low” conditions were unable to effectively digest total HBV DNA. This was most likely
4 302 caused by an inhibition of the enzyme by contaminants present in the extracts or inappropriate
5 303 pH values, since “PSD high” or the use of column-purified +PK DNA for the “PSD low” condition
6 304 remedied this issue (data not shown).

7
8 305 When using cccDNA selective primers, we observed a considerable reduction of cccDNA
9 306 counts after nuclease treatments even in Hirt and -PK DNA extracts, indicating that residual
10 307 HBV RI were still detected following these extractions in this highly infected sample (9×10^8
11 308 HBV DNA GE/ml) (**Fig.2B**). Analysis of the human mitochondrial gene ND2 as a cellular
12 309 surrogate marker for episomal DNA (**Fig.2C**), revealed that mtDNA levels were also lower after
13 310 nuclease digestion albeit to a lesser degree, indicating that the reduced detection of cccDNA
14 311 was not only due to improved primer specificity but partially due to cccDNA loss. Although
15 312 considerable variations were observed among labs, median cccDNA levels were 3.3-fold lower
16 313 after T5 or Exo I/III treatments compared to PSD treatments across all DNA extracts and labs.
17 314 To shed light on the reasons for these differences, we performed a head-to-head comparison
18 315 of qPCR and SB analyses using the same undigested and digested samples (**Fig.2D**). Both
19 316 methods proved that all nuclease digestions reduced HBV DNA copy numbers (qPCR) and
20 317 the typical smear present on the SB. However, PSD did not digest the “slow-migrating” band
21 318 where pf-rcDNA is generally found, while T5 and Exo I/III digested all HBV DNA forms except
22 319 for the cccDNA-containing “fast-migrating” band. Furthermore, cccDNA bands displayed very
23 320 similar densities after exonuclease- or PSD-based treatment within the same extraction,
24 321 indicating that the higher cccDNA PCR counts observed after PSD digestion is due to a co-
25 322 measurement of molecules present in the “slow-migrating” band.

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32 324 **cccDNA and pf-rcDNA are detected by qPCR with the same efficiency**

33 325 To assess whether the HBV DNA species present in the “slow-migrating” band could be
34 326 recognized by the cccDNA PCR with the same efficiency as the cccDNA itself, we performed
35 327 preparative agarose gel electrophoresis, excised and analyzed by PCR the different HBV DNA
36 328 bands individually. Liver samples were analyzed from one untreated HBV-infected mouse and
37 329 two Lamivudine (Lam)-treated mice (six and 12 weeks, respectively; **Supplementary Fig.3B**),
38 330 which were expected to have lower levels of interfering RI. DNA extracted with the -PK method
39 331 was subjected to SB and qPCR after “PSD high” and “T5” digestion. The characteristic smear
40 332 on SB composed of HBV RI in highly infected samples (**Fig.3A**) and total HBV DNA copies by
41 333 PCR (**Fig.3B**) were reduced in Lam-treated mice, thus enabling specific cccDNA
42 334 measurements by qPCR before and after PSD digestion (**Fig.3B**). However, T5 treatment
43 335 removed the “slow-migrating” band, leading to 4-fold lower cccDNA PCR measurements than
44 336 PSD treatment, while the density of the faster migrating cccDNA bands remained the same
45 337 regardless of the nuclease digestion (**Fig.3A**). Interestingly, cccDNA levels determined
46 338 appeared to decrease in a time-dependent fashion in Lam-treated mice compared to the
47 339 untreated mouse.

48 340 Identical samples were used for the preparative agarose gel, where slow- and fast-migrating
49 341 bands were excised separately and analyzed by qPCR for total HBV DNA and cccDNA
50 342 (**Supplementary Fig.6**). The cccDNA band was detected by both PCR assays in a very similar
51 343 fashion and the ratio of total HBV DNA to cccDNA copies was identical across all mice and
52 344 treatments except for the untreated, undigested sample (**Fig.3C**). This observation confirmed
53 345 that the “fast-migrating” band, solely composed of cccDNA, was detected by both PCR assays.
54 346 Interestingly, the same pattern was observed also when the “slow-migrating” band was

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3 347 analyzed, indicating that the DNA species present in this band served as similarly efficient
4 348 templates for the cccDNA PCR as cccDNA itself. The slightly higher ratios in the untreated,
5 349 undigested sample were likely due to the co-detection of HBV RI, presenting a visible smear
6 350 only in this sample. Taken together, the higher cccDNA PCR counts determined in samples
7 351 retaining the slow-migrating band strongly indicate that pf-rcDNA is an efficient template for
8 352 the cccDNA PCR. The precise composition of this band, however, needs further investigations.
9 353 Of note, a potential intermediate for cccDNA formation, the closed minus-strand rcDNA (CM-
10 354 rcDNA), may also be present in that “slow-migrating” band¹⁷. Nicking of the cccDNA (occurring
11 355 during active transcription⁷ or accidentally during the extraction process) would result in the
12 356 loss of supercoiling and nicked cccDNA would migrate together with pf-rcDNA (see below and
13 357 **Supplementary Fig.8C**). Thus, quantification strategies aiming at detecting cccDNA
14 358 contained in the “fast-migrating” band should include T5 or ExoI/III nucleases, whereas PSD
15 359 treatment will guarantee inclusion of potentially damaged, nicked cccDNA.

19 360

21 361 **Comparison of cccDNA extraction and quantification protocols in HepG2-NTCP cells**

23 362 Following the same criteria and protocols used for liver tissues, we comparatively assessed
24 363 the impact of distinct DNA extraction methods on HBV DNA levels in HBV-infected HepG2-
25 364 NTCP cells. Total HBV DNA qPCR measurements indicated that Hirt and -PK extractions
26 365 substantially removed protein-bound HBV DNA forms by 1.7 and 1.5 logs, respectively
27 366 (**Fig.4A**). Accordingly, cccDNA counts were reduced by median 0.9 and 0.8 logs compared to
28 367 +PK extractions indicating improved selectivity for cccDNA (**Fig.4A and B**). We next applied
29 368 different nuclease digestion conditions to all three DNA extraction method (**Fig.4C-F**). In +PK
30 369 extracts, the removal of RI reduced cccDNA counts by PCR. In both Hirt and -PK DNA,
31 370 however, no further substantial cccDNA decline was observed after nuclease digestion,
32 371 suggesting that HBV RI had been sufficiently removed through the extraction process allowing
33 372 for precise cccDNA quantification. The minor reduction of cccDNA levels after all nuclease
34 373 treatments was mirrored in ND2 measurements indicating a general small loss of circular DNA
35 374 molecules (**Fig.4E**). The SB in **Figure 4F** reproduced the characteristic HBV DNA pattern
36 375 similar to liver tissues albeit with less RI-derived smear. Nevertheless, in Hirt and -PK DNA
37 376 extracts, cccDNA levels determined by PCR were 1.5-fold lower after T5 and ExoI/III compared
38 377 to PSD-based methods. Again, the “slow-migrating” band visualized by SB was degraded only
39 378 after exonuclease-based treatments.

44 379 Another factor that can influence cccDNA measurements is the presence of the inoculum,
45 380 which contains high amounts of HBV particles that can persist in culture. To assess the impact
46 381 of input virus on cccDNA quantification, we infected HepG2-NTCP cells with a high-titer
47 382 HepAD38-derived inoculum (MOI 4000) and followed them up for 9 days in the absence or
48 383 presence of the entry inhibitor Bulevirtide (BLV)²⁴. The inoculum contained high levels of pf-
49 384 rcDNA, which persisted until day 9 in BLV-treated cells where the establishment of a productive
50 385 infection was precluded (**Supplementary Fig.7A**). This contaminant could be removed
51 386 through “T5” treatment, resulting in approx. 2-fold lower cccDNA levels detected by qPCR
52 387 (**Supplementary Fig.7B**). Of note, using this highly sensitive bDNA technology, several T5-
53 388 resistant HBV DNA species were detected by SB. Interestingly, these forms are not visible
54 389 under alkaline Hirt extraction conditions (**Supplementary Fig.5B**).

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60 391 **Impact of DNA quality and storage conditions on cccDNA quantification**

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3 392 Nuclease treatment bears some risks and should be employed with caution. First, we observed
4 393 high variations in terms of digestion efficiency between labs and even between replicates within
5 394 one lab (data not shown). Second, excessive digestion conditions can lead to over-digestion
6 395 of cccDNA. Third, the quality of the extracted DNA is of utmost importance since nicking of the
7 396 cccDNA will make it a template for T5 ExoIII, but not for PSD, while all enzymes (except ExoI)
8 397 will act on damaged cccDNA containing double strand breaks. Examples and explanations for
9 398 risks associated with nuclease treatments can be found in the supplementary results and
10 399 **Supplementary Fig.8**.

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13 400 Another factor that can influence the quality of extracted DNA derives from the storage
14 401 conditions. In this study we used freshly frozen, cryopreserved samples; however,
15 402 cryopreservation of liver biopsies is rarely feasible in clinical studies. Instead, tissue
16 403 preservatives are used. To mimic these conditions, cryopreserved small liver pieces from two
17 404 HBV-infected untreated humanized mice and two siRNA-treated mice¹⁹ were moved to
18 405 Allprotect, a common tissue preservative from Qiagen, and stored at -20°C for several months
19 406 before being extracted with -PK protocols and digested with “PSD high” or “T5” (**Fig.5A**).
20 407 Compared to the matched fresh frozen samples analyzed in parallel, the Allprotect-stored
21 408 samples showed an overall higher reduction of cccDNA levels after nuclease digestion by
22 409 qPCR, with PSD reaching approximately 1log and T5 2log reductions. For comparison, the
23 410 cccDNA quantified in freshly frozen liver tissue from siRNA-treated mice were not reduced by
24 411 PSD treatment indicating sufficiently low HBV DNA levels for specific cccDNA quantification in
25 412 this setting. Accordingly, the reduction of mtDNA was even more pronounced than the drop in
26 413 cccDNA following Allprotect storage, while mtDNA levels decreased only modestly in DNA
27 414 from freshly frozen tissue (**Fig.5B**). This data hints at a general DNA damage involving both
28 415 nicking and double strand breaks and warrants extreme caution when using nuclease digestion
29 416 in Allprotect-stored samples.

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36 418 **Discussion and recommendations for cccDNA quantification**

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38 419 To improve our knowledge on cccDNA biology, validate serological biomarkers and assess the
39 420 impact of new therapies on cccDNA levels and activity, reliable and standardized quantitative
40 421 cccDNA assays are paramount. To achieve this goal in a more reliable manner than previously
41 422 possible, it is critical to compare protocols and perform cross-validation experiments across
42 423 laboratories. The results of this concerted effort provide novel information to guide researchers
43 424 and clinical trial investigators in designing and performing protocols to accurately quantify
44 425 cccDNA.

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47 426 The comparative analysis of parallel qPCR and SB results was a strength of our study design
48 427 and allowed us to understand how each method influences the outcome and to identify the
49 428 most critical points. In **figure 6**, we summarized the methodologies that were validated within
50 429 our consortium and the observations relevant to cccDNA quantification. Because all protocols
51 430 must be adapted to the sample type, infection level and treatment, there is not one protocol
52 431 that suits all needs. Instead, we provide guidance and general recommendations, which are
53 432 summarized in **table 1**.

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57 433 Through the comparison of three DNA extraction methods, we could show that not only the
58 434 Hirt procedure, but also the omission of the proteinase K digestion step from a commercial kit
59 435 for fast nucleic acid purification led to efficient reduction of HBV DNA RI, thus improving the
60 436 selectivity of cccDNA PCR measurements. However, -PK or Hirt-based extractions^{13,22,23} might

not be sufficient for specific quantification in highly replicative settings and nuclease treatment will still be needed. Therefore, we recommend performing both a DNA extraction that reduces RI and virions, a nuclease treatment to further reduce non-cccDNA species and a PCR design spanning the cohesive ends region of the rcDNA. The use of such a cccDNA-selective PCR is further supported by the fact that none of the extraction methods tested (-PK, Hirt, alkaline Hirt) was able to guarantee a complete depletion of genomic DNA, which could represent a source of integrated HBV sequences. All nucleases used here reduced RI amounts to various degrees, even when -PK or Hirt DNA extraction procedures had already lowered HBV RI levels. Nevertheless, all nucleases showed specific strengths and weaknesses. PSD did not perform well in +PK-extracted liver DNA, possibly due to impurities present in these extracts, whereas T5 and Exo I/III exonucleases performed similarly well although high concentrations and incubation times bear the risk of cccDNA over-digestion. Additionally, the efficiency of the tested nucleases varied both among labs and even within a given lab. The reasons for these variations are unclear, but could depend on small handling differences, input DNA variations and presence of sample impurities. Moreover, we showed that tissue preservatives are particularly prone to damaging the cccDNA. Consequently, nucleases induced strong reduction of cccDNA PCR levels in Allprotect-stored samples. Since patient liver biopsies are often stored in Allprotect or similar tissue preservatives, omission of nuclease digestions should be considered. Ideally, liver biopsy samples should be fresh-frozen and cryopreserved. Thus, digestion conditions have to be carefully titrated to avoid unspecific side activities potentially leading to cccDNA digestion or to insufficient digestion of other HBV DNA forms. Since it is laborious to determine whether a nuclease treatment is needed for every sample and condition, we recommend including it for fresh and fresh frozen samples.

Additionally, we observed that PSD did not digest the “slow-migrating” band, although this treatment removed most RI from -PK and Hirt samples. Furthermore, we demonstrated that without nuclease treatment, the pf-rcDNA is still present even in the setting of low replication levels and that this “slow-migrating” band is detected by the cccDNA-selective PCR. We therefore recommend using exonuclease-based treatment when detection of this band is not wanted. The precise composition of this “slow-migrating” band detected by SB is not entirely known but it appears to contain a mixture of molecules, which underwent removal of the covalently attached HBV polymerase but that still are unrepaired or at different phases of the repair process, such as DP-rcDNA or CM-rcDNA^{3,4}. Fully repaired HBV DNA molecules that are not yet covalently closed and supercoiled (immature cccDNA) will also appear within this band^{3,4}. In cell culture experiments, a prominent part of the “slow-migrating” band might consist of input virus. Since it is unclear which factors and circumstances (infection status or treatments) may affect the conversion of rcDNA to cccDNA, the intensity of the “slow-migrating” band may also vary between samples and experimental settings. Additionally, the choice of the extraction method will influence the detected population of HBV DNA molecules. In the side-by-side comparison of the original Hirt with a modified alkaline Hirt known to preferentially extract supercoiled DNA, the “slow-migrating” bands – potentially resulting from circular HBV DNA with different degrees of supercoiling – appeared lost (Supplementary Fig.5). Thus, further studies are needed to assess the biological meaning of such differences and cccDNA quantification strategies including the “slow-migrating” band are justified.

For in vitro infection studies, we recommend employing exonuclease-based treatments (T5 or Exo I/III) to remove the non-cccDNA species present in the inoculum. This contaminant was present as a prominent “slow-migrating” band on SB and persisted until day 9 post infection of HepG2-NTCP cells despite the use of an entry inhibitor (Bulevirtide), known to abrogate the establishment of productive HBV infection²⁴. Although the example shown here used an

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3 485 extremely high MOI (4000), T5 exonuclease efficiently reduced this contaminant in Hirt-
4 486 extracted samples allowing specific cccDNA measurements by qPCR. Thus, it is advisable to
5 487 include an entry inhibitor control in cell culture to rule out interferences due to input HBV DNA.

7 488 Because cccDNA that contains nicks or double strand breaks will become a template for
8 489 nucleases and migrate together with pf-rcDNA on SB, it is of utmost importance to assess the
9 490 quality of the DNA in every extract. We recommend using mitochondrial DNA – an episomal
11 491 dsDNA – as a surrogate for cccDNA and to quantify a mitochondrial gene by PCR in every
12 492 sample before and after nuclease digestion. Based on our experience, a reduction of less than
13 493 1log indicates sufficiently intact DNA, while more than 1log reduction indicates damaged DNA.
14 494 Over-digestion of mtDNA after exonuclease-based but not PSD-based digestions, indicates
15 495 that the DNA contains single-strand nicks. Consequently, cccDNA will also be nicked and
16 496 reduced after exonuclease treatment. PCR assessment of mtDNA levels will indicate the
17 497 quality of the DNA in the sample and after the extraction.

20 498 We acknowledge that the present methods to quantify cccDNA are not optimal yet and
21 499 encourage the optimization or development of new methods for both DNA extraction and
22 500 cccDNA quantification²⁵. Ideally, improved PCR-based methods should have higher specificity
23 501 for cccDNA in the presence of contaminating HBV DNA species and should be robust,
24 502 sensitive and suitable for all virus isolates. A milestone will be reached when novel procedures
25 503 allow to avoid the use of nucleases. The implementation of digital PCR (dPCR) instead of
26 504 qPCR has allowed a significant increase in sensitivity and brought the major advantage of
27 505 absolute quantification without PCR standards, thus limiting the variability thereof^{12,26}.
28 506 However, the limited specificity for cccDNA in a complex mixture of sequence-identical HBV
29 507 DNA species remains even when using dPCR. Novel methodologies to visualize cccDNA in
30 508 infected cells are being developed and can complement quantitative analyses and serve to
31 509 corroborate PCR and SB results²⁷. Additionally, more research is needed to ascertain the
32 510 nature of all HBV DNA forms, their role in the life-cycle of HBV and how they are influenced by
33 511 various manipulations.

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4	1. Reduce HBV RI and rcDNA through means of the DNA extraction
5	<ul style="list-style-type: none"> • Extract DNA using Hirt or -PK method to lower RI and rcDNA contained in HBV capsids. This procedure will facilitate specific cccDNA quantification together with nuclease treatments and cccDNA-selective PCR measurements.
6	<ul style="list-style-type: none"> • PSD digestion has been shown to work more reliably after -PK or Hirt DNA extractions than after +PK extraction. Exonuclease-based methods are less frail, but low RI and rcDNA content is preferred in any case.
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11	2. Further reduce HBV RI and virions through nuclease digestion
12	<ul style="list-style-type: none"> • Perform nuclease digestion to further reduce non-cccDNA species.
13	<ul style="list-style-type: none"> • To exclusively measure the cccDNA, exonuclease-based treatments should be used. To quantify both cccDNA and species contained in the “slow-migrating” band, the use of PSD is recommended.
14	<ul style="list-style-type: none"> • The “slow-migrating” band contains nicked cccDNA, caused mostly by technical damage. Exonuclease digestion may thus result in a loss of these cccDNA forms and lower cccDNA levels detected by PCR.
15	<ul style="list-style-type: none"> • The digestion conditions should be carefully titrated for every new sample type and extraction protocol (by PCR analysis of total HBV DNA and cccDNA in the undigested and digested sample and a direct comparison by SB) and monitored routinely (PCR analysis of total HBV DNA and cccDNA in undigested and digested samples).
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25	3. Assess the quality of the extracted DNA
26	<ul style="list-style-type: none"> • Use mitochondrial DNA as a surrogate for cccDNA (circular dsDNA). A mitochondrial gene should be quantified in every sample before and after nuclease digestion.
27	<ul style="list-style-type: none"> • A reduction of <1Log10 after nuclease digestion indicates intact DNA; a reduction of >1Log10 indicates damaged DNA (DNA extract should be discarded).
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32	4. Determine the optimal normalization strategy
33	<ul style="list-style-type: none"> • Check for differential enrichment of genomic and mitochondrial DNA during the DNA extraction process to choose the optimal normalization strategy.
34	<ul style="list-style-type: none"> • The total amount of recovered DNA can also be used for normalization. In human chimeric mice, cccDNA numbers need to be normalized to the amounts of human hepatocytes present in every liver specimen.
35	<ul style="list-style-type: none"> • Control whether the treatments you want to test affect cell viability or mitochondria levels. Mitochondria count may vary between patients and samples.
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40	5. Report all methodological details for cccDNA quantification in publications
41	<ul style="list-style-type: none"> • To allow independent assessment of the data, all methodological details should be reported including the DNA extraction method, nuclease digestion, qPCR conditions and normalization strategy.
42	<ul style="list-style-type: none"> • Employ only one optimized method in a particular study for cccDNA extraction, nuclease digestion, and qPCR quantification.
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47	6. Considerations for the establishment of new assays
48	<ul style="list-style-type: none"> • For novel PCR assays, determine the degree of specificity towards cccDNA by measuring total HBV DNA and cccDNA in the untreated sample and calculate the ratio of total HBV DNA to cccDNA copy numbers. A ratio <100:1 is recommended. Copy numbers and not CT values should be used for comparison to avoid biases due to different sensitivities of PCR assays. Note that specificity ratios might also vary between types of samples and thus, falling below this ratio does not guarantee specific measurements in any case.
49	<ul style="list-style-type: none"> • <u>Novel DNA extraction methods should assess the enrichment of cccDNA in comparison to RI and rcDNA. The optimal ratio of input sample and buffer volume has to be determined empirically. The extraction efficiency can be controlled by spiking the sample with known copy numbers of an unrelated supercoiled plasmid DNA.</u>
50	<ul style="list-style-type: none"> • Assess the specificity to detect cccDNA in every new method including DNA extraction, nuclease digestions, PCR assays or other novel methodologies.
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- Confirm the results by performing Southern blotting.

513 **Table 1:** Recommendations for cccDNA quantification

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Confidential: For Review Only

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3 590 **Figure legends**

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5 591 **Figure 1: The effect of different DNA extraction methods on cccDNA quantification by**
6 592 **qPCR and SB in HBV-infected USG mouse liver tissue.** (A) Schematic presentation of the
7 593 experimental design used for the cross-validation. (B) SB analysis on nondigested DNA
8 594 extracts using HBV DNA probes in three of the labs. (C) qPCR measurements of total HBV
9 595 DNA and cccDNA in the DNA extracts. Bars depict the median and range across all four labs.
10 596 (D) qPCR measurements of cccDNA shown separately for every lab, relative to the amount in
11 597 the +PK DNA extractions. Bars depict the mean of duplicate measurements. Hirt, Hirt DNA
12 598 extraction, which does not include a proteinase K digestion; +PK, total DNA extraction with
13 599 proteinase K digestion; -PK, total DNA extraction without proteinase K digestion; SB, Southern
14 600 blot.

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17 601 **Figure 2: The effect of nuclease digestions on different DNA extracts in HBV-infected**
18 602 **USG mouse liver tissue.** The bar graphs depict qPCR measurements of total HBV DNA (A)
19 603 and cccDNA (B) in all DNA extracts and labs without nuclease digestion (hatched bars) or after
20 604 the indicated nuclease treatments. The bars depict the median and range of the values from
21 605 three labs. Every lab performed the nuclease digestion in duplicates. The values (copies/PCR)
22 606 after nuclease treatment were first normalized to the nondigested value in the respective DNA
23 607 extract, then all values derived from Hirt or -PK DNA extracts were normalized to the +PK
24 608 extract. (C) qPCR of mtDNA DNA via the mitochondrial gene ND2, depicted as arbitrary units
25 609 normalized to the nondigested values in the respective DNA extract. (D) SB analysis in one of
26 610 the labs using a second stably HBV-infected and untreated USG mouse and all three DNA
27 611 extracts and four nuclease digestion conditions using HBV DNA probes (top panel) and
28 612 densitometric analysis of the cccDNA band (lower panel). The "X" denotes a sample that could
29 613 not be quantified because of high background staining. The samples were run on two separate
30 614 blots but identical amounts of nondigested DNA, with the help of which densitometry was
31 615 normalized between blots. ND2, mitochondrially encoded NADH:ubiquinone oxidoreductase
32 616 core subunit 2.

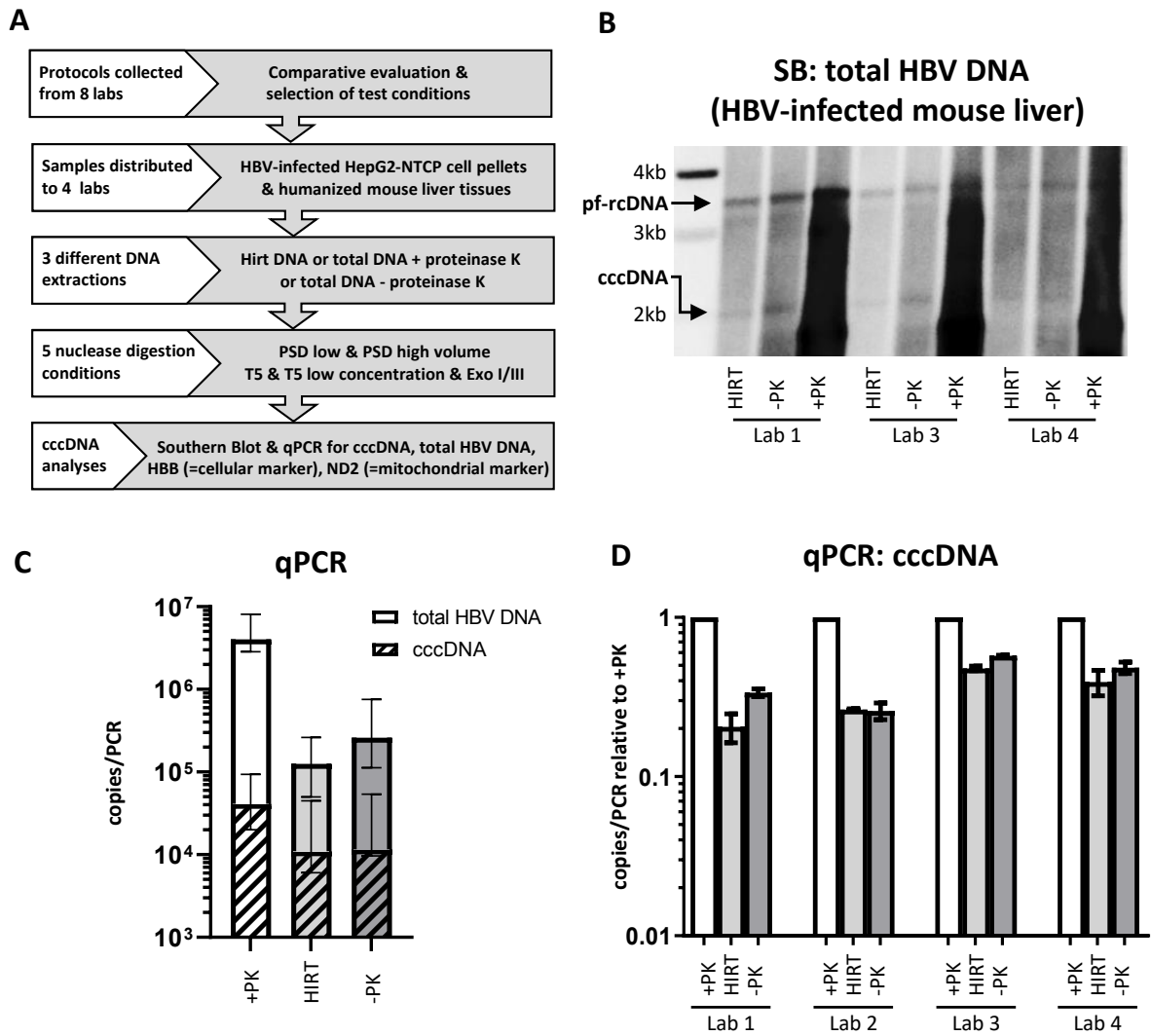
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36 617 **Figure 3: The pf-rcDNA is detected with the same efficiency as cccDNA by cccDNA-**
37 618 **selective qPCR but is removed through T5 exonuclease treatment.** Parallel SB (A) and
38 619 qPCR (B) analysis in three stably HBV-infected USG mice (after six or 12 weeks of Lamivudine
39 620 treatment, or untreated). Liver DNA was extracted with the -PK, digested with nucleases or left
40 621 undigested before analysis. (A) SB using HBV DNA probes (top panel) and densitometric
41 622 analysis of the pf-rcDNA (middle panel) and cccDNA band (lower panel). DNA amounts were
42 623 normalized to ND2 via qPCR with human-specific primers before digestion to ensure loading
43 624 of equal amounts of DNA derived from human cells. (B) qPCR measurements of total HBV
44 625 DNA (grey bars) and cccDNA (checked bars) normalized to human hepatocytes via human
45 626 HBB counts in the nondigested DNA extract. The cccDNA copy numbers/cell are depicted
46 627 above each bar. (C) Preparative agarose gel using the same samples as in (A) and identical
47 628 settings for the gel electrophoresis. The upper and lower bands were excised separately, DNA
48 629 was extracted and used for qPCR analysis (total HBV DNA and cccDNA). The ratio of total
49 630 HBV DNA copies to cccDNA copies was calculated for all samples derived from the upper SB
50 631 band (top) and the lower band (bottom), respectively. Lam, Lamivudine; NT, non-treated.

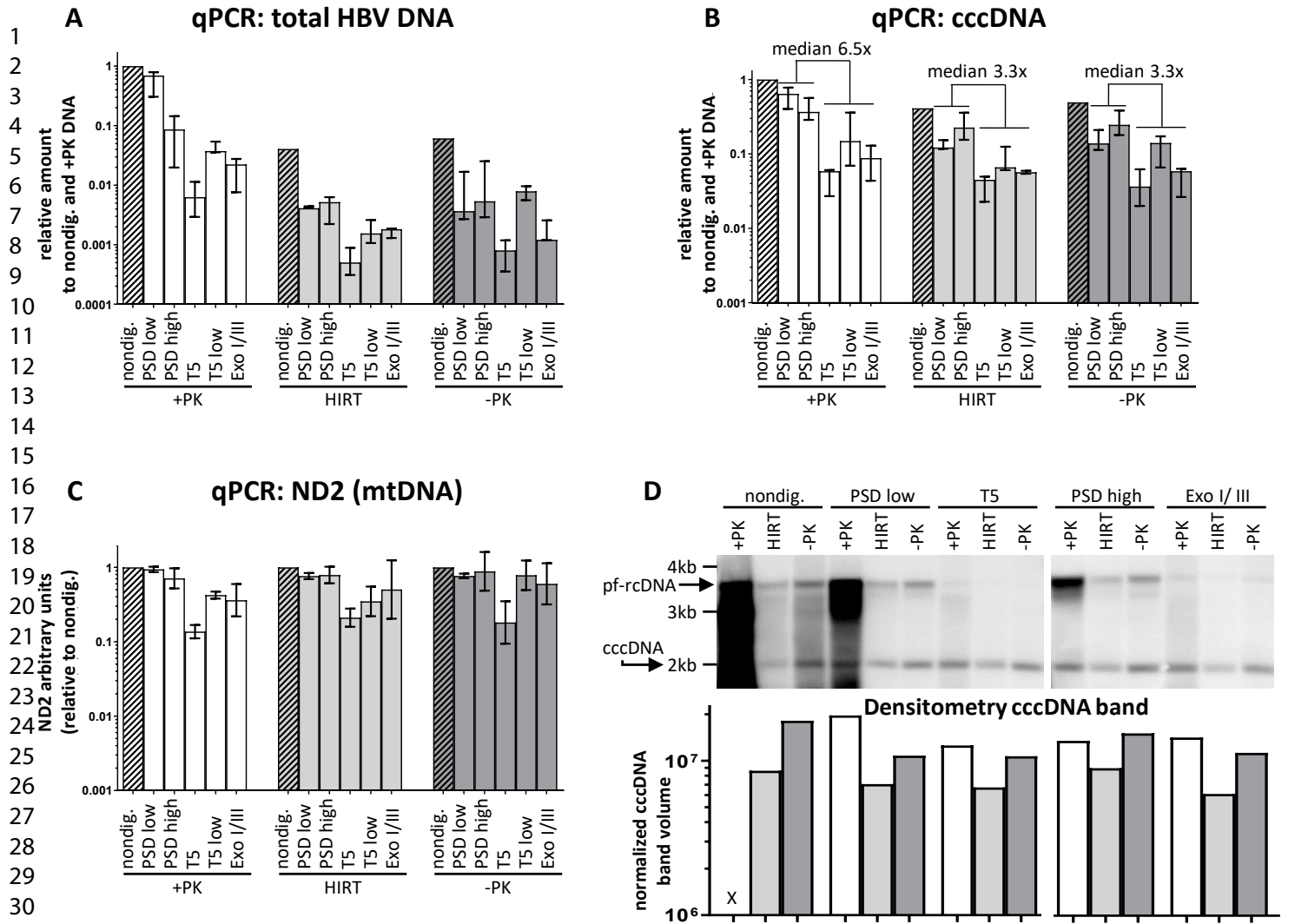
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53
54 632 **Figure 4: The effect of different DNA extraction methods and nuclease digestions on**
55 633 **cccDNA quantification by qPCR and SB in HBV-infected HepG2-NTCP cells.** (A-F) Frozen
56 634 cell pellets harvested at day nine post infection were shipped to the participating labs. (A)
57 635 qPCR measurements of total HBV DNA and cccDNA in the undigested DNA extracts. Bars
58 636 depict the median and range across all four labs. (B) PCR measurements of cccDNA shown
59 637 separately for every lab and relative to the amount in the +PK DNA extractions. Bars depict
60 638 the mean of duplicate measurements. (C, D) qPCR measurements of total HBV DNA (C) and
639 639 cccDNA (D) in all DNA extracts and labs either without nuclease digestion (hatched bars) or

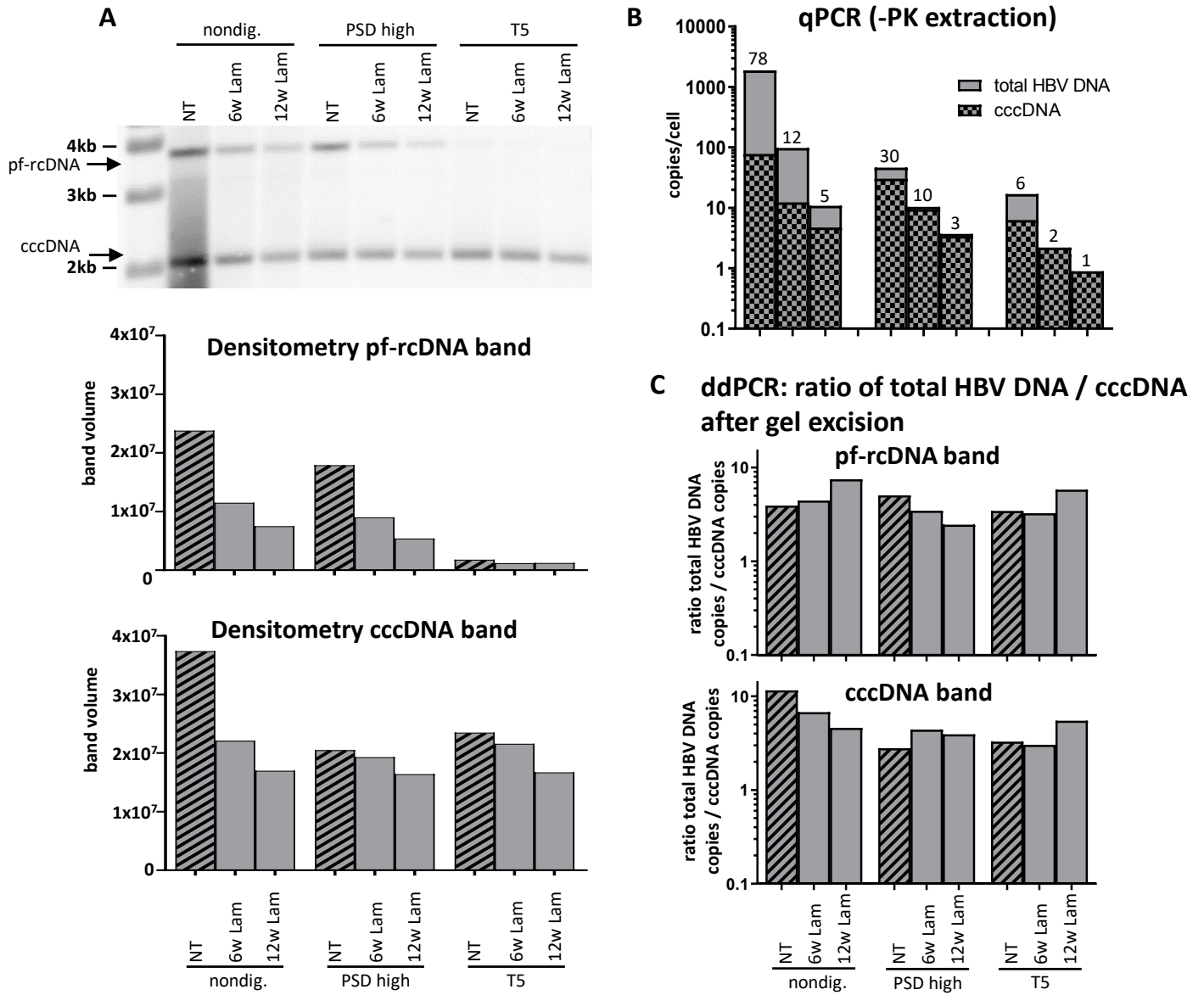
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3 640 after the indicated nuclease treatments (performed in duplicates). The bars depict the median
4 641 and range of the values from three labs. The values (copies/PCR) after nuclease treatment
5 642 were first normalized to the nondigested value in the respective DNA extract, then all values
6 643 derived from Hirt or -PK DNA extracts were normalized to the +PK extract. (E) qPCR of mtDNA
7 644 DNA via the mitochondrial gene ND2, depicted as arbitrary units normalized to the nondigested
8 645 values in the respective DNA extract. (F) SB using HBV DNA probes (top panel) and
9 646 densitometric analysis of the cccDNA band (lower panel). The "X" denotes a sample that could
10 647 not be quantified because of high background staining. The samples were run on two separate
11 648 blots with identical amounts of nondigested DNA, with the help of which densitometry was
12 649 normalized between blots.

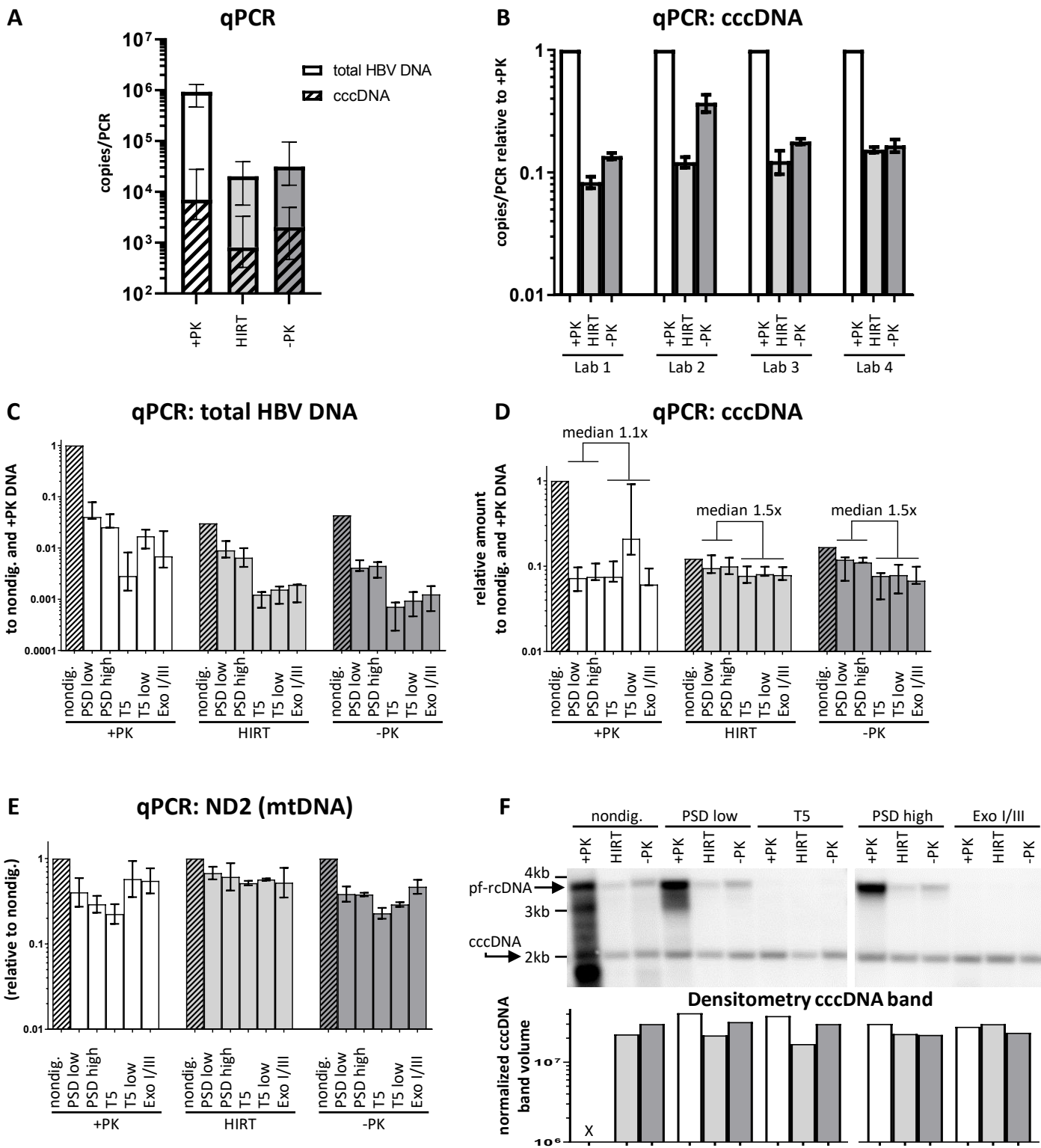
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15 650 **Figure 5: Nuclease treatment bears the risk of over-digesting cccDNA in Allprotect-**
16 651 **stored samples.** Comparison of nuclease digestion in fresh frozen liver tissue or liver tissue
17 652 preserved in Allprotect. Liver DNA was extracted using the -PK method from 2 untreated HBV-
18 653 infected mice and 2 mice treated with siRNA targeting all HBV transcripts for 6 weeks. DNA
19 654 was digested with PSD or T5 exonuclease and subjected to qPCR for cccDNA (A) and ND2
20 655 (B). Every dot depicts a single mouse, bars the median. siRNA, small interfering RNA.

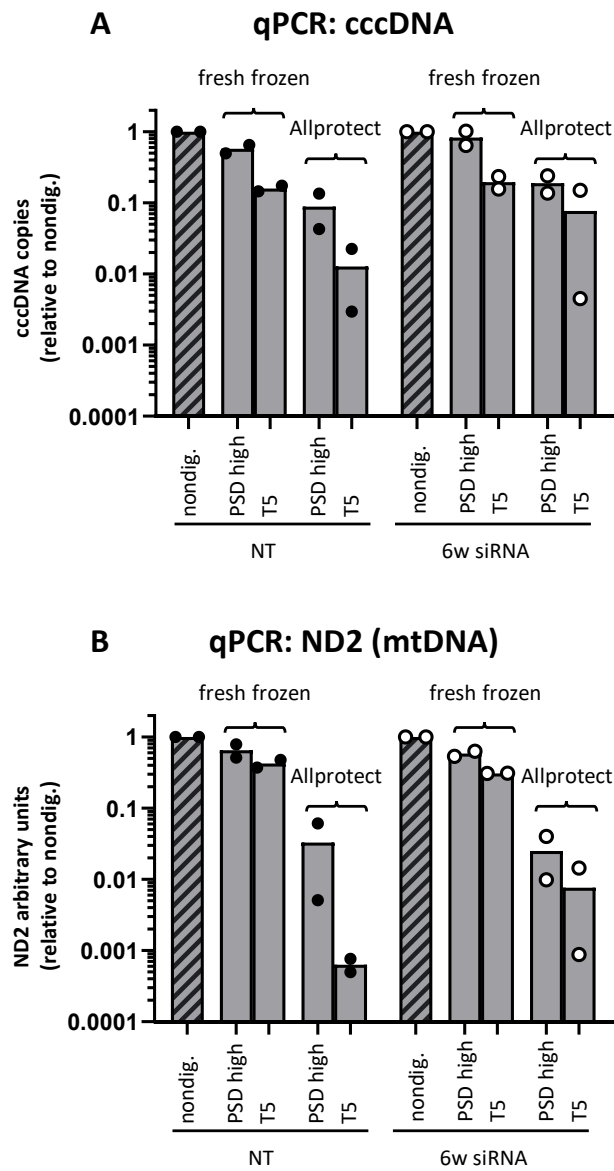
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23 656 **Figure 6: Schematic presentation of the main findings of the study.** The flow chart
24 657 summarizes the experimental flow for cccDNA quantification and highlights optimal and
25 658 suboptimal results for both qPCR and SB, including the major caveats.

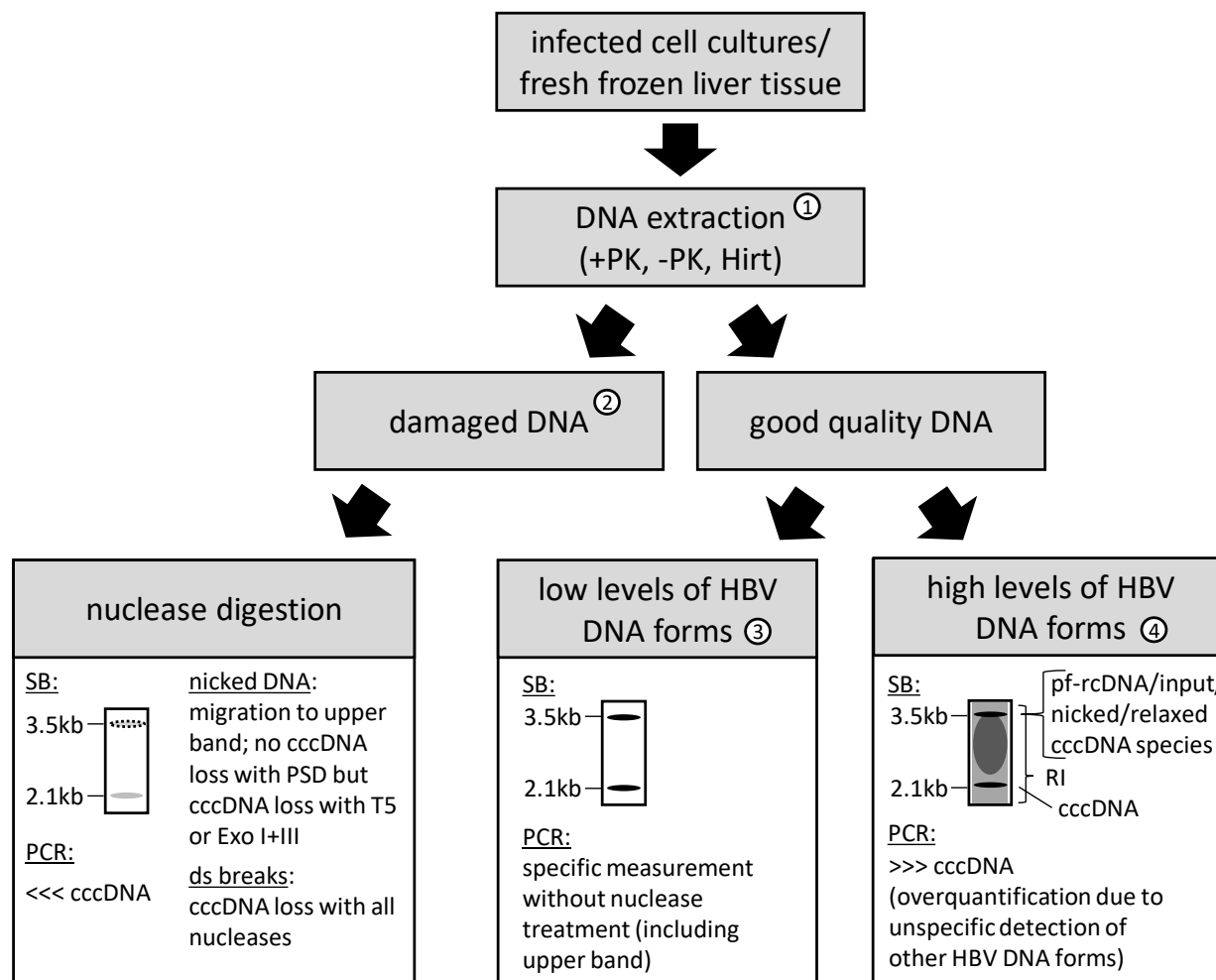






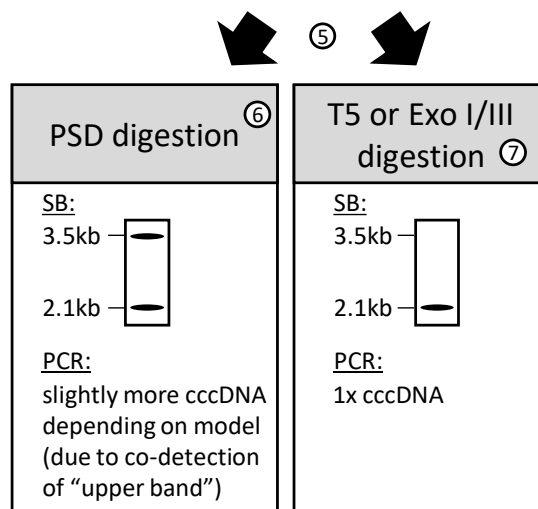






Caveats

- 1) differences in extraction efficiency with different protocols or lysis buffers will affect recovery and normalization
- 2) liver stored in the tissue preservative Allprotect is particularly prone to damage
- 3) i.e. in -PK or Hirt extractions or samples with low infection/replication levels
- 4) i.e. in +PK extractions or samples with high infection/replication levels (without antiviral treatment)
- 5) high variations with all nucleases
- 6) PSD doesn't work well in dirty DNA (in particular +PK): purify or dilute
- 7) too much enzyme/incubation destroys cccDNA



Quantification of the Hepatitis B Virus cccDNA: Evidence-based guidelines for monitoring the key obstacle of HBV cure

Short Title: cccDNA quantification harmonization

Lena Allweiss^{1,2}, Barbara Testoni^{3,4}, Mei Yu⁵, Julie Lucifora^{3,4}, Chunkyu Ko^{6*}, Bingqian Qu^{7**}, Marc Lütgehetmann^{8,2}, Haitao Guo^{9,10}, Stephan Urban^{7,2}, Simon P. Fletcher⁵, Ulrike Protzer^{6,2}, Massimo Levrero^{3,4}, Fabien Zoulim^{3,4}, Maura Dandri^{1,2}

1. I. Medical Clinic and Polyclinic, University Medical Center Hamburg-Eppendorf, Hamburg, Germany

2. German Center for Infection Research (DZIF), Germany

3. Cancer Research Center of Lyon, INSERM U1052, Lyon, France

4. ANRS AC34

5. Gilead Sciences, Foster City, California, United States of America

6. Institute of Virology, Technical University of Munich, Munich, Germany

* Current affiliation: Infectious Diseases Therapeutic Research Center, Therapeutics & Biotechnology Division, Korea Research Institute of Chemical Technology (KRICT), 34114 Daejeon, Republic of Korea

7. Department of Infectious Diseases, Molecular Virology, University Hospital Heidelberg, Germany

** Current affiliation: Division of Veterinary Medicine, Paul Ehrlich Institute, Germany

8. Institute of Medical Microbiology, Virology and Hygiene, University Medical Center Hamburg-Eppendorf Hamburg, Germany

9. Indiana University School of Medicine, Indianapolis, Indiana, United States of America

10. Current affiliation: Department of Microbiology and Molecular Genetics, Cancer Virology Program, UPMC Hillman Cancer Center, University of Pittsburgh School of Medicine, Pittsburgh, United State of America

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Supplementary material and methods

Generation, infection, treatment and viral characterization of human liver chimeric. All animal experiments were performed in accordance with the European Union directive 2010/63/EU and approved by the ethical committee of the city and state of Hamburg in accordance with the ARRIVE guidelines. The generation of USG (uPA/SCID/beige/IL2RG^{-/-}) mice reconstituted with human hepatocytes was conducted as previously reported¹. HBV infection was established upon a single intraperitoneal injection of HBV-containing USG mouse serum (1×10^7 HBV DNA copies/mouse, genotype D, HBeAg-positive). Blood samples were taken retro-orbitally during the experiments. Viral DNA was extracted from serum samples using the QiAamp MinElute Virus Spin Kit (Qiagen, Hilden, Germany) and quantified with HBV-specific primers and probes (TaqMan® Gene Expression assay ID: Pa03453406_s1). HBV core antigen on cryostat liver sections was visualized by immunofluorescence staining as described earlier¹. Some mice received Lamivudine (Lam) (Epivir, ViiV Healthcare, Zeist, Netherlands) for six or 12 weeks supplemented in the drinking water (20mg/100ml).

HBV infection and preparation of HepG2-NTCP cell culture samples. HepG2-NTCP cells were cultured and infected as described elsewhere². Briefly, cells were infected with HepAD38-derived virus (genotype D) at an MOI of 100 genome equivalents (GE) / cell and harvested at day 9 post infection. The cells were pooled before being divided and shipped to the four participating labs. Every lab received a frozen cell pellet of approximately 1×10^7 cells, which upon arrival was dissolved in 900 μ l 10 mM Tris-HCl / 10 mM EDTA buffer and distributed equally for the three DNA extractions. HepG2-NTCP cells for the SB in **Figure 4F** were infected with an MOI of 250 GE / cell and harvested at day 9 post infection as described elsewhere³. For **Supplementary Figure 7**, HepG2-NTCP cells were generated by transfection of expression vector pEF1/v5-His-B (Thermo Fisher Scientific) encoding the human NTCP human into HepG2 cells (ATCC). Transfected HepG2 cells were selected with G418 at 1 mg/ml for 3 weeks and the G418-resistant colonies expanded and tested for NTCP functional activity by monitoring uptake of tritium labeled taurocholate ($^3\text{H}(\text{G})$]-taurocholic acid 250 μ Ci, 9.25MBq, Perkin Elmer). Cells were infected with an MOI of 4000 GE / cell.

Alkaline Hirt DNA extraction. HBV cccDNA was extracted from HBV-infected humanized mouse liver tissue and HepG2-NTCP cells with a modified Hirt DNA extraction method as described previously^{4,5}. Cell lysis in an alkaline milieu irreversibly denatures genomic DNA and all non-cccDNA HBV DNA species. After rapid neutralization, only supercoiled cccDNA renatures and remains in the supernatant after centrifugation. Briefly, 6×10^6 cells or 10mg liver tissue were diluted and homogenized in 400 μ l 10mM Tris-HCl (pH 7.5)/10mM EDTA (pH 8.0)/0.2% NP40. Cell lysis was achieved by the addition of 400 μ l 6%SDS/0.1M NaOH and 30min incubation at 37°C with agitation. The alkaline lysate was neutralized by the addition of 200 μ l of 3M potassium acetate (pH 4.8) and centrifuged for 15 min at 4°C and 14,500g. The supernatant was extracted with phenol (pH>7.2) followed by an additional extraction with phenol/chloroform/isoamyl alcohol (25:24:1). The DNA was precipitated with isopropanol, pelleted by centrifugation, washed twice in 70% ethanol and dissolved in 10mM Tris-HCl/1mM EDTA buffer.

Nuclease digestions. The plasmid-safe ATP-dependent DNase (PSD)⁶ selectively hydrolyses linear dsDNA and with a lower efficiency single-stranded DNAs (ssDNA). Notably, it does not affect nicked circular dsDNAs (with a single discontinuous strand). PSD also digests virion-derived rcDNA⁶ and intracellular capsid-associated rcDNA⁷ but not rcDNA after Hirt DNA extraction⁷⁻⁹. The T5 exonuclease is a dsDNA-specific exonuclease with ssDNA-specific endonuclease activity⁹ and in contrast to PSD also acts on nicked dsDNA. This bears the risk

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3 of degrading transcriptionally active cccDNA forms that must be temporarily nicked¹⁰.
4 Exonuclease I catalyzes the removal of nucleotides from linear ssDNA, while exonuclease III
5 removes nucleotides from linear or nicked dsDNA. Together, both enzymes remove HBV RI,
6 but leave closed single and double strands undigested^{11,12}.
7

8
9 Unless otherwise indicated, the same amount of initial starting material was used for all
10 downstream nuclease digestion and PCR analyses to enable a direct comparison of all settings
11 within and among the participating labs. The nuclease digestion assays were run in
12 independent duplicates. The DNA content was determined with the Qubit™ dsDNA BR Assay
13 Kit (Thermo Fisher Scientific) and approximately 100ng or 500ng DNA from HepG2-NTCP or
14 mice, respectively, was used for all the following conditions: “PSD low”⁶: 10U PSD (Lucigen),
15 2µl 25 mM ATP, 2µl of the proprietary reaction buffer, and water for a total volume of 20 µl;
16 incubation at 37°C for 6h, heat inactivation at 70°C for 30 min. “PSD high”¹: 30U PSD
17 (Lucigen), 8µl 25 mM ATP, 20 µl of the proprietary reaction buffer, and water for a total volume
18 of 200 µl; incubation at 37°C for 2 h, heat inactivation at 70°C for 30 min. “T5”⁹: 10U T5
19 exonuclease (T5; NEB, Ipswich, MA, USA), 2 µl NEB reaction buffer 4, and water for a total
20 volume of 20 µl; incubation at 37°C for 45 min, heat inactivation at 70°C for 30 min. “T5 low”²:
21 5U T5, 2µl NEB reaction buffer 4, and water for a total volume of 20µl; incubation at 37°C for
22 30 min, heat inactivation at 70°C for 30 min. “Exo I/III”^{11,12}: 20U exonuclease I (Exo I; NEB),
23 25U exonuclease III (Exo III; NEB), 2µl cutsmart™ buffer (NEB), and water for a total volume
24 of 20µl; incubation at 37°C for 2h, heat inactivation at 80°C for 20 min. Digested and
25 nondigested samples were column-purified using the Genomic DNA Clean & Concentrator™-
26 25 (Zymo Research, Irvine, CA, USA) before downstream analyses. In preparatory studies,
27 the effect of heat denaturation on PSD digestion efficiency was tested in several sample types.
28 HBV-infected HepG2-NTCP cells, rcDNA extracted from infectious mouse serum and an HBV
29 DNA containing plasmid as a cccDNA surrogate mixed with DNA from an uninfected
30 humanized mouse liver were used. Before digestion with PSD low and high conditions, the
31 input DNA (500ng) was denatured by 5 min incubation at 85°C.
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37 **Quantitative PCR measurements.** Quantitative PCR measurements were performed using
38 Taqman™ chemistry and the Taqman™ Fast Advanced Master Mix (Thermo Fisher Scientific).
39 PCR was run in triplicates. cccDNA was quantified with cccDNA-selective primers and probe
40 as published previously¹³ using improved PCR conditions (final concentration of forward primer
41 100 nmol/l; reverse primer 800 nmol/l; cycling conditions: 10 min initial denaturation at 95°C
42 followed by 40 cycles of 95°C for 1 sec and 65°C for 1 min)¹⁴ (**Supplementary Fig. 2B**). Total
43 HBV DNA was quantified with primer and probe from the Taqman™ Gene Expression System
44 (assay ID: Pa03453406_s1; Thermo Fisher Scientific). This assay was tested against 16 HBV
45 isolates including genotypes A, B, C, D, E, and G as per manufacturer’s specifications. The
46 final concentration of both primers was 250 nmol/l; cycling conditions were: 20 sec initial
47 denaturation at 95°C followed by 40 cycles of 95°C for 1 sec and 65°C for 20 sec. Known
48 amounts of an HBV DNA plasmid were amplified to establish a standard curve for absolute
49 quantification of cccDNA and total HBV DNA. For the absolute quantification of cccDNA in gel-
50 extracted DNA (**Fig. 3C**), digital droplet PCR (ddPCR) was employed. Template DNA, the
51 same primers and probe as above were diluted in ddPCR Supermix for Probes (Biorad,
52 Feldkirchen, Germany) to the same final concentration as above. After droplet generation and
53 PCR (cycling conditions: 10 min initial denaturation at 95°C followed by 40 cycles of 94°C for
54 30 sec and 65°C for 1 min), droplets were analyzed on a QX100 droplet reader (Biorad). The
55 sensitivity of the cccDNA-selective ddPCR assay has been determined elsewhere¹⁵. Viral DNA
56 was normalized to the number of human cells by measuring the human single copy gene
57 hemoglobin beta (assay ID Hs00758889_s1) or to mitochondrial DNA by measuring the human
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3 mitochondrial gene ND2 (assay ID #Hs02596874_g1). Human genomic DNA (Roche Applied
4 Science, Mannheim, Germany) was used to establish a standard curve for quantification.
5

6 **Preparative agarose gel electrophoresis.** Total DNA extracted without proteinase K was
7 loaded on a 1.2% TAE agarose gel. After gel electrophoresis at 25 V for 21 h, all the upper
8 and lower HBV DNA bands were excised separately by comparison to a 1 Kb DNA ladder
9 (Thermo Fisher Scientific). DNA was extracted from the gel with the help of the QIAquick gel
10 extraction kit (Qiagen) following the manufacturer's instructions. The extracted DNA was
11 analyzed by ddPCR as described above. For comparison, a SB was prepared with equal
12 amounts of the same samples and run in parallel. Because liver samples from three different
13 chimeric mice were used for this assay, samples had to be normalized to the degree of human
14 repopulation in order to compare viral loads across mice. This was done by qPCR
15 measurements of human mitochondrial DNA (via ND2) in the undigested samples and loading
16 of normalized amounts on the gel.
17
18

19 **Southern blot analyses.** SB analysis was performed as previously described^{14,16}. Briefly, DNA
20 was separated on an agarose gel and blotted on a Nytran membrane using downward capillary
21 transfer. HBV DNA was detected with the help of branched DNA (bDNA) technology using the
22 QuantiGene Singleplex assay (Thermo Fisher Scientific) and a full genome HBV probe (assay
23 ID #VF1-12525). A detailed version of this protocol can be found on the ICE-HBV protocol
24 database ([https://ice-hbv.org/protocol/a-sensitive-and-rapid-southern-blot-assay-based-on-
25 branched-dna-technology-for-the-detection-of-hbv-dna-in-cell-culture-and-liver-tissue-
26 samples/](https://ice-hbv.org/protocol/a-sensitive-and-rapid-southern-blot-assay-based-on-branched-dna-technology-for-the-detection-of-hbv-dna-in-cell-culture-and-liver-tissue-samples/)).
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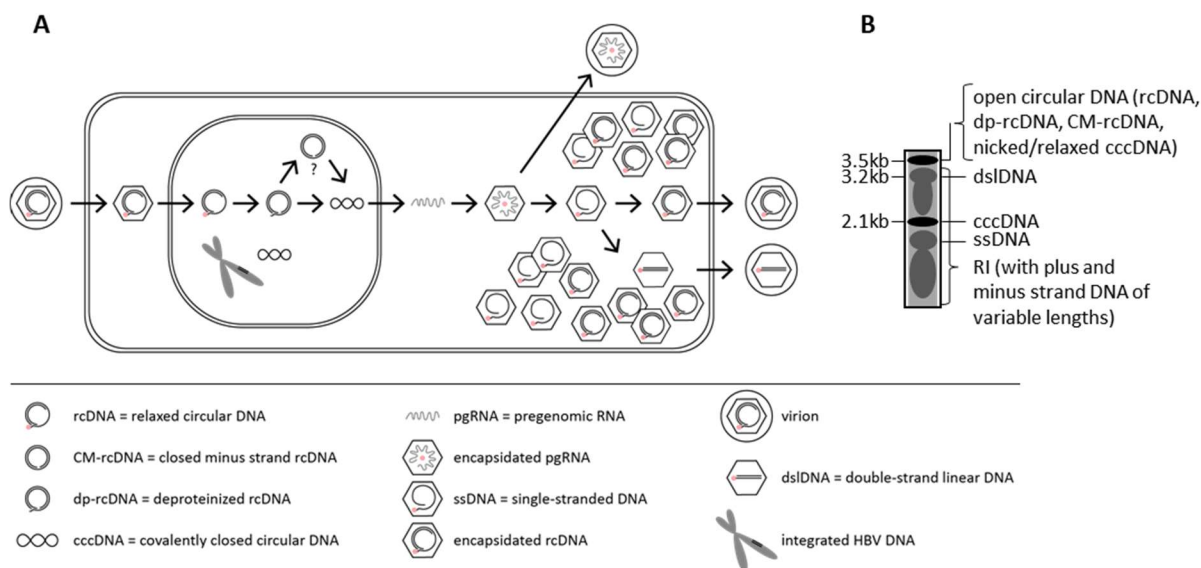
Supplementary results

Impact of DNA quality on cccDNA quantification

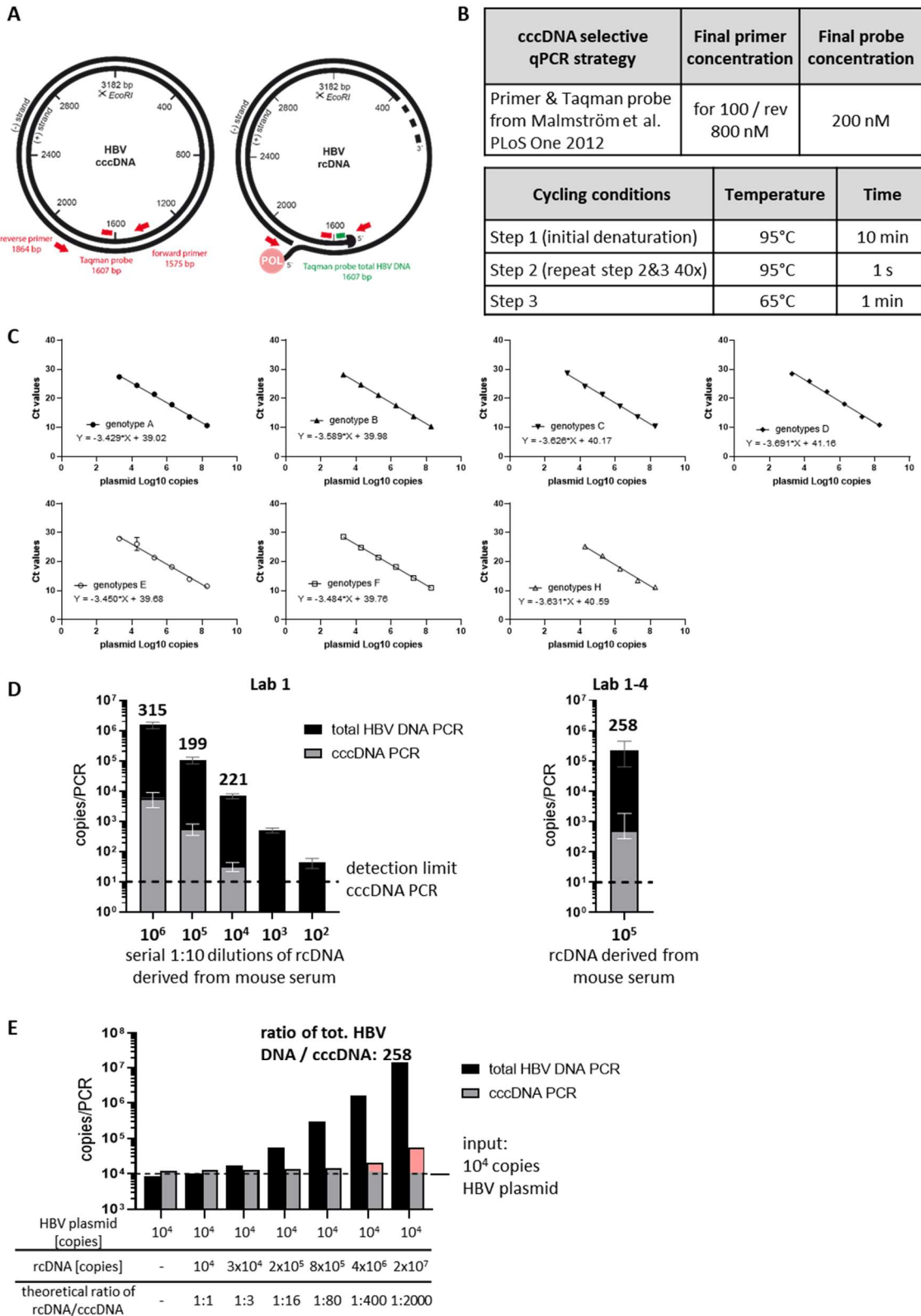
While Hirt and -PK DNA extractions were sufficient to remove replicative intermediates to a degree that makes it possible to specifically detect cccDNA (including pf-rcDNA) in low replicative samples (NA treatment), nuclease digestion was still needed in highly infected samples to remove the “upper band”. However, nuclease treatment bears some risks and should be employed with caution. First, throughout the cross-validation experiments, we observed high variations in terms of digestion efficiency between the labs and even between replicates within one lab (data not shown). Second, excessive digestion conditions could lead to over-digestion of cccDNA. We therefore compared the standard “PSD high” and “T5” conditions used throughout this study with conditions where enzymatic units were increased by 4-fold and the incubation time was extended to 6 hours (T5-augmented). The SB and densitometric analysis of the cccDNA band in -PK extracted DNA from infected mouse liver tissue shows unaltered cccDNA levels with either PSD conditions, but 2-fold lower cccDNA levels after T5-augmented conditions (**Supplementary Fig.8A**). Although the chosen conditions were extreme, these results indicate that extended digestion conditions may become detrimental when using the T5 exonuclease. In an attempt to make the pf-rcDNA accessible to digestion by PSD, we included a heat denaturation step prior to “PSD low” and “PSD high” digestion reactions⁸. Heat denaturation increased the digestion efficiency of rcDNA derived from mouse serum (**Supplementary Fig.8B**) because the enzyme could then act on the denatured single strands. However, this experiment created the highest variations and appeared to digest nicked cccDNA because of its separation into single strands. Indeed, we could observe a much stronger reduction of the cccDNA PCR counts of an HBV DNA plasmid and HBV-infected HepG2-NTCP cells using PSD and heat denaturation compared to PSD alone, indicating that the plasmid preparation contained nicks. Because of this concern and the additional need to experimentally adapt the heat denaturation conditions to the amount and viscosity of the DNA sample, this approach did not prove to be advantageous over the other conditions described here for a PCR-based cccDNA quantification.

A common characteristic of all tested nucleases is their ability to hydrolyze linear or open DNA molecules but spare covalently closed circular forms from digestion. Thus, the quality of the extracted DNA is of utmost importance. Any condition provoking nicking of the cccDNA will make it a template for T5 exonuclease and exonuclease III, but not for PSD, while all enzymes (except exonuclease I) will act on damaged cccDNA containing double strand breaks. We occasionally obtained low quality DNA with detrimental effects on cccDNA measurements after nuclease digestions. **Supplementary figure 8C** serves as an example for accidental nicking showing two independent -PK DNA extractions from the same mouse liver tissue. In one of the extracts, however, the SB revealed a prominent “slow-migrating” band and only a faint “fast-migrating” band, indicating that the cccDNA was nicked and migrated as a relaxed circular form during electrophoresis. Notably, cccDNA measurement by qPCR was still possible using PSD treatment. **Supplementary figure 8D** shows an example of -PK extracted DNA that was severely damaged, containing nicks and double-strand breaks. By comparison to the high-quality -PK extracts in the cross-validation, this sample showed 0.6log lower cccDNA levels after digestion with all nucleases. Mitochondrial DNA was reduced by 2.1log on average during all nuclease digestions demonstrating damage of this circular DNA species as well.

Supplementary figures

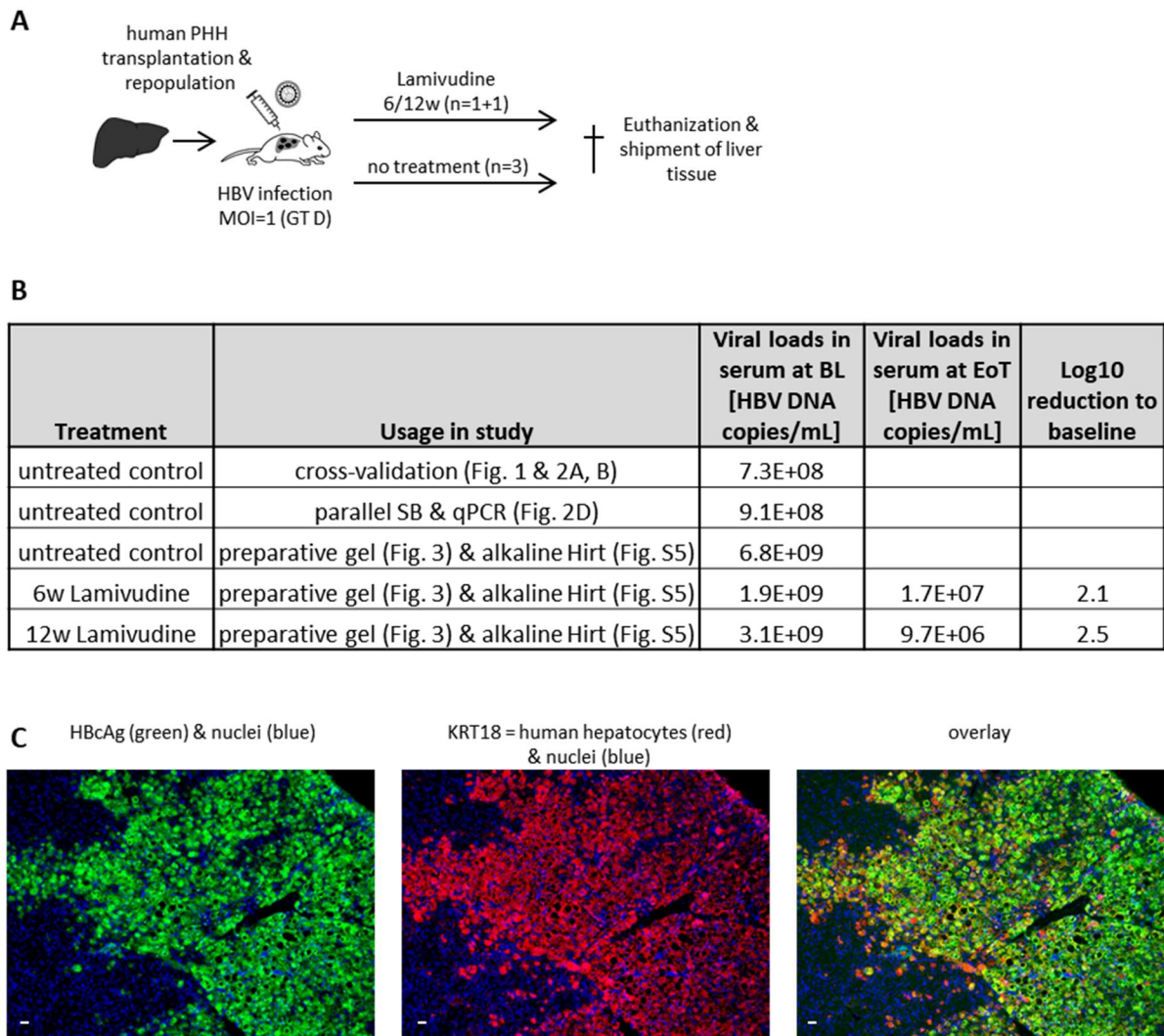


Supplementary figure 1: (A) Simplified HBV life-cycle with a focus on HBV DNA forms present in the cell. The pf-rcDNA is also known as dp-rcDNA. The removal of the viral polymerase might occur in the cytoplasm or the nucleus. The CM-rcDNA is a putative intermediate between pf-rcDNA and cccDNA. The encapsidated replicative intermediates occur with variable lengths of minus and plus strand DNA; however, only the defined intermediates i.e. pregenomic RNA, single-stranded DNA and relaxed circular DNA are depicted. The encapsidated rcDNA might be shuttling back to the nucleus to refill the cccDNA pool. **(B)** Schematic Southern blot pattern derived from highly HBV-infected samples depicting a typical picture with major bands. The blot is labelled on the right-hand side with HBV DNA forms that are present in the respective bands or smears.

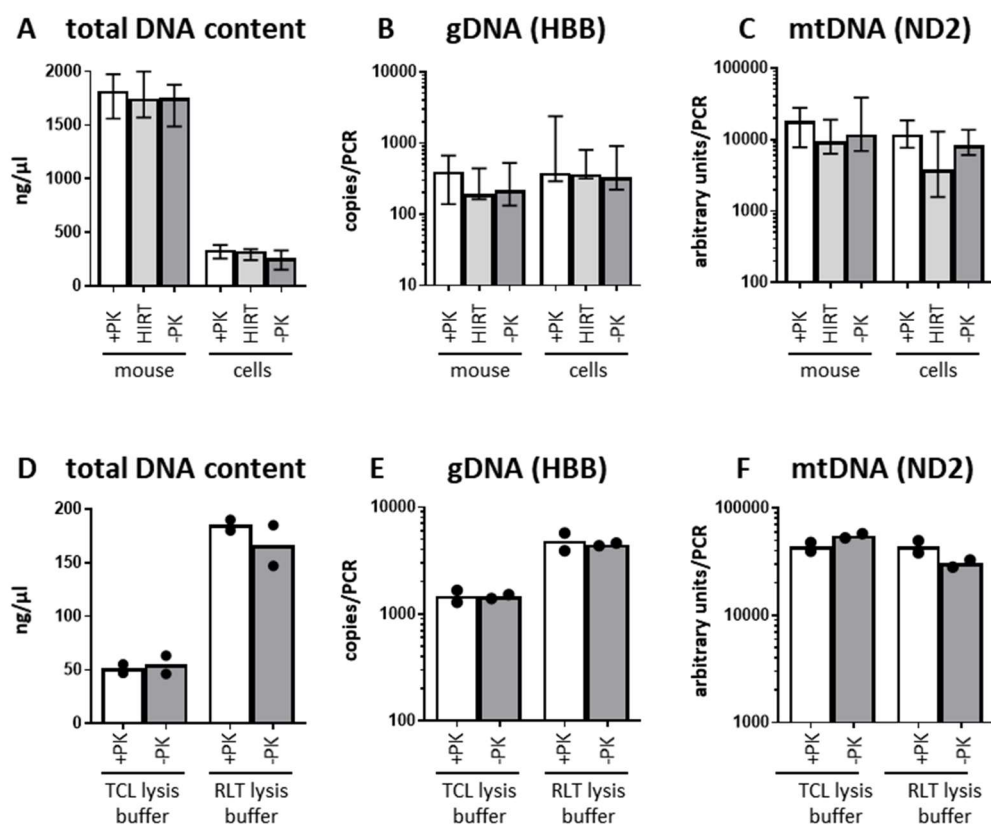


Supplementary figure 2: Characterization of the cccDNA-selective qPCR strategy used in this study. **(A)** A schematic presentation of the primer and probe binding sites on cccDNA and rcDNA is shown in red. The binding site of the probe for the qPCR detecting total HBV DNA is shown as a green dash. **(B)** The table summarizes the qPCR conditions for the cccDNA-selective PCR used throughout the study. **(C)** This qPCR strategy detects all HBV genotypes except genotype G with comparable efficiencies. Serial dilutions of plasmids each containing

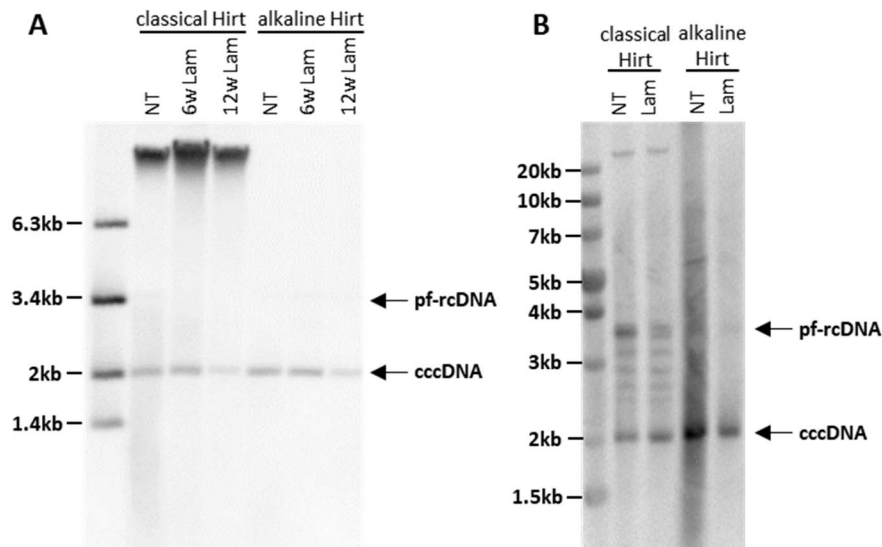
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3 the consensus sequence built from the HBVdb database (<https://hbvdb.lyon.inserm.fr/HBVdb/>)
4 for every genotype were run in triplicates and the standard curve was computed. (D) rcDNA
5 derived from two mice was analyzed by qPCR for cccDNA (grey bars) and total HBV DNA
6 (black bars) showing the median and range. The false detection ratio (determined by the total
7 HBV DNA copy number divided by the copy number detected by the cccDNA-selective PCR)
8 is depicted on top of the bars and was around 250 indicating that rcDNA is amplified in the
9 cccDNA-selective PCR in a false-positive manner with a ratio of 1:250. The PCR strategy was
10 implemented in every lab and showed comparable cccDNA specificity in serum-derived
11 rcDNA. (D) A fixed amount of an HBV containing plasmid (10^4 copies/per reaction) was mixed
12 with increasing concentration of mouse serum derived rcDNA as indicated below the graph.
13 Liver DNA from an uninfected USG mouse was included in every reaction to simulate
14 conditions in actual infectious liver samples. These artificial mixtures were analyzed by qPCR
15 for cccDNA (grey bars) and total HBV DNA (black bars). Red color indicates the fraction of
16 cccDNA counts that is detected in a false-positive manner. The number on top of the bar
17 depicts the false detection ratio (i.e. total HBV DNA copy numbers / cccDNA copy numbers) in
18 this sample. This experiment illustrates the effect of this false-positive detection in mixtures of
19 an HBV plasmid (as a surrogate for cccDNA) and increasing amounts of serum-derived rcDNA
20 mimicking the situation in infected samples. When rcDNA levels exceed HBV DNA plasmid
21 levels by more than 250 fold, measured cccDNA levels increase due to the false-positive
22 detection of rcDNA and a precise quantification of cccDNA is not possible.
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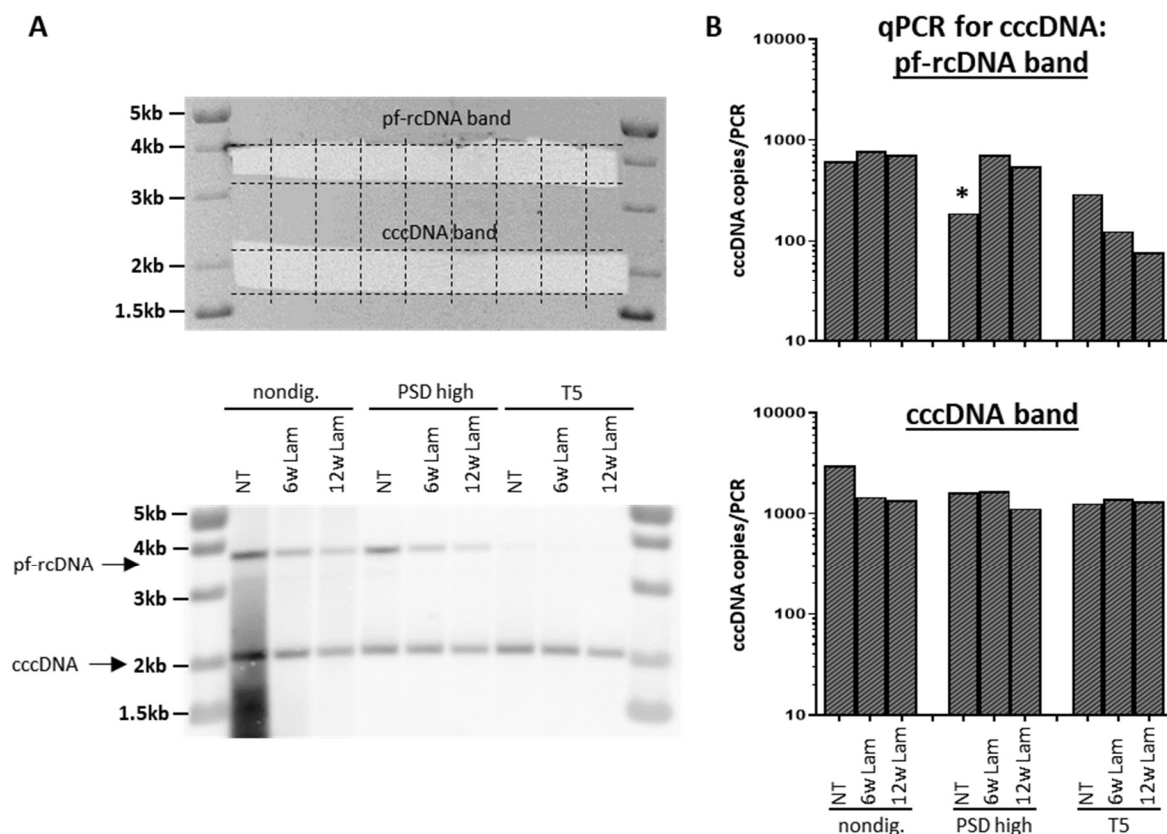
Supplementary figure 3: Sample preparation and virological characterization. **(A)** Schematic presentation of the generation and treatment of humanized liver chimeric mice used in this study. **(B)** The table summarizes the mice, their usage for the presented experiments, their final HBV DNA titers in the serum and, where applicable, their titer at the end of treatment and reductions from baseline. **(C)** Immunofluorescence co-staining for HBV core antigen (green) and the cytokeratin 18 (KRT18) in red as a marker for human hepatocytes in cryopreserved liver sections. Nuclei were stained with Hoechst 33258 (blue). Scale bar = 50 μ m; BL, baseline; EoT; end of treatment.



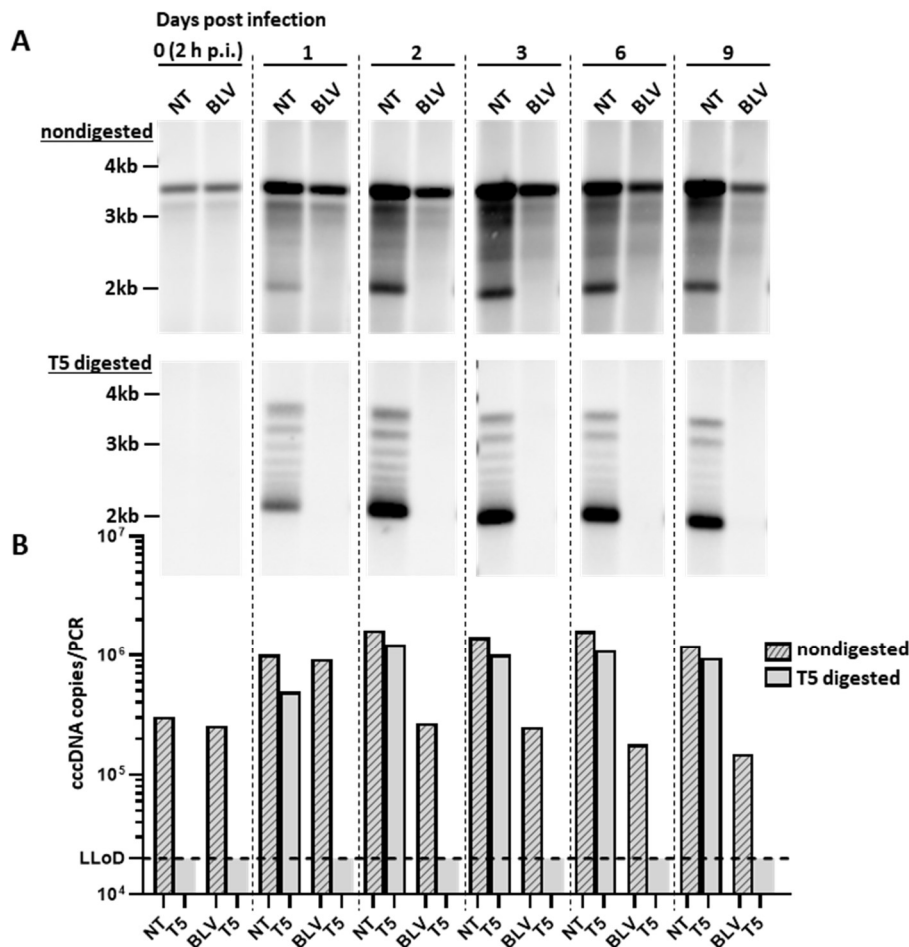
Supplementary Figure 4: The DNA extraction protocol affects the recovery of different types of DNA which in turn influences the normalization strategy. (**A-C**) The recovery of total DNA (measured by spectrophotometry) (**A**), genomic DNA (measured by qPCR for the human single-copy gene HBB) (**B**), and mitochondrial DNA (measured by qPCR for the human mitochondrial gene ND2) (**C**) are depicted as bar graphs for the three tested extractions and the two type of samples as indicated below the graphs. The bars show the median and range of the measurements in four labs. (**D-F**) The total DNA extraction with and without proteinase K treatment was tested head-to-head with the proprietary TCL buffer (Epicentre) and an alternative lysis buffer RLT (Qiagen) using two HBV-infected, untreated humanized mice. Every dot depicts one mouse, the bars the mean. The recovery of total DNA was measured by fluorometry (**D**), genomic DNA by qPCR for the human single-copy gene HBB (**E**), and mitochondrial DNA by qPCR for the human mitochondrial gene ND2 (**F**). gDNA, genomic DNA; HBB, hemoglobin subunit beta; mtDNA, mitochondrial DNA; ND2, mitochondrially encoded NADH:ubiquinone oxidoreductase core subunit 2.



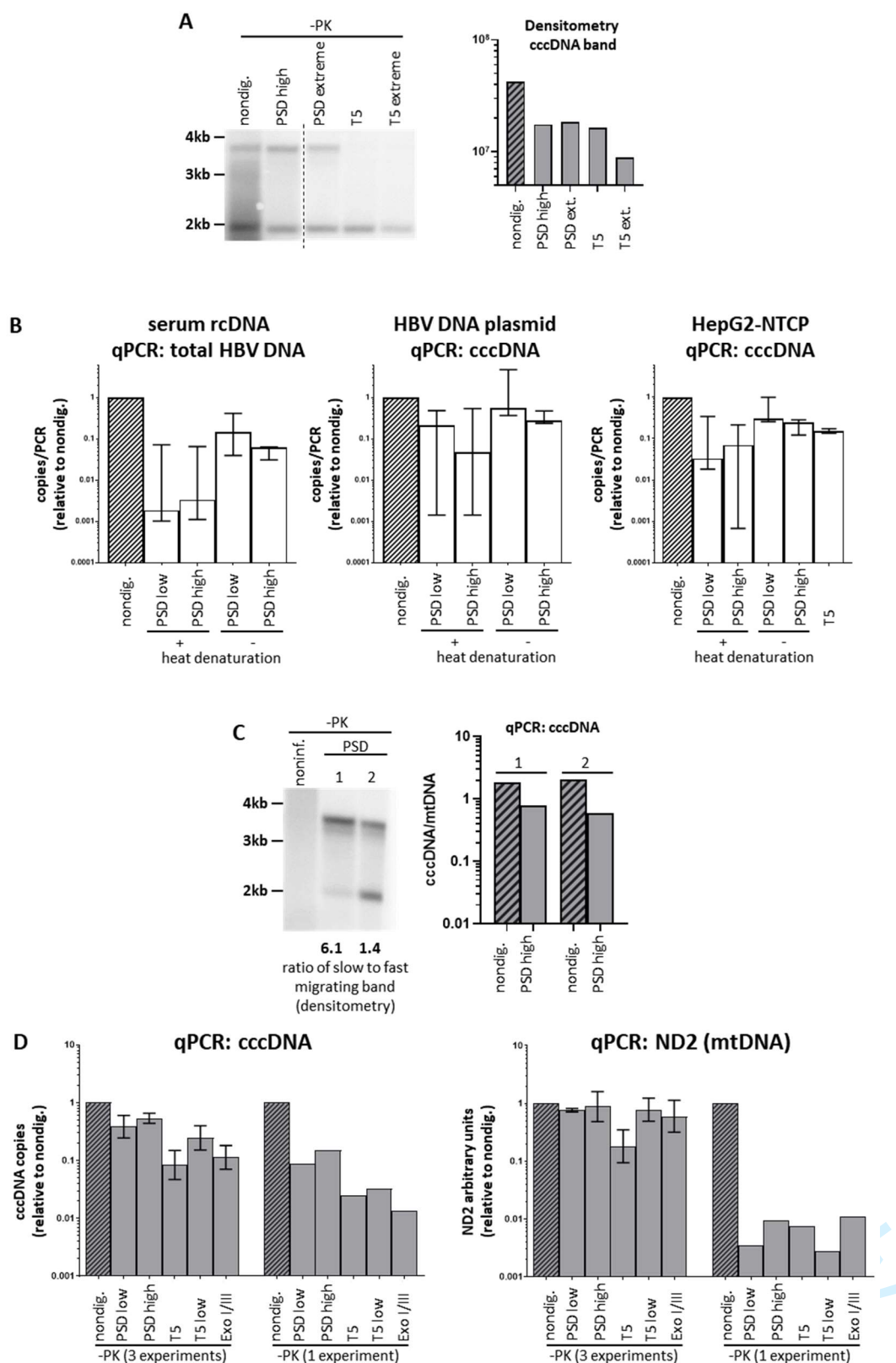
Supplementary Figure 5: Side-by-side comparison of classical and alkaline Hirt procedures. DNA was extracted with the alkaline and the classical Hirt method and subjected to SB as described in Supplementary Materials and Methods. **(A)** Liver DNA from three stably HBV-infected USG mice (after six or 12 weeks of Lamivudine treatment, or untreated, same mice as in **Figure 3**). **(B)** DNA from HepG2-NTCP cells infected with HBV (HepAD38-derived virus at MOI 250 GE / cell) and cultured for 9 days with or without Lamivudine treatment (10uM). In contrast to the classical method, cells are lysed in an alkaline milieu leading to the irreversible denaturation of genomic DNA and all non-supercoiled HBV DNA species, which are removed by centrifugation after rapid neutralization. As can be seen on the upper part of the blot, genomic DNA is visible only in the classical Hirt DNA extracts, confirming the higher capacity of alkaline extraction to deplete it. However, qPCR for HBB as an indicator of genomic DNA showed that genomic DNA was still present to varying extents (data not shown). In cell culture derived samples **(B)**, most of the slow-migrating, relaxed HBV DNA forms, as well as “T5-resistant forms” (see **Supplementary Fig. 7**) are absent in the alkaline Hirt DNA extracts. These forms are not detected in either classical or alkaline Hirt extracts of mice livers **(A)**, probably due to sensitivity issues or the high quality of the obtained DNA, i.e. no contribution of nicked cccDNA to the slow-migrating upper band. A smear in the alkaline Hirt-derived sample is visible in cell culture extracts **(B, lane 4)**, which is absent under Lamivudine treatment (lane 5), suggesting that it is specific to HBV DNA. Lam, Lamivudine; NT, non-treated.



Supplementary Figure 6: The pf-rcDNA is detected with the same efficiency as cccDNA by cccDNA-selective qPCR. **(A)** The upper and lower bands of a parallel gel (same samples as in Figure 3) were excised separately and the DNA was extracted. The top photograph shows the agarose gel after excision; the lower photograph shows the parallel SB for comparison. **(B)** The upper graph depicts qPCR measurements for cccDNA in samples originating from the upper band in copies / PCR assay. The lower graph depicts the measurements from the lower band. The asterisk (*) marks a sample where some of the material was lost during the gel extraction process. Lam, Lamivudine; NT, non-treated.



Supplementary figure 7: Persistent pf-rcDNA from input virus interferes with cccDNA measurements in cell culture but can be removed by T5 exonuclease treatment. (**A, B**) HepG2-NTCP cells were infected with HBV (HepAD38-derived virus at MOI 4000 GE / cell) and followed up for nine days in the presence of Bulevirtide (185 nM) or without treatment. Hirt DNA was extracted at the indicated time points and subjected to SB (**A**) and cccDNA-selective qPCR (**B**) analyses either without additional nuclease digestion or after T5 exonuclease digestion. Samples treated with T5 exonuclease are shown in the bottom blot or with hatched bars, respectively. On the bottom blot, twice as much DNA as on the top blot was loaded. BLV, Bulevirtide; NT, non-treated.



Supplementary Figure 8: Nuclease treatment bears the risk of over-digesting cccDNA when digestion conditions are exaggerated or when the input DNA is damaged. **(A)** SB analysis (left) and densitometry of the cccDNA band (right) of -PK extracted liver DNA from one stably infected untreated USG mouse after various nuclease treatments. The standard conditions for PSD and T5 were compared to extreme conditions: “PSD high”: 30 U PSD in 200 μ l, 2 h incubation vs. “PSD extreme”: 120 U PSD in 200 μ l, 6 h incubation and “T5”: 10 U T5

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3 exonuclease in 20 μ l; 45 min incubation vs “T5 extreme”: 40 U T5 exonuclease in 20 μ l; 6 h
4 incubation. Note that the higher band volume of the nondigested sample determined by
5 densitometry is due excessive background staining in this lane. **(B)** Comparison of PSD
6 digestion efficiency with and without prior heat denaturation of the input DNA. DNA from
7 HepG2-NTCP cells was extracted with the +PK extraction protocol. Serum rcDNA was
8 extracted from humanized mouse serum using the QiAamp MinElute Virus Spin Kit. Extracted
9 rcDNA and purified HBV DNA plasmid was diluted in +PK extracted DNA from an uninfected
10 humanized mouse before nuclease digestion. The bar graphs show total HBV DNA or cccDNA
11 copy numbers normalized to the nondigested levels. Bars depict the median and range of
12 measurements from four labs. The sample type and qPCR are depicted above the respective
13 graphs. **(C)** SB analysis (left) and qPCR for cccDNA (right) in two individual -PK DNA extracts
14 from the same untreated HBV-infected USG mouse (denoted as 1 and 2). The ratio of upper
15 and lower band was determined by densitometry. qPCR measurements of cccDNA normalized
16 to mitochondrial DNA via ND2 are shown beside the blot before and after nuclease digestion.
17 **(D)** qPCR measurements of cccDNA and ND2 in -PK extracted liver DNA from an HBV-infected
18 USG mouse liver tissue, digested with nucleases as indicated below the graph or left
19 undigested (hatched bars) The left-hand side of each graph shows three independent DNA
20 extraction; the right-hand side shows the results of a failed -PK DNA extraction in one
21 experiment, which resulted in damaged DNA. Bars depict the median of three experiments.
22 Copy numbers per qPCR assay were normalized to the values in the nondigested sample.
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Confidential: For Review Only

In silico analysis of the inclusivity of the qPCR used in this

Method: The latest 10,000 HBV genome sequence entries were retrieved. Eight sequences did not show any complementarity for either probe or reverse primer. The remaining 9,992 HBV sequences with known genotype information as per their TaxIDs were

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s study for the detection of HBV cccDNA

from NCBI GenBank. Of these 10,000 sequences, 8,959 sequences had full cover
verse primer sequence and were excluded from the alignment (see end of the ta
e analyzed separately (see following tabs).

probe sequence	reverse primer sequence
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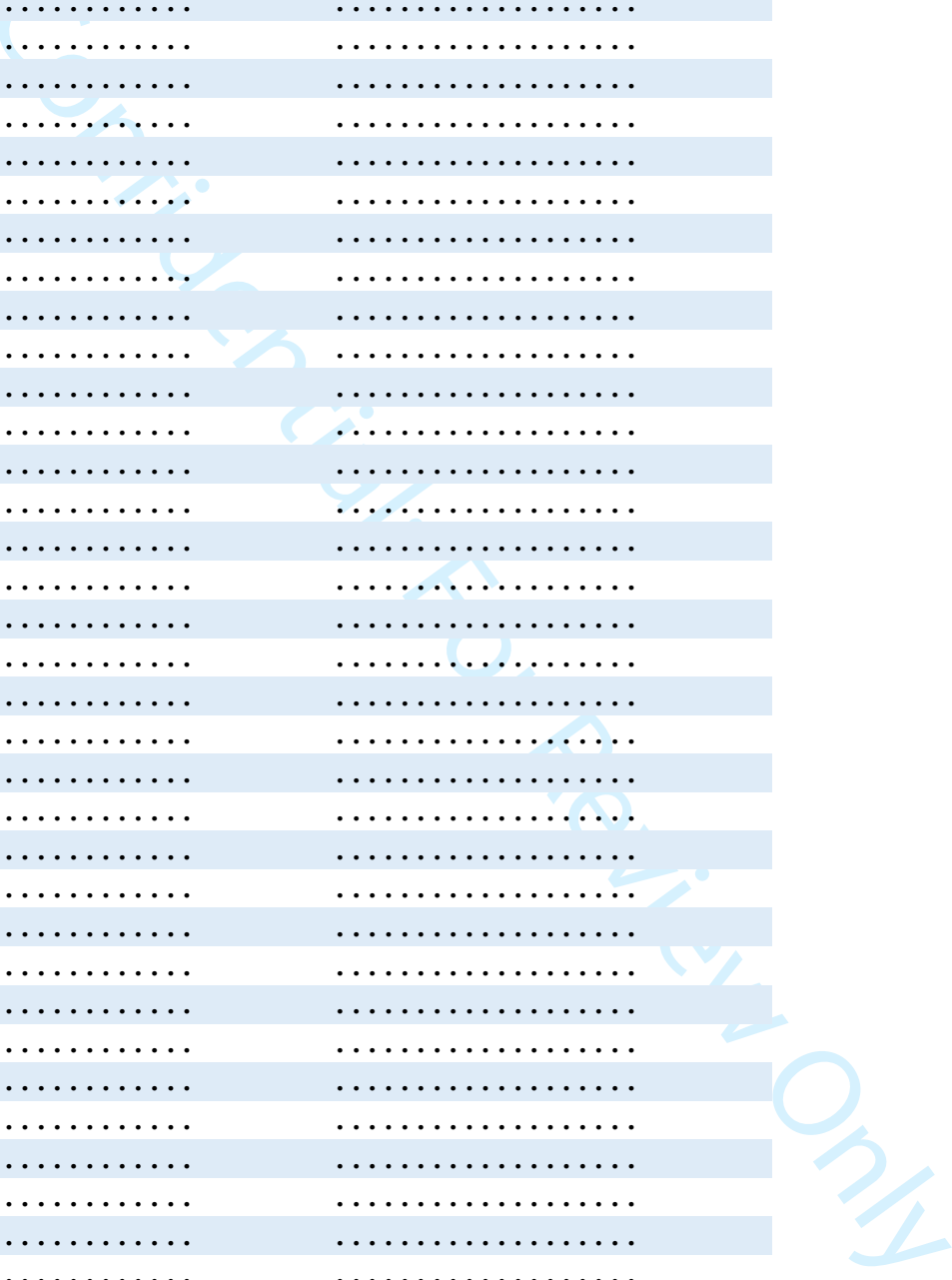
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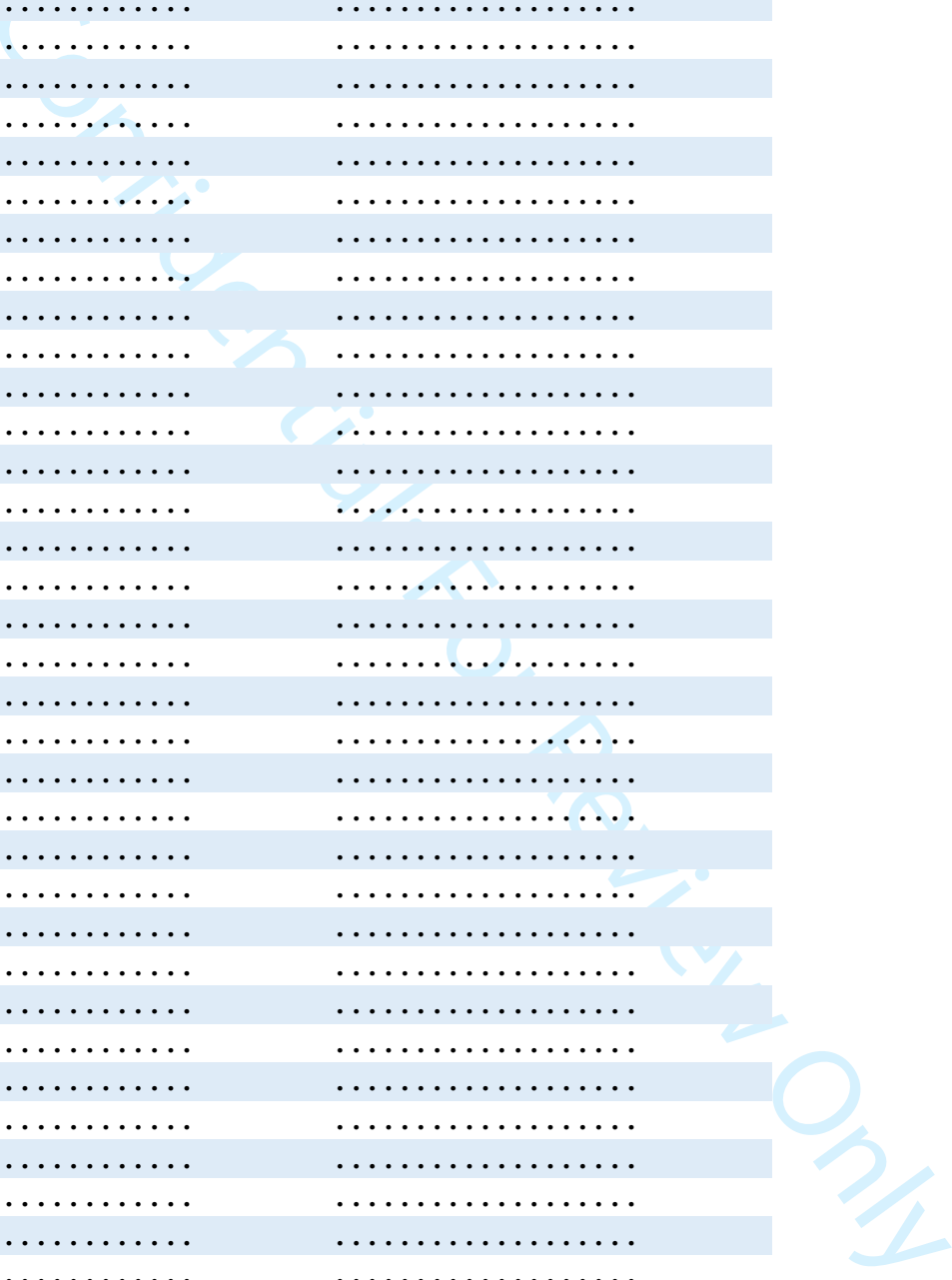
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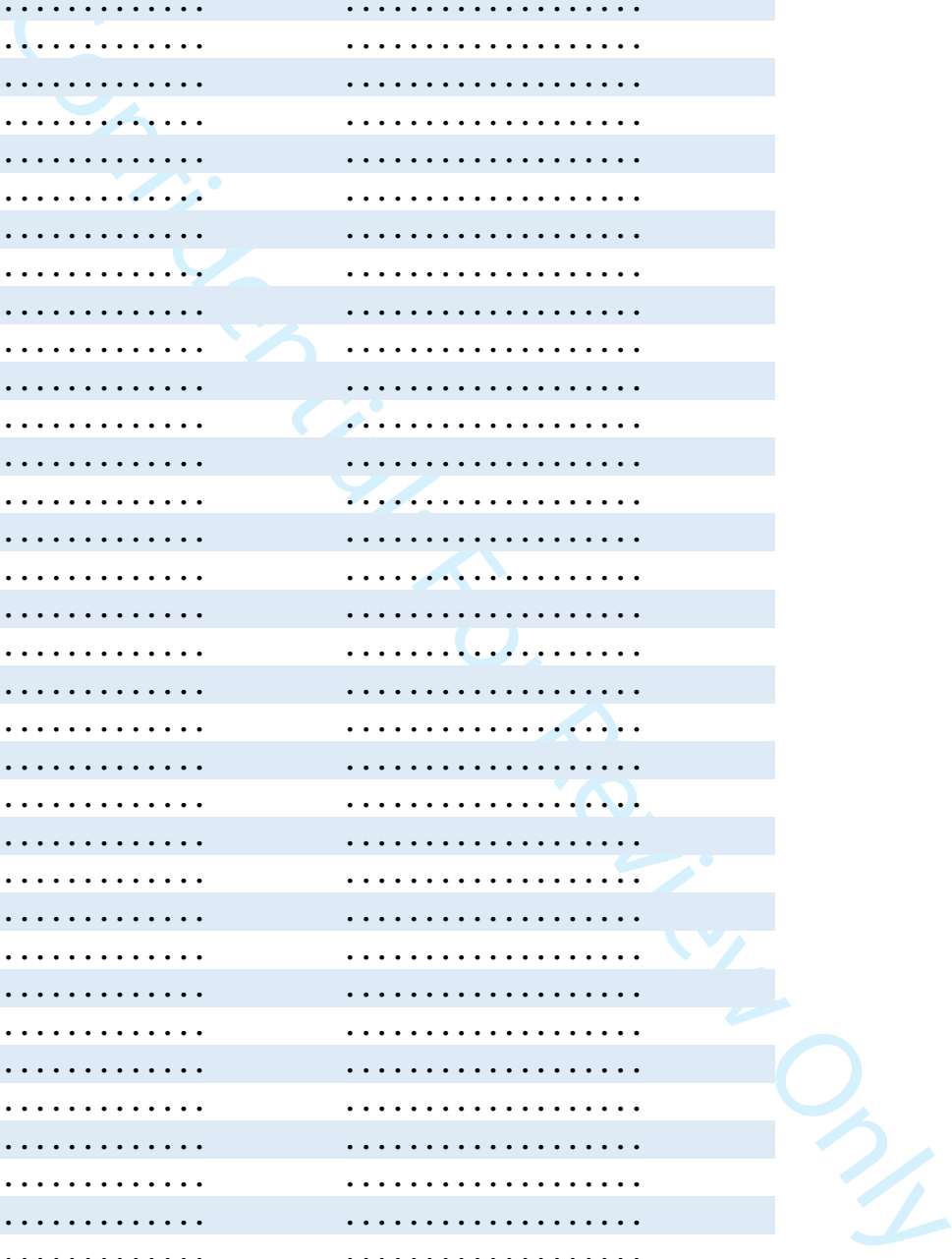
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18 h reverse primer
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	forward primer sequence	probe sequence
NCBI accession number	CCGTGTGCACTTCGCTTCA	CATGGAGACCACCGTGAACGCC
HE974371.1
HE974364.1
HE974374.1
HE974383.1
HE974376.1
AP007263.1
LC533934.1
HE974375.1
HE974370.1
HE974381.1
LC519788.1
HE974362.1
LC519791.1
LC519817.1
LC519794.1
LC519806.1
HE974365.1
LC519823.1
LC519819.1A.....
LC519815.1A.....
LC519798.1A.....
LC519811.1A.....
LC519820.1A.....
HE974367.1C.....
LC488828.1C.....
HE974363.1R.....

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2 **reverse primer sequence**
3 **TCAAGCCTCCAAGCTGTGC**
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1
2 **sequence of forward primer, probe and reverse primer stitched**

3 **CCGTGTGCACTTCGCTTCACATGGAGACCACCGTGAACGCCCTCAAGCCTCCAAGCTGTGC**

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number of mismatches	number of sequences with this particular pattern of mi
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1	5
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	% of analyzed sequences
4	69.23%
5	69.23%
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31	19.23%
32	7.69%
33	7.69%
34	3.85%

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	forward primer sequence	probe sequence
NCBI accession number	CCGTGTGCACTTCGCTTCA	CATGGAGACCACCGTGAACGCC
LC500247.1
LC060789.1
LC064380.1
LC064372.1
LC064376.1
LC064373.1
LC064366.1
LC057377.1
LC060790.1
LC064375.1
LC064377.1
LC064381.1
LC064368.1
LC064378.1
LC064371.1
LC057378.1
LC064367.1
LC064369.1
LC063767.1
LC064370.1
AB540582.1
LC036263.1
AB554017.1
LC456127.1
AB981581.1
AB981582.1
AB981583.1
AB819611.1A.....
AB819612.1A.....
AB819613.1A.....
AB819614.1A.....
LC064379.1A.....
AB602818.1A.....
LC064374.1A.....
LC456112.1A.....

	number of mismatches	number of sequences with	% of analyzed sequences
1	0	27	77.14%
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4	0	27	77.14%
5	0	27	77.14%
6	0	27	77.14%
7	0	27	77.14%
8	0	27	77.14%
9	0	27	77.14%
10	0	27	77.14%
11	0	27	77.14%
12	0	27	77.14%
13	0	27	77.14%
14	0	27	77.14%
15	0	27	77.14%
16	0	27	77.14%
17	0	27	77.14%
18	0	27	77.14%
19	0	27	77.14%
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21	0	27	77.14%
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25	0	27	77.14%
26	0	27	77.14%
27	0	27	77.14%
28	0	27	77.14%
29	0	27	77.14%
30	0	27	77.14%
31	0	27	77.14%
32	0	27	77.14%
33	0	27	77.14%
34	0	27	77.14%
35	0	27	77.14%
36	0	27	77.14%
37	1	8	22.86%
38	1	8	22.86%
39	1	8	22.86%
40	1	8	22.86%
41	1	8	22.86%
42	1	8	22.86%
43	1	8	22.86%
44	1	8	22.86%
45	1	8	22.86%
46	1	8	22.86%

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60**forward primer sequence**

NCBI accession number	CCGTGTGCACTTCGCTTCA
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AB644281.1
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AB554015.1
AB554014.1
AB554021.1
AB644286.1
AB644283.1
AB644284.1
LC516605.1
LC360507.1
LC155818.1
LC155816.1
LC155819.1
LC155817.1
AB540584.1
LC516606.1
LC064754.1
LC064755.1
LC170474.1
LC535928.1
LC456130.1
LC535912.1
LC456116.1
LC456115.1
LC456121.1
LC456126.1
LC456129.1
LC456132.1
LC456128.1
LC456131.1
LC535913.1
LC535923.1
LC456110.1
LC456111.1
LC535916.1
LC535917.1
LC535931.1
LC535949.1

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LC456135.1
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LC519821.1
LC535938.1
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LC535927.1
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LC519804.1
LC456118.1
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LC519818.1
LC456122.1
LC519796.1
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LC456117.1
LC456125.1
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AB819616.1
AB819617.1
AB819618.1
LC516607.1
LC170475.1
LC535915.1
LC456119.1
LC456114.1
LC456113.1
LC535950.1
LC519800.1
LC519801.1
LC535942.1
LC456120.1
LC519790.1
LC519792.1
LC519799.1
LC519812.1
LC535936.1
LC516608.1
LC516609.1
LC516610.1

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AY123041.1
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LC155820.1
LC456134.1
LC535939.1
AB540585.1
AB540583.1
LC519807.1
LC519805.1

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	forward primer sequence	probe sequence
NCBI accession number	CCGTGTGCACTTCGCTTCA	CATGGAGACCACCGTGAACGCC
HE974382.1
HE974373.1
HE974378.1
LC519824.1
LC519809.1
LC519808.1
AB267090.1
LC519795.1
LC519814.1
LC519793.1
LC519789.1
LC488706.1
LC519810.1
LC519816.1
AB554024.1
AB554016.1
AB554023.1
HE815465.1
HE974379.1
LC519787.1
HE974377.1
HE974372.1A.....
LC519802.1A.....G.....

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2 **reverse primer sequence**
3 **TCAAGCCTCCAAGCTGTGC**
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	number of mismatches
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number of sequences with this particular pattern of mismatches
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	% of analyzed sequences
4	91.30%
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18	91.30%
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NCBI accession number	forward primer sequence
HE974380.1
LC513654.1
LC513657.1
AP007262.1
LC513651.1
LC513652.1
LC513656.1
HE974384.1

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probe sequence	reverse primer sequence
CATGGAGACCACCGTGAACGCC	TCAAGCCTCCAAGCTGTGC
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sequence of forward primer, probe and reverse primer stitched

CCGTGTGCACTTCGCTTCACATGGAGACCACCGTGAACGCCCTCAAGCCTCCAAGCTGTGC

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3 **number of mismatches**

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	number of sequences with this particular pattern of mismatches
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% of analyzed sequences

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NCBI accession number	forward primer sequence
HE974368.1
HE974366.1
HE974369.1

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probe sequence	reverse primer sequence
CATGGAGACCACCGTGAACGCC	TCAAGCCTCCAAGCTGTGC
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sequence of forward primer, probe and reverse primer stitched

CCGTGTGCACTTCGCTTCACATGGAGACCACCGTGAACGCCCTCAAGCCTCCAAGCTGTGC

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number of mismatches
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	number of sequences with this particular pattern of mismatches
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% of analyzed sequences
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	forward primer sequence	probe sequence
NCBI accession number	CCGTGTGCACTTCGCTTCA	CATGGAGACCACCGTGAACGCC
AB625343.1A...G..A.....A..T
AB625342.1A...G..A.....A..T
AP007264.1A...G..A.....A..T

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reverse primer sequence

TCAAGCCTCCAAGCTGTGC

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sequence of forward primer, probe and reverse primer stitched

CCGTGTGCACTTCGCTTCACATGGAGACCACCGTGAACGCCCTCAAGCCTCCAAGCTGTGC

.....A...G..A.....A..T.....

.....A...G..A.....A..T.....

.....A...G..A.....A..T.....

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3 **number of mismatches**

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	number of sequences with this particular pattern of mismatches
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NCBI accession number	forward primer sequence
AB516394.1
AB516393.1
LC491577.1
AB846650.1
AB298362.1
AP007261.1
AY090454.1G....
AB516395.1

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probe sequence	reverse primer sequence
CATGGAGACCACCGTGAACGCC	TCAAGCCTCCAAGCTGTGC
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sequence of forward primer, probe and reverse primer stitched

CCGTGTGCACTTCGCTTCACATGGAGACCACCGTGAACGCCCTCAAGCCTCCAAGCTGTGC

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number of mismatches

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	number of sequences with this particular pattern of mismatches
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% of analyzed sequences
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	forward primer sequence
NCBI accession number	CCGTGTGCACTTCGCTTCA
AF241411.1

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probe sequence	reverse primer sequence
CATGGAGACCACCGTGAACGCC	TCAAGCCTCCAAGCTGTGC
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sequence of forward primer, probe and reverse primer stitched
CCGTGTGCACTTCGCTTCACATGGAGACCACCGTGAACGCCCTCAAGCCTCCAAGCTGTGC
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3 **number of mismatches**

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number of sequences with this particular pattern of mismatches

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3 **% of analyzed sequences**

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