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REVIEW

Multiple Inhibitory Factors Act in the Late Phase of HIV-1 Replication: a Systematic Review of the Literature

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SUMMARY The use of lentiviral vectors for therapeutic purposes has shown promising results in clinical trials. The ability to produce a clinical-grade vector at high yields remains a critical issue. One possible obstacle could be cellular factors known to inhibit human immunodeficiency virus (HIV). To date, five HIV restriction factors have been identified, although it is likely that more factors are involved in the complex HIV-cell interaction. Inhibitory factors that have an adverse effect but do not abolish virus production are much less well described. Therefore, a gap exists in the knowledge of inhibitory factors acting late in the HIV life cycle (from transcription to infection of a new cell), which are relevant to the lentiviral vector production process. The objective was to review the HIV literature to identify cellular factors previously implicated as inhibitors of the late stages of lentivirus production. A search for publications was conducted on MEDLINE via the PubMed interface, using the keyword sequence "HIV restriction factor" or "HIV restriction" or "inhibit HIV" or "repress HIV" or "restrict HIV" or "suppress HIV" or "block HIV," with a publication date up to 31 December 2016. Cited papers from the identified records were investigated, and additional database searches were performed. A total of 260 candidate inhibitory factors were identified. These factors have been identified in the literature as having a negative impact on HIV replication. This study identified hundreds of candidate inhibitory factors for which the impact of modulating their expression in lentiviral vector production could be beneficial.

KEYWORDS cell-mediated immunity, host resistance, human immunodeficiency virus, immunology, infection control, viral immunity, virology, virulence regulation, virus-host interactions

INTRODUCTION

The use of viral vectors for therapeutic gene delivery capitalizes on the coevolution of viruses and mammalian host cells (1), which makes them efficient gene transfer agents. A number of naturally occurring viruses have been adapted as viral vectors for gene therapy (2). Lentiviruses are particularly suited for this purpose

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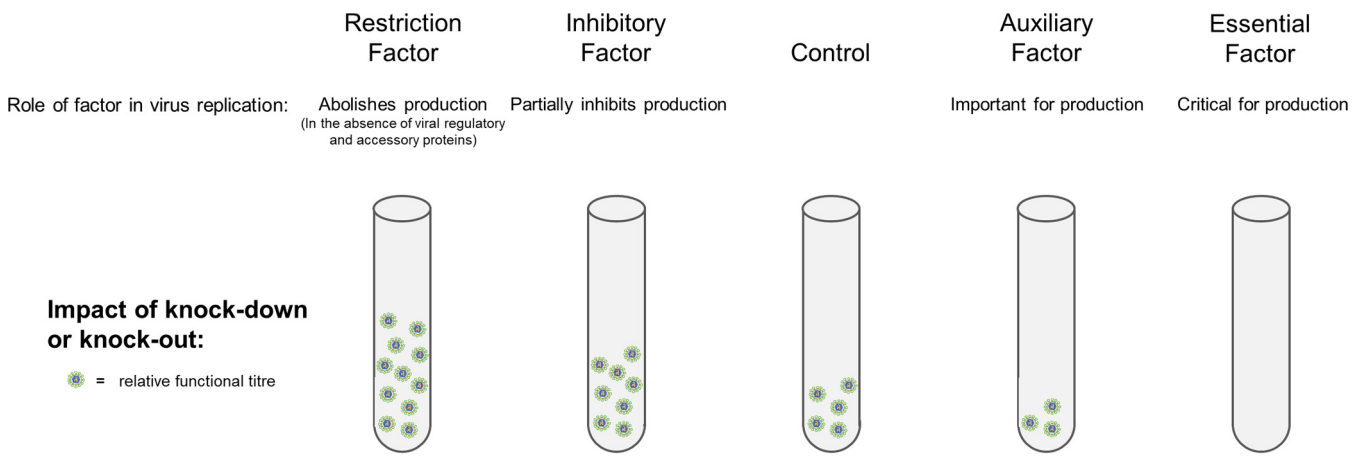

FIG 1 Categorization of cellular factors involved in virus replication and predicted impact of their knockdown/knockout on virus production. For the purposes of this review, cellular factors involved in virus replication were classified into four categories: restriction, inhibitory, auxiliary, and essential. The anticipated impact of the knockdown or knockout of genes in each category on subsequent virus production is indicated schematically.

because they can integrate into the host genome, have a large transgene capacity, and can transduce both dividing and nondividing cells (3). Therapeutic lentiviral vectors have encountered preclinical success in *ex vivo* clinical trials for the treatment of leukemia (4–6) and disorders associated with hematopoietic stem cells (7–10) and are being evaluated in early *in vivo* clinical trials for Parkinson's disease (11) and age-related macular degeneration (12). Multiple cell therapy products underpinned by lentiviral vectors are in development, with one having been approved for the therapy of acute lymphoblastic leukemia (13).

HIV Essential Factors

In order to replicate, viruses have evolved to exploit a large number of cellular factors, with an estimated 9.5% of human protein-coding genes proposed to affect human immunodeficiency virus type 1 (HIV-1) replication (14). These genes can be classified into four categories: essential, auxiliary, restriction, and inhibitory factors. Essential factors, also identified elsewhere as "dependency factors" (15, 16), are categorized as those factors for which there is an absolute requirement for virus replication, such that the knockdown or knockout of genes encoding essential factors will either be extremely detrimental to virus replication or completely abolish it (Fig. 1). Essential factors accomplish cellular functions that are required to produce viruses or are exploited by the virus to complete its life cycle. A few examples include CD4, which is required for cellular entry of wild-type HIV-1 (17, 18); RANBP2, which is essential for the nuclear import of the HIV-1 preintegration complex (19); CCNT1 (cyclin T1), which is a Tat cofactor mediating TAR RNA binding (20, 21); DDX3, a cofactor required for the Rev-RRE export function (22); RAB9, which facilitates vesicular transport from the late endosome to the *trans*-Golgi network, a process implicated in HIV-1 particle assembly and export (23); and TSG101, a factor involved in budding (24, 25). The impact of these genes on lentiviral vector production might differ from their impact on HIV-1 replication, as in vector production, early steps in replication are bypassed either by transfection of the crucial virus factors or by their activation in stable producer cell lines. Furthermore, lentiviral vectors have been modified and "pseudotyped" with a non-HIV-1 envelope protein(s) to enhance their cell-specific targeting. Other host genes that have a positive impact on, but are not absolutely required for, virus production are identified here as auxiliary factors. In contrast to essential factors, decreasing the amounts of these factors is expected to reduce, but not abolish, virus replication (Fig. 1).

HIV Restriction Factors

Mammalian cells also express specific factors to minimize virus replication, known as restriction factors; they constitute a first line of defense even before the innate and

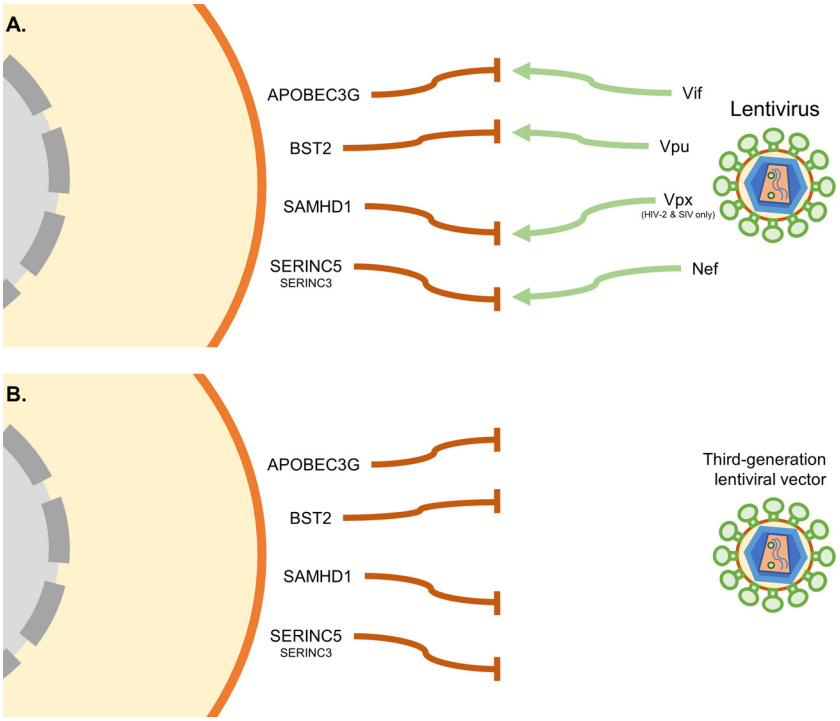

FIG 2 Lentiviral restriction factors along with their viral antagonists. ABOBEC3G, BST2 (tetherin), SAMHD1, SERINC3, and SERINC5 are factors that restrict lentivirus replication. (A) In lentiviral infection of human cells, viral accessory proteins antagonize the effects of these restriction factors: APOBEC3G by Vif, BST2 by Vpu, SAMHD1 by Vpx (in HIV-2 and simian immunodeficiency virus [SIV] only), and SERINC5 (and, to a lesser extent, SERINC3) by Nef. (B) In third-generation lentiviral vector production and transduction, none of the accessory proteins are present, rendering the vector susceptible to these host cell factors.

adaptive immune systems have a chance to exert their antiviral action. Through mutual evolution, viruses have developed their own endogenous factors to counteract the activity of these host restriction factors in an ongoing "arms race." This is because virion production would be greatly impaired if cellular restriction factors were not inhibited. In the case of lentiviruses, the regulatory and accessory proteins encoded in the lentiviral genome oppose cellular restriction factors (Fig. 2). HIV-1 is one of the most intensely studied viruses, generating a rich literature describing cellular factors that restrict HIV-1 replication, including APOBEC3G, BST2 (tetherin), SAMHD1, and SERINC3/5.

APOBEC3G was identified as the principal restriction factor mediating HIV-1 restriction in the absence of Vif (26). APOBEC3G is packaged into virions (26) and acts when the virus infects a subsequent cell, causing extensive mutations in the viral genome and terminating the life cycle at the reverse transcription step (27–29). Vif prevents APOBEC3G incorporation into virions by depleting its intracellular levels (30–35). APOBEC3G can also restrict the replication of incoming viruses in target cells at the reverse transcription step (36). Other members of the ABOBEC3 family have also been linked with HIV-1 restriction, in particular APOBEC3F (reviewed in reference 37).

BST2, also known as tetherin, was found to be a Vpu-antagonized HIV-1 restriction factor (38, 39). BST2 localizes to lipid rafts (40), where HIV-1 budding occurs, and prevents virion release through a tethering mechanism whereby virions at the cell surface are linked to the cellular membrane and to each other (41). Additionally, BST2 can act as an innate sensor through the activation of NF-κB (42). Vpu acts by downregulating BST2 from the cell surface, thus counteracting this cellular antiviral defense mechanism (38).

SAMHD1 is a restriction factor counteracted by Vpx (43, 44) and functions as a deoxynucleoside triphosphate (dNTP) triphosphohydrolase (45, 46). It restricts HIV

replication by depleting the cytoplasmic pool of dNTPs necessary for reverse transcription (47). Exogenous Vpx strongly reduces SAMHD1 in dendritic cells and macrophages (43, 44).

SERINC5 and, to a lesser extent, SERINC3 were shown to restrict HIV-1 infectivity and to be counteracted by Nef (48, 49). SERINC5 is localized in the plasma membrane, is incorporated into budding virions, and acts as a restriction factor by impairing their ability to translocate their content into the target cells' cytoplasm. Nef prevents virion incorporation of SERINC5 by redirecting it to an endosomal compartment (48).

The roles of these intrinsic restriction factors are well known in lentiviral infection, but they are also present in producer cells during lentiviral vector production. Importantly, third-generation lentiviral vectors have been stripped of their accessory proteins for increased safety, leaving the vector form of the lentivirus at the mercy of the host cell's restriction factors, which could have a subsequent impact on the production titer (Fig. 2B). Helpfully, the human embryonic kidney 293 (HEK 293) cell line, frequently used for lentiviral vector production, is known to express very low levels of the main restriction factors acting late in the HIV-1 life cycle (APOBEC3G, BST2, and SERINC5) (50). This means that HEK 293-derived cells constitute a better choice for lentiviral vector production than, for example, HeLa cells, which express seven times more APOBEC3G and 252 times more BST2 (50, 51).

HIV Inhibitory Factors

It would be surprising, of course, if a process as complex as virus inhibition could be achieved by using only four cellular restriction factors. Therefore, this calls for another category of cellular proteins, which have an adverse effect on virus production or infectivity but which are not so crucial as to abolish virus production. Although such proteins are usually referred to as restriction factors in the literature, here they are termed inhibitory factors as they are not sufficiently critical to necessitate a direct countermeasure from the virus in the form of regulatory or accessory proteins. Such factors can, for example, accomplish cellular functions that indirectly inhibit virus production or affect cell growth. Importantly, most reviews of HIV-1–cell interactions focus only on the canonical restriction factors described above (52–57), disregarding the inhibitory factors discussed here.

Inhibitory factors have been studied mostly in regard to virus entry, with several factors, such as CH25H, DDX58 (RIG-I), and MX2 (MxB), being described as having an impact on the initial steps of HIV-1 infection/replication. CH25H converts cholesterol into 25-hydroxycholesterol, a soluble antiviral factor which broadly inhibits the growth of enveloped viruses, including HIV-1 (58). DDX58 is a cytoplasmic viral RNA sensor that is inhibited by the HIV-1 protease (59), while MX2 was shown to be an interferon-induced inhibitor of HIV-1 infection (60).

A key method to identify new factors involved in viral replication is high-throughput screening, a drug discovery process that uses automation to assay the biological or biochemical activities of numerous drug-like compounds. It is a powerful strategy that allows the identification of factors involved in virus replication not previously linked to virus infection as well as the confirmation of previously established relationships. Most high-throughput screens for genes affecting HIV-1 infection reported to date tended to focus on essential/auxiliary factors (Table 1). Only one high-throughput screen reported to date specifically focused on inhibitory factors (61), addressing the early steps of the viral life cycle (virus entry to integration), as these steps are most relevant as targets for drugs blocking early stages of infection. Therefore, there is a gap in the knowledge concerning inhibitory factors acting late in the HIV-1 life cycle (from transcription to infection of a new cell) (Fig. 3); such late-acting inhibitory factors, which are highly relevant to lentiviral vector production, are much less well defined. These cellular factors might negatively affect virus production, and conventional cell lines therefore might not be optimal for lentiviral vector production. Assuming that such factors are also active in the lentiviral vector production environment, it is hypothesized that this search will lead to the identification of gene targets that could be "knocked down" or

TABLE 1 Comparison of high-throughput screens for essential, auxiliary, and inhibitory factors implicated in HIV-1 replication[a]

Reference	Technology	Targets	No. of targets	HIV-1 life cycle steps covered	No. of hits found
445	cDNA	Essential/auxiliary factors	15,000 genes	Entry to release	315
15	siRNA	Essential/auxiliary factors	21,121 genes	Entry to infectivity	273
446	siRNA	Essential/auxiliary factors	19,628 genes	Entry to translation	295
440	siRNA	Essential/auxiliary and inhibitory factors	19,709 genes	Entry to infectivity	232 (81)[b]
447	shRNA	Essential factors	59,509 transcripts	Entry to release	252
61	siRNA	Inhibitory factors	19,121 genes	Entry to translation	114
16	CRISPR-Cas9	Essential factors	18,543 genes	Entry to translation	5

[a]siRNA, small interfering RNA; shRNA, short hairpin RNA; CRISPR-Cas9, clustered regularly interspaced short palindromic repeats and CRISPR-associated protein-9.
[b]A total of 232 preliminary and 81 confirmed hits.

"knocked out" in order to increase production yields. To address this, we performed a review of the HIV-1 literature to assess the current knowledge of these factors.

METHODS

Systematic Investigation of the Literature

This systematic review of the literature was conducted according to Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (62) as much as feasible; considering that this is not a medical systematic review, portions of the guidelines were not applicable or impractical to implement.

The research strategy is summarized in Fig. 4. A search for publications was conducted on MEDLINE via the PubMed interface, using the keyword sequence "HIV restriction factor" or "HIV restriction" or "inhibit HIV" or "repress HIV" or "restrict HIV" or "suppress HIV" or "block HIV," with a publication date up to 31 December 2016. Published studies in any language were considered. This search term combination led to the identification of 2,862 records; of these, PubMed identified 408 records as reviews, and these records were excluded from the search results. A further 151 records, not tagged as reviews, were found to be reviews, news articles, editorials, or comments

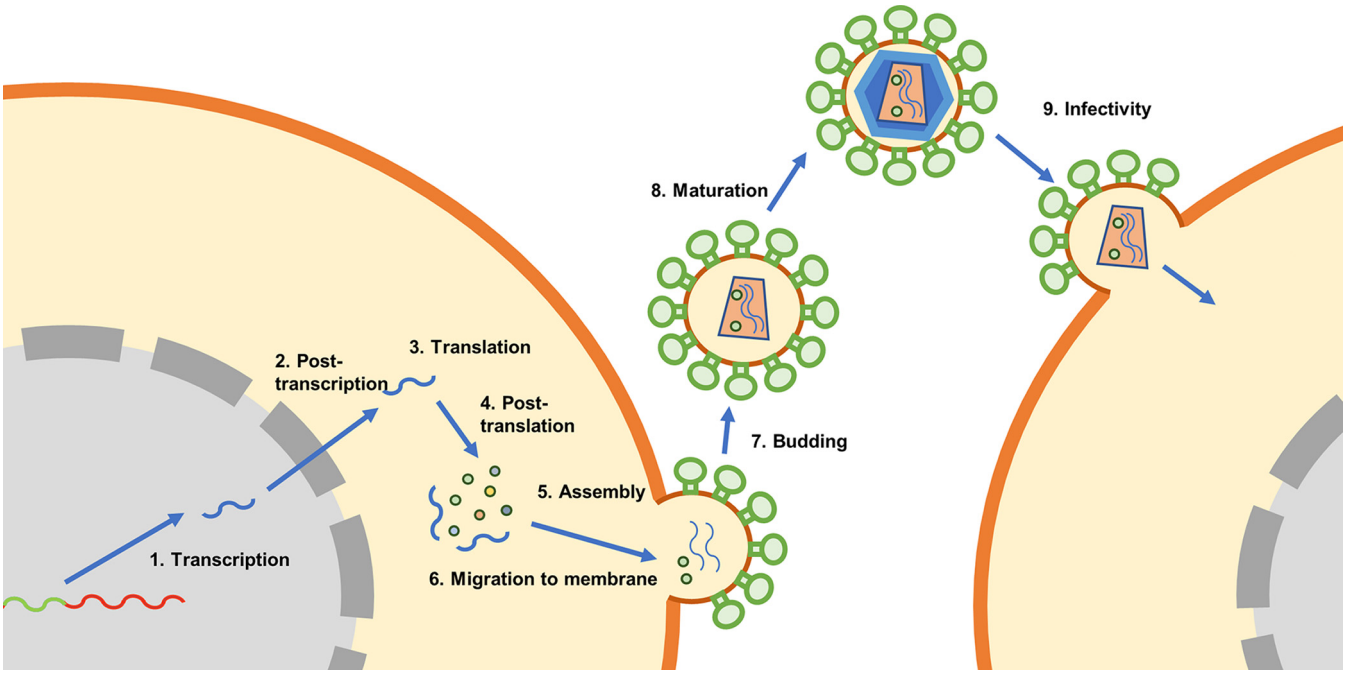

FIG 3 Schematic showing stages in the late phase of the HIV-1 life cycle. The production of lentiviral vectors via producer cell lines, or transient transfection, involves only the late steps of the HIV-1 life cycle. The genes identified in the literature search are identified by the step in which they are presumed to be active. Life cycle steps depicted are transcription (step 1), posttranscription (step 2), translation (step 3), posttranslation (step 4), assembly (step 5), migration to the cell membrane (step 6), budding (step 7), maturation (step 8), and infectivity (step 9) of the produced virions.

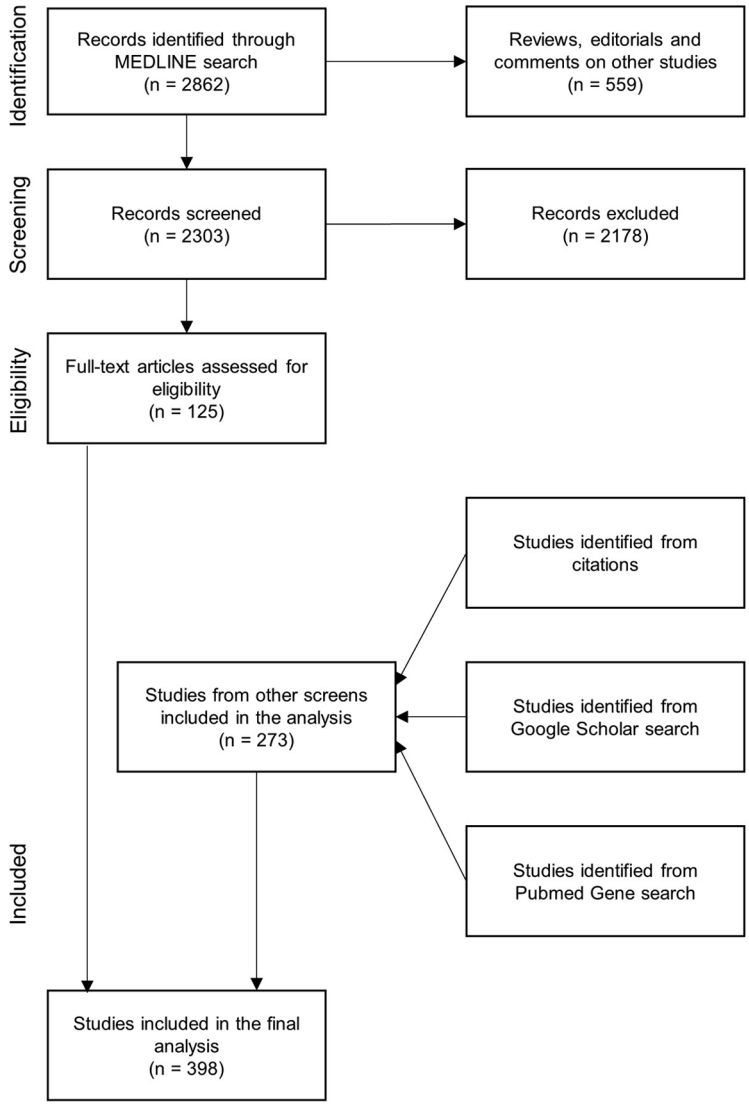

FIG 4 Schematic of stages of the systematic review.

on other articles and were also excluded from the search results. The titles of the remaining 2,303 articles were screened to select papers that identified genes that have an adverse impact on the late phase of the HIV-1 life cycle (Fig. 3), with a review of the abstract if there was any ambiguity. Of these records, the majority were rejected because they did not address the subject matter (1,215 records related to HIV medication or treatment; 507 about HIV biochemistry, biology, immunology, or pathology; 239 not related to HIV or related to nonhuman experiments; 89 related to public health or epidemiology studies; and 19 related to essential factors for HIV replication), which was unsurprising due to the broad query terms. Records related to inhibitory factors that were found to act only early in the HIV-1 life cycle (110 records) were not included in the results, but records related to genes for which a step in the life cycle could not be identified were retained. Finally, 125 records were included in the analysis.

The genes identified in the selected records were termed "candidate inhibitory factors," as they could potentially adversely affect lentiviral vector production. Each candidate inhibitory factor is identified with its HUGO Gene Nomenclature Committee official symbol (63) in tables and figures; alternative names used in cited papers are listed in parentheses in Table S1 in the supplemental material. The reference lists of the papers identified in the search were also consulted to identify any published studies missed by the database search

TABLE 2 Restriction and candidate inhibitory factors acting in the late phase of the HIV-1 life cycle identified in the literature review

Step	Factor(s)
Transcription (step 1)	*ACTL6A, APOL1, APOL6, ARHGEF1, ARID1A, BANP, BCL11A, BCL11B, BIRC2, CAV1, CBX3, CDKN1A, CEBPB, CHD1, CHD3, CIITA, CNP, COMMD1, CPSF3, CTNNB1, CYLD, DDX5, DENND4A, DICER1, DKC1, DNAJA1, DNAJB1, DNAJB6, DNAJC5, DROSHA, E2F1, EHMT2, EIF3F, EIF3L, FCGR3A, FOXP3, GADD45A, GADD45B, GADD45G, GNA13, GRN, HDAC1, HDAC2, HDAC3, HEXIM1, HEXIM2, HIF1A, HLA-B, HMGB1, HMOX1, HSPA12A, HSPA12B, HSPA13, HSPA14, HSPA1A, HSPA1B, HSPA2, HSPA4, HSPA5, HSPA6, HSPA8, HSPA9, HSPB1, IFI44, INTS11, LEF1, LIF, MCM2, MIR17, MIR17HG, MIR198, MIR20A, MIR27B, MMP3, MST1R, MTA1, MTA2, MYC, NELFB, NELFE, NFKB1, NFKBIA, POU2F1, POU2F2, PRDX1, PRDX2, PRDX4, PRKAA1, PRKAA2, PRMT6, RBPJ, RHOA, RN7SK, RNF7, SETDB1, SIRT1, SLC40A1, SMARCA4, SMARCB1, SP3, SUPT6H, SUV39H1, TARDBP, TCF4, TFAP4, TFCP2, TRIM11, TRIM22, UBASH3A, UBASH3B, UBP1, XRCC5, YY1, ZNF10, ZNF175, ZNF350*
Posttranscription (step 2)	*AXIN1, DGCR8, DICER1, DUSP1, IFITM1, IFITM2, IFITM3, ISG15, MIR155, NEAT1, NFKBIA, PRMT6, SFPQ*
Translation (step 3)	*ADAR, AGO2, APOL3, AXIN1, BST2, DDX6, DICER1, DROSHA, DUSP1, EIF2AK2, IFITM1, IFITM2, IFITM3, LSM1, MIR106B, MIR125B1, MIR125B2, MIR150, MIR15A, MIR15B, MIR16-1, MIR16-2, MIR20A, MIR223, MIR28, MIR29A, MIR29B1, MIR29B2, MIR29C, MIR382, MIR93, MOV10, PRKRA, RNASEL, ROCK2, SLFN11, TNRC6A, XRN1, ZC3H12A*
Posttranslation (step 4)	*DICER1*
Assembly (step 5)	*AGO2, APOL1, CAV1, CAV2, CCDC8, CNP, DHX30, HERC5, HSP90AB1, IFI30, IFITM1, IFITM2, IFITM3, LGALS3BP, MIR146A, MOV10, NEAT1, RSAD2, TRIM21, TRIM22, TSPO, XRCC5, ZC3H12A*
Migration to membrane (step 6)	*RNF115, TRIM22*
Budding (step 7)	*ABCA1, BST2, CC2D1A, CC2D1B, CD151, CD209, CD37, CD53, CD63, CD81, CD82, CD9, CHMP5, CLEC4M, DDX5, HAVCR1, HAVCR2, HGS, ISG15, MIR146A, MIR888, TIMD4, TRIM22, TSG101, TSPAN7, UBA7, UBE2L6*
Maturation of virions (step 8)	*CIITA, LGALS3BP*
Infectivity (step 9)	*ABCA1, APOBEC3A, APOBEC3B, APOBEC3C, APOBEC3D, APOBEC3F, APOBEC3G, APOBEC3H, APOL1, CAV1, CCDC8, CD37, CD53, CD63, CD81, CD82, CD9, DDX5, DLG1, EZR, GBP5, HSPA12A, HSPA12B, HSPA13, HSPA14, HSPA1A, HSPA2, HSPA4, HSPA5, HSPA6, HSPA8, HSPA9, IFITM1, IFITM2, IFITM3, LGALS3BP, MAP3K5, MARCH8, MB21D1, MIR146A, MOV10, RN7SL1, RN7SL2, RN7SL3, SERINC3, SERINC5, SPN, SUMO1, SUMO2, TRIM37, TSPAN7*
Apoptosis	*BCL2L1, CFLAR, KAT5, MAP3K5, XIAP*
Unknown	*AMT, BCL2, CD164, CD3E, CD3G, CDH23, CDK13, CTR9, EIF3E, EPSTI1, GM2A, HAS2, HSF1, HSP90AA1, IFI16, KCNK3, LPP, MECP2, MIR1236, MIR133B, MIR138-1, MIR138-2, MIR149, MIR326, MIR92A1, MIR92A2, NRON, NTRK3, OAS1, PARP14, PINX1, RTP4, RUVBL2, SLC51A, TDRD7, TNFRSF10A, TNFRSF10D, TRAF6, TRIM15, TRIM26, TRIM32*

as well as papers citing the identified records. An additional inquiry was run in Google Scholar using the names of candidate inhibitory factors (and alternative names used in the corresponding records) and the keyword "HIV" to find further articles confirming findings. The PubMed gene database also provided supplemental studies that were investigated. From these additional searches, 84 studies providing contradictory results on the status of the candidate inhibitory factor were included and are listed in parentheses in Table S1 in the supplemental material to provide a more complete picture of the current state of knowledge on each of the identified genes. Some studies listed very large numbers of genes; in these cases, only the information on genes identified in other studies was retained. These additional searches added 273 records. Some records did not identify the specific gene from a gene family that was being targeted, so the whole family is listed as individual candidate inhibitory factors.

RESULTS

A total of 398 records (15, 24–28, 30–33, 35, 36, 38, 39, 42, 48, 49, 64–444) that identified 260 candidate inhibitory factors were retained from the systematic search, and the results were tabulated as 830 reference points (see Table S1 in the supplemental material). Where possible, the HIV-1 life cycle step(s) where the gene is described or expected to be active is indicated. The steps covered are transcription (step 1), posttranscription (step 2), translation (step 3), posttranslation (step 4), assembly (step 5), migration to the cell membrane (step 6), budding (step 7), maturation (step 8), and infectivity (step 9), as indicated in Fig. 3. Two genes affected the ability of the cell to undergo apoptosis. Candidate inhibitory factors are listed according to the steps with which they are associated in Table 2, with some appearing in more than one category.

Each record was scrutinized to determine the techniques that led to the identification of the candidate inhibitory factor. A ranking was established to evaluate the

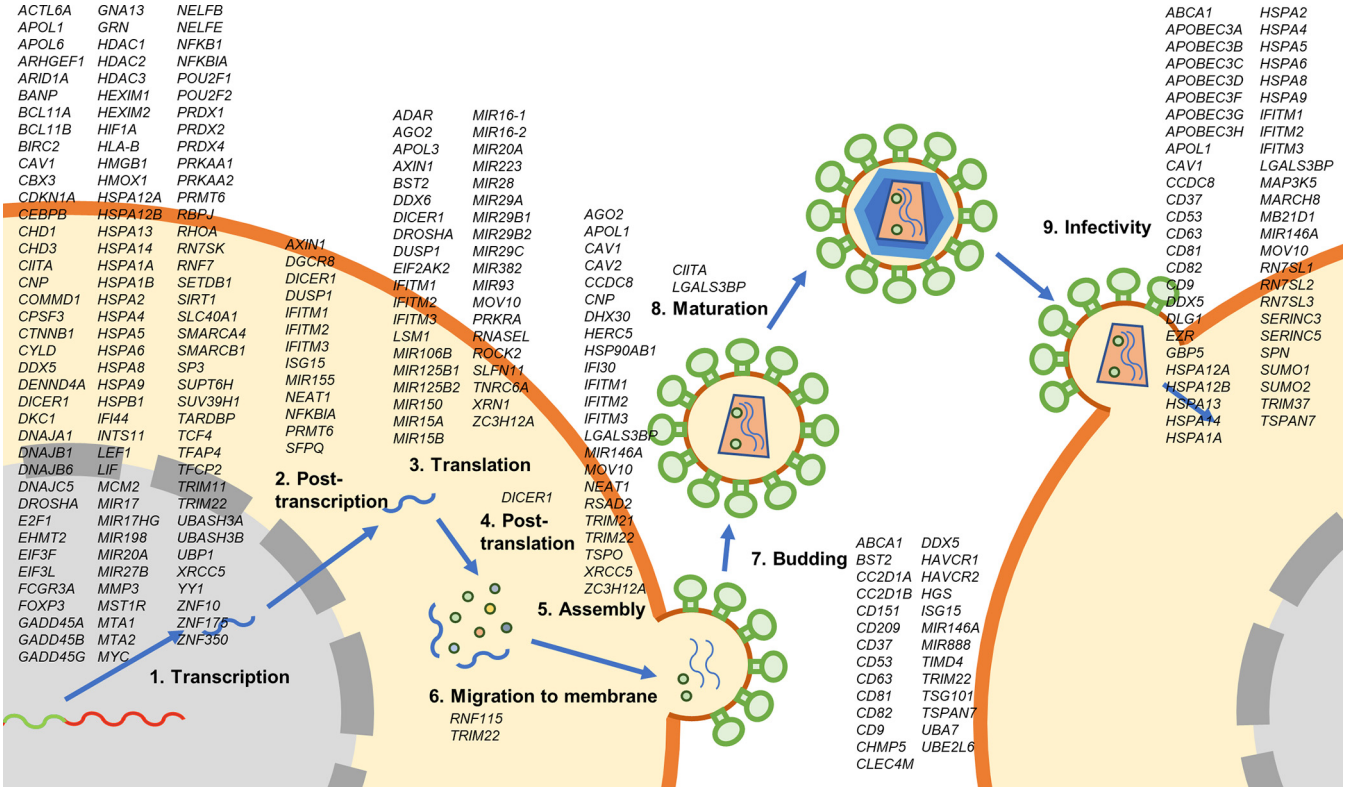

FIG 5 Candidate inhibitory factors and the step in the late phase of the HIV-1 life cycle in which they are inferred to act. The genes identified as candidate inhibitory factors in the literature search are indicated in the diagram near the step where they are presumed to be active in the late stages of the HIV-1 life cycle, as derived from the literature review. Steps depicted are transcription (step 1), posttranscription (step 2), translation (step 3), posttranslation (step 4), assembly (step 5), migration to the cell membrane (step 6), budding (step 7), maturation (step 8), and infectivity (step 9) of the produced virions. Genes lacking an identified step are not shown.

perceived relative "value" of the data presented in the papers. We decided that the data that were most likely to be informative were obtained from silencing or knockout studies (ranked 1); data from other experimental approaches were ranked as follows: overexpression studies (ranked 2), detection of virion incorporation of a gene product (ranked 3), active downregulation by the virus during cell culture studies (ranked 4), change in expression levels in HIV-infected patients (ranked 5), and any other evidence (ranked 6) (tabulated as screen types in Table S1). The reliability of the identification of a specific gene as a candidate inhibitory factor involved in HIV-1 inhibition could be further be evaluated based on the number of publications citing the gene, with more confidence being given to genes identified in multiple studies. For example, there were 101 publications that investigated the role of APOBEC3G (Table S1).

DISCUSSION

In this study, the literature was investigated to identify candidate inhibitory factors involved in the late phase of HIV-1 replication, the manipulation of which could potentially increase titers during lentiviral vector production. A total of 260 genes expressing potential inhibitory factors were identified and are shown in Fig. 5, alongside the respective step where they are thought to act in the viral life cycle. Approximately 38.1% of these candidate inhibitory factors (99/260) were identified in papers published since 2010, indicating that this is a dynamic field of research. The literature investigation conducted here was performed by using broad research terms, followed by a repeated-search strategy using the gene names in two additional databases to extend the findings. It was observed that some studies identified through these additional searches used only the term "human immunodeficiency virus" rather than the abbreviation "HIV" as used in the primary search, explaining why they were not originally identified.

Despite our attempts to expand the search space, it is reasonable to assume that some published studies and, hence, some candidate inhibitory factors may have been overlooked. Nevertheless, with >200 genes being implicated, this systematic search is more likely to be representative of a complex phenomenon such as the inhibition of viral infection than limiting discussion to the small number of restriction factors (APOBEC3G, BST2, SAMHD1, and SERINC3/5) (Fig. 2A) often cited in published reviews for the entire HIV-1 life cycle (52–57). This literature review therefore constitutes a first step to explore inhibitory factors exclusively in the late phase of HIV-1 replication.

Not all types of evidence identifying candidate inhibitory factors were deemed to be of equal value. Nearly half of these candidate genes (115/260; 44.2%) were identified in a single article and did not appear to have been validated in further studies. Furthermore, the techniques used to identify the genes varied considerably. Overexpression studies create an "artificial" expression profile that might never exist in a normal cell, while gene-targeted "knockdown" and "knockout" studies give results that are more representative of the effect of a gene. Knockdown and knockout techniques were used to identify more than half (161/260; 61.9%) of the genes found here. Only three studies induced a complete knockout of a gene, using clustered regularly interspaced short palindromic repeat (CRISPR)-Cas9 technology, but it is expected that many more studies using this technology will be reported in the future. Several studies used a combination of both knockdown and overexpression strategies to assess the effect of a gene on HIV-1 production. Other types of evidence for identifying candidate inhibitory factors were the following: the packaging of a protein into virions and increased or decreased levels either during infection or between infected patients and uninfected individuals. While these techniques might hint at a specific role for a particular gene in HIV-1 replication, they are not sufficient to confirm the effect. Fortunately, most genes identified by using these techniques were also identified in studies using RNA interference (RNAi)-mediated knockdown.

The number of factors identified in this review supports the complex nature of the virus-cell interaction in the context of HIV infection. Many of these factors could also be at play in the context of lentiviral vector production. Understanding the role of such factors and their impact on lentiviral vector production, either singly or in combination, might be beneficial for improving manufacturing yields.

SUPPLEMENTAL MATERIAL

Supplemental material for this article may be found at https://doi.org/10.1128/MMBR.00051-17.

SUPPLEMENTAL FILE 1, XLSX file, 0.1 MB.

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J.-F.G. performed the literature search. J.-F.G., D.R.G., and S.C.H. prepared and reviewed the manuscript.

J.-F.G., D.R.G., and S.C.H. are named inventors on patents and/or patent applications in the field of lentiviral vector design and manufacturing. Some patent claims relate to genes identified in this publication.

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