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College of Liberal Arts

INVESTIGATING INTRINSIC IMMUNE FUNCTIONS OF IFI16 AND IFIX

A Thesis in Biochemistry and Molecular Biology

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Abstract

Scientists have recently identified IFI16 as a Pattern Recognition Receptor (PRR) that senses foreign DNA. In this role, it plays an important part in the initiation of the innate immune response to many viral infections. Along with its innate immune function, IFI16 has been implicated in various other immune functions largely involved in intracellular defense from viral infection. These immune functions are categorized as intrinsic immune functions. A family member of IFI16, known as IFIX, has significant structural similarities to IFI16, and has also been identified as a PRR for foreign DNA. Unlike IFI16, however, the intrinsic immune functions of IFIX have not been as extensively explored. This study, therefore, aimed to explore in greater detail the similarities between IFI16 and IFIX in order to better explore the individual roles they play in immune response to viral infection. We started by performing a phylogenetic analysis on the primate orthologs of IFI16 and IFIX, through which we identified multiple duplication events that led to the emergence of two IFI-like PYHIN proteins in lemurs and simians, respectively. From there, we went on to explore a specific immune function of IFI16: the inhibition of the HIV-1 promoter, the Long Terminal Repeat (LTR). We correctly hypothesized that given the structural and functional similarities between IFI16 and IFIX, they would share in their inhibitory function of the LTR. We then went on to show that IFIX binds to APOBEC3A, a cytosine deaminase that also inhibits the LTR and had been shown previously to physically interact with IFI16. From these data we concluded that IFIX like IFI16 likely plays a role in intrinsic immune defense against HIV-1, and likely has other intrinsic immune functions as well.

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Abbreviations

5FMC: 5 Friends of Methylated Chromatin

AIDS: Acquired Immune Deficiency Syndrome

AIM2: Absent in Melanoma 2

ALR: AIM2-Like Receptors

AP-1: Activator Protein 1

APOBEC3: Apolipoprotein B mRNA Editing Enzyme Catalytic Polypeptide-like

BLASTn: Basic Local Alignment Search Tool (Nucleotide)

CD4+: Cluster of Differentiation 4 positive

cGAMP: cyclic Guanine Monophosphate-Adenosine Monophosphate

cGAS: cyclic Guanine Monophosphate-Adenosine Monophosphate synthase

CLR: C-type Lectin Receptor

DDT: Diothiothreotol

DMEM: Dulbecco's Modified Eagle's Medium

DNA: Deoxyribonucleic Acid

DNA-PK: DNA-Protein Kinase

(H)CMV: (Human) Cytomegalovirus

HEK293: Human Embryonic Kidney cell line 293

HIN-200: Heopoietic IFN-inducible nuclear proteins (200-amino acids)

HIV: Human Immunodeficiency Virus

HSV: Herpes simplexvirus

IFI16: Interferon gamma inducible protein 16

IFIX: Interferon gamma inducible protein X

IFN: Interferon

IL: Interleukin

IP: Immunoprecipitation

IRF: Interferon regulatory factor

ISG: Interferon stimulated gene

KAP1: KRAB-Associated Protein 1

kDa: Kilodaltons

LTR: Long Terminal Repeat

MNDA: Myeloid Nuclear Differentiation Antigen

NCBI: National Center for Biotechnology Information

NF-κB: Nuclear Factor kappa-light-chain-enhancer of activated B cells

NLR: Nod-Like Receptors

PAMP: Pathogen-Associated Molecular Pattern

PCR: Polymerase Chain Reactions

PMA: Phorbol Myristate Acetate

PRR: Pattern Recognition Receptor

PYHIN: Pyrin-and-HIN-200 containing protein

RL-TK: Renilla Luciferase controlled by TK promoter

RLR: RIG-I-Like Receptor

RNA: Ribonucleic Acid

RPM: Rotations per Minute

RPMI: Roswell Park Memorial Institute Medium

SAINT: Significance Analysis of Interactome

SDS-PAGE: Sodium Dodecylsulfate- Polyacrylamide Gel Electrophoresis

STING: Stimulator of Interferon Genes

TBST: Tris-Buffered Saline with Tween

TNF-α: Tumor Necrosis Factor alpha

WCL: Whole Cell Lysate

Introduction

One of the first rules of biology is structure is driven by function. This is apparent in all aspects of biology, from the organismal level down to the molecular. This rule is exemplified is in the human immune system, where a host of organs, cells, and molecules work together to protect the body from the environment. The outermost layer of immunity consists of barrier defenses (Marshall et al., 2018). These defenses – structures such as skin, mucosal linings, and stomach acidity – function to physically prevent pathogens from entering the body and infecting cells within it. If a pathogen can subvert those physical barriers, it faces a secondary set of defenses within the cell categorized as intrinsic immunity (Bieniasz, 2004). These defenses, a set of constitutively expressed enzymes, transcription factors, and other molecules, function as the first internal defense for a cell. They can act in immediate response to a pathogen, without having to change cellular expression characteristics or recruit external immune elements. Concurrent with the intrinsic immune response is the innate immune response, which relies on the recognition of broad classes of pathogens as different from the host, and the subsequent recruitment of cells and molecules which defend the body against them (Marshall *et al.*, 2018). These cells include phagocytes such as macrophages and neutrophils as well as granulocytes such as basophils and mast cells which release signaling molecules like histamine which drive inflammation. Barrier, intrinsic, and innate immunity are all similar in that the responses they mediate are not dependent on the pathogen that they are defending against, which allows them to respond quickly to threats.

The final and most specific layer of the immune system is adaptive immunity. This layer of the immune system is populated by millions of unique immune cells known

as lymphocytes, each of which express receptors that have the potential to bind to specific portions of individual pathogens. The two major categories of adaptive lymphocytes are B cells and T cells. B cells are responsible for the production of antibodies that bind specifically to pathogens can prevent them from continuing to infect the body through a variety of mechanisms, such as increasing their susceptibility to phagocytosis in a process known as opsonization or neutralizing them by preventing them from binding to host cells. T cells have a variety of jobs centered around purging the body of an infectious agent. CD8+ cytotoxic T cells, target and kill infected host cells, while CD4+ helper T cells recruit various innate immune cells (i.e., macrophages, neutrophils) to sites of infection. These hyper-specific cells function to formulate an immune response dependent on the characteristics of the individual pathogen. Adaptive and innate immunity are often directly contrasted. While innate immune defenses are generally faster-acting and remain the same each time a pathogen is encountered, the adaptive immune system acts more slowly, but through "memory cells" its response to the same pathogen improves with the number of times that pathogen is encountered.

Despite this seemingly rigid categorization of the immune system, all parts are interconnected and function as a whole to defend the body from pathogens (Marshall *et al.*, 2018). Within the barrier immune structures like skin and mucosa are innate and adaptive immune cells. As previously stated, intrinsic immunity exists in all cells at all times as a defense mechanism against infectious agents. More than just physical integration, however, the different layers of the immune system functionally interact with one another as well. The pathogens trapped by physical barriers or trafficked to lymph node hubs by blood and lymph are more easily sensed by innate immune cells, which go

on to not only defend the body but also signal for the activation of the adaptive immune system. If any one portion of the immune system were to be dysfunctional, it would go on to affect the overall quality of immune function.

The ability to act as a sentinel system and trigger the adaptive immune response is part of what makes innate immunity such an essential part of the immune system. It is dependent on innate immune cells being able to differentiate between "self" molecules, or those present in the human body and "non-self" molecules, or those that are foreign and most often found in various pathogens. These cells identify non-self molecules found in pathogens through the detection of shared molecular characteristics called pathogen-associated-molecular patterns (PAMPs) (Mogensen, 2009). These molecular patterns represent broad classes of molecules that are commonly found on pathogens, such as the peptidoglycans that compose bacterial cell walls, bacterial motor proteins such as flagellin, or viral nucleic acid. By being able to identify these commonly found structures, the innate immune system well equipped to rapidly respond to any foreign substance it encounters, as ideally all necessary cells would be able to identify pathogens based on their shared characteristics with one another.

The sensors that bind to these molecules are known as pattern recognition receptors (PRRs). The functionality of the innate immune system revolves around the ability of various PRRs to differentially target "non-self" molecules, those found in pathogens, from "self" molecules, which are present in one's own body. If the innate immune system were unable to make this distinction, it would be unable to selectively defend the body from a broad variety of harmful pathogens. At the same time, however, if the scope of the innate immune system were too narrow, there would be many

pathogens that went undetected, allowing them to evade the immune response and proliferate throughout the body at the expense of the host. There are five major classes of PRRs; the Toll-like receptors (TLRs) were the first to be discovered (Jang et al., 2015). Membrane-embedded TLRs are involved in bacterial and fungal PAMP sensing, while various cytoplasmic TLRs sense single- and double-stranded RNA and in some cases DNA, so long as it follows a specific molecular pattern of base pairs. The next class, known as NOD-like receptors (NLRs), are intracellular receptors that are involved with bacterial PAMP sensing. C-type lectin receptors (CLRs) are carbohydrate receptors that have the potential to sense a variety of pathogens based on their composition. RIG-like receptors (RLRs) are cytoplasmic receptors for viral RNA. Finally, AIM-2-like receptors (ALRs) are intracellular DNA sensors that share similar structural domains (Unterholzner et al., 2010). They are the most recently characterized class of PRRs and there is still much that is not known about their function in the broader scheme of immune defense, as there is evidence of them having functions outside of DNA sensing.

PRR signal transduction pathways utilize a variety of proteins that ultimately activate transcription factors to trigger expression of biological signaling proteins known as cytokines (Figure 1). Prominent signal transduction pathways of this nature usually activate certain transcription factors (i.e., NF-κB, AP-1, IRFs). These transcription factors target specific promoter sequences in DNA that, upon binding, allow transcription of genes for signaling molecules known as cytokines. Through autocrine or paracrine signaling, cytokines are responsible for inducing the immune response (Mogensen, 2009). One major role that cytokines play in the immune response is the initiation of the inflammatory response. All of the aforementioned transcription factors play a role in

initiating the inflammatory response by inducing the expression of specific cytokines, notably interleukins (IL) IL-1β and IL-6, interferon (IFN) and TNF-α (Chen et al., 2018). The diversity of PRRs allows the innate immune system to defend against a broad variety of pathogens, despite lacking the individualized specificity of the cells in the adaptive immune system.

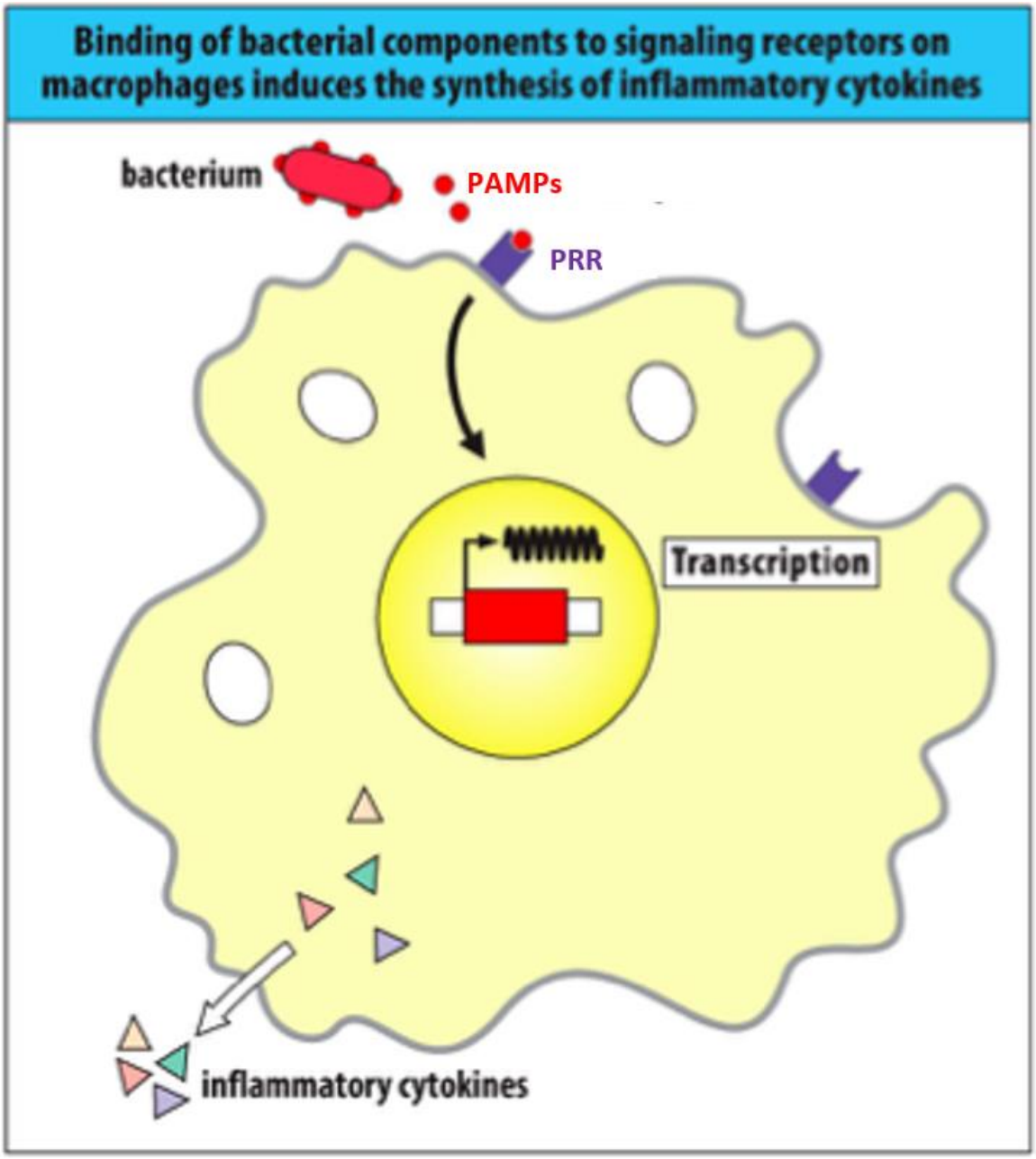


Figure 1: PRR Signal Transduction Pathway. The innate immune system relies on PRR sensing of PAMPs, which leads to subsequent activation of immune cell-signaling inflammatory cytokines.

The most recently described class of PRRs are the AIM2-Like receptors (ALRs). Because these protein have in their sequence one pyrin domain (N-terminus) and at least one HIN-200 domain (C-terminus), they are grouped into a protein family known as PYHIN proteins (Cridland et al., 2012). Pyrin domains are amino acid sequences that are known to be involved in protein-protein interactions. They are most notably found in proteins which comprise the inflammasome, or a wheel of caspases and other proteins which trigger events that result in pyroptosis, or the "explosive" death of the cell due to inflammation (Guo et al., 2015). HIN-200 domains, the other parts of PYHIN proteins, are unique because they are only found in PYHIN proteins, and PYHIN proteins are only found in mammals. This quality makes useful structures for analyzing the evolutionary development of PYHIN proteins and better characterizing individual proteins in the family as a whole. Literature identifies three broad categories of HIN-200 domains: HIN-200a, HIN-200b, and HIN-200c. All of the HIN-200 domains are canonically characterized as nonspecific DNA-binding domains found in PYHIN proteins (Shaw and Liu, 2014). There is evidence, however, that HIN-200 domain subtypes may have greater binding preference towards certain sequences or structures of DNA than others or may have roles outside of just DNA binding (Cridland *et al.*, 2012; Diner et al., 2015; Gray et al., 2016; Monroe et al., 2014; Unterholzner *et al.*, 2010). Evidence such as this illustrates that there is still more to learn about the function of these proteins, and conclusions made in previous literature may be affected by these presumptions.

The four human PYHIN proteins are Absent in Melanoma 2 (AIM2), Myeloid Nuclear Differentiation Antigen (MNDA), IFN-γ Inducible Protein 16 (IFI16), and IFN-γ Inducible Protein X (IFIX), also known as PYHIN1 (Diner *et al.*, 2015). AIM2 is unique

in that it is the only human PYHIN known to have a HIN-200c domain. IFI16, IFIX, and MNDA all have HIN-200a domains, however IFI16 also has HIN-200b domain on its C-terminus, making it the only human PYHIN protein to have 2 HIN-200 domains. This unique quality is also present in the mouse PYHIN protein p204 (encoded by the mouse gene *ifi204)* (Cridland *et al.*, 2012). These structural similarities lead researchers to often use p204 as the mouse analog of IFI16, however both phylogenetic and functional analyses indicate that the proteins play different roles in the two species (Burleigh et al., 2020; Cridland *et al.*, 2012; Unterholzner *et al.*, 2010). Phylogenetic analysis has indicated that PYHIN proteins are only present in mammals and marsupials, indicating a relatively recent emergence of these genes (Cridland *et al.*, 2012). In this same analysis, it is predicted that the common PYHIN ancestor underwent one duplication event which led to the emergence of two groups: AIM2 orthologs and IFI orthologs, and then several other duplication events occurred in different mammalian lineages that lead to the diversification of the more IFI-like PYHIN proteins. It is hypothesized that proteins with two HIN-200 domains such as IFI16 and p204 emerged in humans and mice lineages respectively occurred in more species-specific or evolutionarily localized events. It is also important to note that while humans have four PYHIN proteins, up to 13 unique PYHIN proteins have been identified in mice (Cridland *et al.*, 2012). This evidence suggests that there may be broader differences between human and mice when it comes to DNA-sensing immune pathways. Such was indicated when Burleigh and colleagues identified a DNA sensing pathway that was present in humans, but not in mice (Burleigh *et al.*, 2020). In sum, recent literature indicates that mice may not be an ideal model for IFI16-related immune pathways, which is important because many studies commonly cited in

reference to PYHIN proteins have used mouse cells as models for IFI16 function, or even used p204 as a complete functional ortholog of IFI16. Phylogenetic, structural, and functional data all suggest that this notion is false. All in all, this reemphasizes the idea that current literature surrounding IFI16 may contain incomplete or even incorrect conclusions about what it does or does not do.

PYHIN protein-mediated DNA sensing is especially important during viral infection. While AIM2, the first described PYHIN, induces the expression of IL-1β, both IFI16 and IFIX have both been shown to induce IFNβ expression (Diner *et al.*, 2015; Fernandes-Alnemri et al., 2009). IFNβ is a type I interferon (IFN-I) cytokine conventionally expressed during viral infection, and its signaling triggers the expression of *interferon stimulated genes* (ISGs) and induces various other transcriptional changes in cells that make them less susceptible to viral infection (Schneider et al., 2014). ISGs number in the hundreds and control a wide range of cellular processes (Schneider *et al.*, 2014). As a way of priming the immune system, a mainstay in the antiviral state is increased peptide fragment presentation through MHC expression, and increased PAMP sensing through increased PRR expression. ISGs also work to prevent viral infection in the cell at almost every possible point of viral infection, including viral entry, protein coat shedding, mRNA translation to protein or reverse transcription to DNA, DNA transcription to mRNA, post-translational degradation of the viral proteins, viral packaging and assembly, and viral budding. Because of viral utilization of host cell machinery, this predictably has deleterious impacts on host cell function, and along with viral replication host cells see a severe decrease in functionality due to dampened expression.

IFI16 has been shown previously to induce IFN-I through its interaction with the STimulator of INterferon Genes (STING) protein complex pathway (Unterholzner *et al.*, 2010) (Figure 2). Canonically, another DNA sensor, cyclic GMP/AMP synthase (cGAS), catalyzes the production of cyclic GMP/AMP (cGAMP). The effector protein STING, upon binding to cGAMP, then activates transcription factor IRF3, which induces expression of IFN-I (Unterholzner *et al.*, 2010). Although it has not been demonstrated how specifically IFI16 is involved in this pathway, evidence supports the theory that IFI16 may be involved in enhancing the speed and magnitude of the IFN-I response in macrophages, as the pyrin domain of IFI16 has been shown to interact with cGAS (Diner et al., 2016; Shannon et al., 2018). Gray and colleagues and Jønsson and colleagues provide evidence by showing that within 6 hours and 18 hours respectively, there was an attenuated, but not completely dissipated, IFN-I response to foreign viral DNA in the absence of IFI16 (Gray *et al.*, 2016; Jønsson et al., 2017). Moreover, although IFI16 was not required for immediate IFN-β expression, its absence led to an attenuated long-term IFN-β response (Hansen et al., 2014). Jønsson and colleagues also showed that there was direct binding between IFI16's pyrin domain and STING that promoted the dimerization and phosphorylation of STING through TANK-binding kinase 1 (TBK1), which led to the enhanced IFN-β expression. Based off of evidence such as this, it has been assumed that IFI16 solely plays a role in the initial portion of the cGAS-STING pathway as a secondary DNA sensor which amplifies the IFN response.

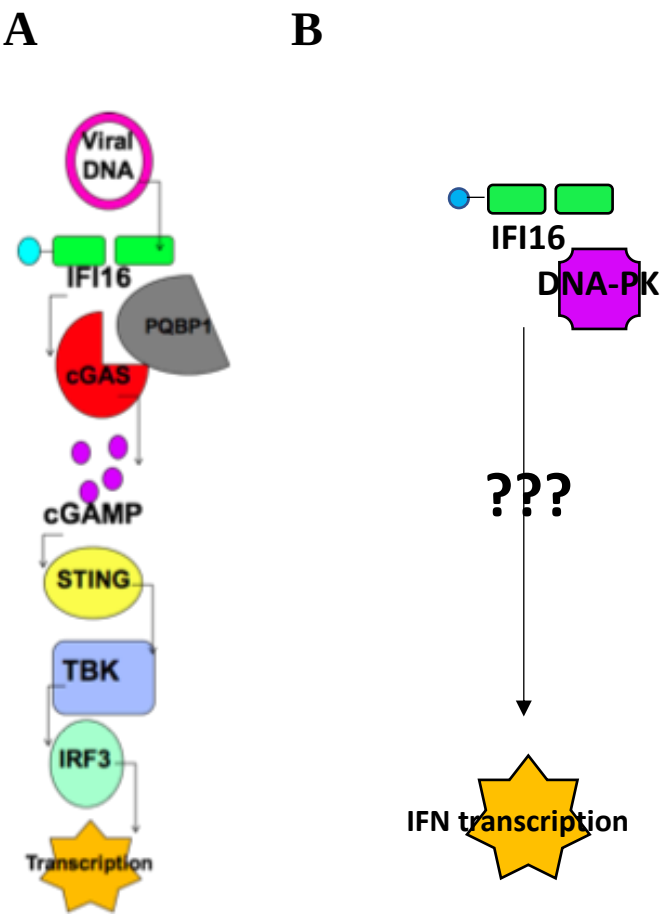


Figure 2: Role of IFI16. A) Canonical IFI16 pathway indicates IFI16 is an upstream sensor of DNA, however there is evidence both for and against this theory. B) Recent evidence suggests a STING-independent pathway involving DNA-PK and IFI16, which also triggers IFN transcription.

More recently, however, scientists have been investigating other possible roles IFI16 may play in the cGAS-STING pathway. Data showed that upon infection of HSV-1 or human cytomegalovirus (HCMV), cGAS localization was not dependent on IFI16 expression, but IFI16 knockdown alone led to a decreased interferon response (Diner *et al.*, 2016). This led researchers to hypothesize that IFI16 was acting downstream of STING activation, because if the role of cGAS in the pathway was not changed based on expression of IFI16, but there was still an attenuated response, it implies that the role of IFI16 is somewhere else in the pathway. Separately, researchers have recently theorized a new, STING-independent IFN activation pathway involving DNA-dependent protein kinase (DNA-PK), a DNA damage protein triggered by, among other molecules, foreign DNA (Burleigh *et al.*, 2020). Previous lab work by Uma Kantheti has shown DNA-PK's physical association with IFI16 and correlated a knockout of IFI16 to an attenuated DNA damage response (Kantheti 2019). This novel pathway may involve IFI16 either as a PRR or a downstream activator (Figure 2). The role of IFI16 as more than just an upstream DNA sensor is one that is being increasingly explored in recent literature.

Despite the structural similarity between IFI16 and IFIX, far less investigation has been done into the specificities of IFIX's DNA sensing pathway. In 2015, Diner and colleagues published data suggesting that IFIX's HIN-200a domain binds to dsDNA in a sequence independent manner similar to that of IFI16 (Diner *et al.*, 2015). It also showed that in HEK293 cells, an interferon response was dependent on the expression of IFIX, thereby establishing IFIX as an innate immune sensor of DNA. Elucidating similarities and differences in the mechanism of these PYHINs' DNA sensing would provide important clues about areas of structural importance in their amino acid sequences.

Chronic IFN-I expression is hypothesized to contribute to disease states triggered by viral infection. In 2017, Cheng and colleagues demonstrated that while IFN-I responses were beneficial for curbing the replication of HIV-1 in already infected individuals, chronic interferon signaling led to the depletion of host T cells, causing immune dysfunction that characterizes the progression of HIV infection to Acquired ImmunoDeficiency Syndrome (AIDS) (Cheng et al., 2017). Evidence also shows increased IFN-I expression in autoimmune diseases such as Lupus (Lambers et al., 2019). The pathogenesis that results in this overactivity of the immune system may be related to upstream activators of IFN expression, such as IFI16 and IFIX. In fact, a study done in 2014 indicated that IFI16 was necessary for the cell-controlled death of CD4+ T cells infected with HIV, and that the presence of IFI16 was correlated with an increased type-I interferon response (Monroe *et al.*, 2014). The same study attempted to identify whether IFIX played a similar role in the death signaling of the CD4+ T cells; however, because IFIX was not sufficiently knocked down in the cells, the data did not have statistical significance, making the results inconclusive.

The connection of PYHIN proteins to both IFN-I expression and possible viral disease-associated effects is interesting when the evolutionary history of the protein is once again considered. Bats do not express PYHIN proteins, despite them being expressed in every other mammalian species, and some marsupials (Ahn et al., 2016). When it comes to viral infection, bats are unique because they can host a large number of viral infections seemingly without a major impact to their health or lifespan. Scientists have hypothesized that this is because bats have an extremely regulated inflammatory response, which prevents them from being harmed by an overactive immune system. The

absence of PYHIN genes despite the presence of other DNA sensors (i.e. cGAS) contributes to this theory because PYHIN proteins are the DNA sensors that trigger the inflammatory response (Ahn *et al.*, 2016).

Outside of their DNA-sensing capabilities, there are other described functions of PYHIN proteins that make them an even more interesting target of study. AIM2, IFI16, and IFIX have all shown antitumor activity through binding interactions with p53, the most well-studied tumor suppressor protein, which is central to preventing transformation of healthy cells to cancerous cells (Ding et al., 2004; Kondo et al., 2012). IFI16 was initially characterized as a transcriptional regulator and was shown to be involved in the DNA damage repair pathway (Yan et al., 2008). MNDA has been implicated in myeloid cell differentiation as well as neutrophil apoptotic pathways (Fotouhi-Ardakani et al., 2010). These functions, all of which revolve around the control of the cell cycle and replication, imply that PYHIN proteins' function may rely on their ability to bind not just foreign but also host DNA, which is central to the above processes.

IFI16 and IFIX have also been implicated in a wide range of other antiviral functions. These intrinsic immune functions are varied and often are unique responses to particular viruses. IFI16 has been shown to restrict transcription of both host and viral DNA. IFI16 restricts transcription of HIV through binding of the transcription factor Sp-1, preventing its association with the HIV promoter region (Hotter et al., 2019). IFI16 was also shown to restrict the transcription of HSV-1; however, it did so through a different mechanism: epigenetic silencing (Johnson et al., 2014). Unlike freshly replicated viral DNA, host DNA exists in the cell in the form of chromatin, a complex of DNA strands tightly wrapped around histone octamer proteins in a continuous linkage of

structures called nucleosomes (Johnson *et al.*, 2014). These nucleosomes are also surrounded by various proteins involved in protecting, stabilizing, and transcribing the DNA as part of general cellular functions. The level of compaction of DNA around histones determines the rate of expression of nearby genes by manipulating the access of transcriptional proteins to the DNA: the more tightly wound DNA is less accessible for proteins. Histones are modified to regulate how tightly they wrap DNA; histone methylation is a common form of transcriptional repression, while acetylation is a form of activation (Johnson *et al.*, 2014). When HSV-1's genome enters the nucleus, it is also incorporated into histones, and Johnson and colleagues showed that IFI16 was part of the process to recruit histone methylation enzymes, and similar to HIV also prevented the binding of transcription factors necessary for transcription of the viral genome (Johnson *et al.*, 2014). IFIX has also been shown to be a transcriptional repressor (Diner *et al.*, 2015). A closer look at the functional interactome of IFIX confirmed that its involvement in transcriptional repression is through the recruitment of epigenetic silencers, such as the five friends of methylated chromatin (5FMC) complex (Crow and Cristea, 2017). In fact, one component of the 5FMC complex was shown to block Sp-1 transcription factor binding, providing yet another connection to IFI16 (Diner *et al.*, 2015). As further proof of IFIX's antiviral function, and its similarity to IFI16, both HCMV and HSV-1 have been shown to target IFIX for degradation through interactions with the same proteins as with IFI16 (Cristea et al., 2010; Crow and Cristea, 2017; Diner *et al.*, 2015).

Despite their many similarities, however, there are still differences in the generally accepted functions of IFI16 and IFIX. While IFI16 knockdown was sufficient in rescuing CD4+ T cells from cell death post-HIV infection, the same could not be said

for IFIX knockdowns (although as previously stated the knockdowns were incomplete at best) (Monroe *et al.*, 2014). Evidence suggests that IFIX IFN-β activity is independent from the STING-cGAS pathway, as overexpression of IFIX with cGAS in human embryonic kidney (HEK293) cells did not lead to a heightened IFN-β response, while it did in THP-1 cells (Diner *et al.*, 2015; Jønsson *et al.*, 2017). Research also implies that the HIN-200A domain of IFIX has different affinity to dsDNA than those of IFI16; however, specific comparisons of the HIN-200a domain of IFI16 and IFIX were not done (Gray *et al.*, 2016). Nevertheless, further research into the shared and unique functions of IFI16 and IFIX may prove useful in the understanding of both PYHINs' antiviral function.

A functional list of IFI16's binding partners during HSV-1 infection was created using Significance Analysis of INTeractome (SAINT) software (Diner *et al.*, 2016). This interactome distinguished between proteins that bound more significantly to the pyrin domain from those that bound to either of IFI16's two HIN-200 domains. It implicated a family of proteins in interacting with the pyrin domain of IFI16: the APOBEC3 proteins (Diner *et al.*, 2016). The cells used to generate the interactome were human foreskin fibroblasts (HFFs), through which researchers showed the interaction of IFI16 and APOBEC3C upon HSV-1 infection. The APOBEC3 proteins are cytidine deaminases, enzymes that catalyze the conversion of cytidine nitrogenous bases in nucleic acid to uracil (Stenglein et al., 2010). The APOBEC proteins promote the clearance of viral DNA specifically in HIV-1 through this conversion, indicating a shared viral target between this family of proteins and IFI16 (Bieniasz, 2004). One of the APOBEC3 proteins in particular, APOBEC3A, has been shown to be selectively expressed in

myeloid immune cells such as macrophages, monocytes, and neutrophils (Stenglein *et al.*, 2010). Because this protein is in the same family as the one in the screen, and it is expressed in the same cells where IFI16 is expressed in large quantities, it is not unrealistic to predict the two may in some way work together to defend against HIV-1 infections. It was found that APOBEC3A was involved in the selective clearance of foreign DNA through recognition and mutation, and APOBEC3A's expression was induced by IFN signaling (Stenglein *et al.*, 2010). Independent of this cytidine deaminase activity, APOBEC3A was shown to silence HIV expression (Taura et al., 2019). The proposed mechanism behind APOBEC3A's HIV silencing was through binding to the same region of the HIV promoter sequence (LTR) that would usually be bound by Sp-1 and recruiting the epigenetic silencer KAP1 (Taura *et al.*, 2019). This evidence illustrated an even greater probability that APOBEC3A and IFI16 work in conjunction with one another, as promoter sequence for the same transcription factor which is bound and inhibited by IFI16 was now shown to be silenced by APOBEC3A. Our lab hypothesized physical interaction between IFI16 and APOBEC3A. We predicted that the reason this interaction was not observed in the SAINT screen was because APOBEC3A is not expressed in HFFs. Previous evidence from out lab supported this hypothesis (Potts 2020). Continued exploration may yet determine more specifics concerning a mechanism by which they interact and allow for greater understanding of HIV silencing mechanisms.

Project Overview

This project aims to investigate if IFI16 and IFIX function similarly, or even in cooperation with APOBEC3A. Literature currently characterizes these PYHIN proteins as DNA sensors of the innate immune system, however a wealth of novel data now show

that there may be many non-canonical intrinsic immune functions that they play a role in. Describing the role of IFI16 and IFIX as it relates to these experiments therefore would provide further evidence for the intrinsic immune function. Moreover, if IFI16 and IFIX are found to have a shared function, it would provide evidence for which functional domain is responsible for the function, allowing further, more specific experiments to be done to better characterize the molecular mechanisms of action for these proteins.

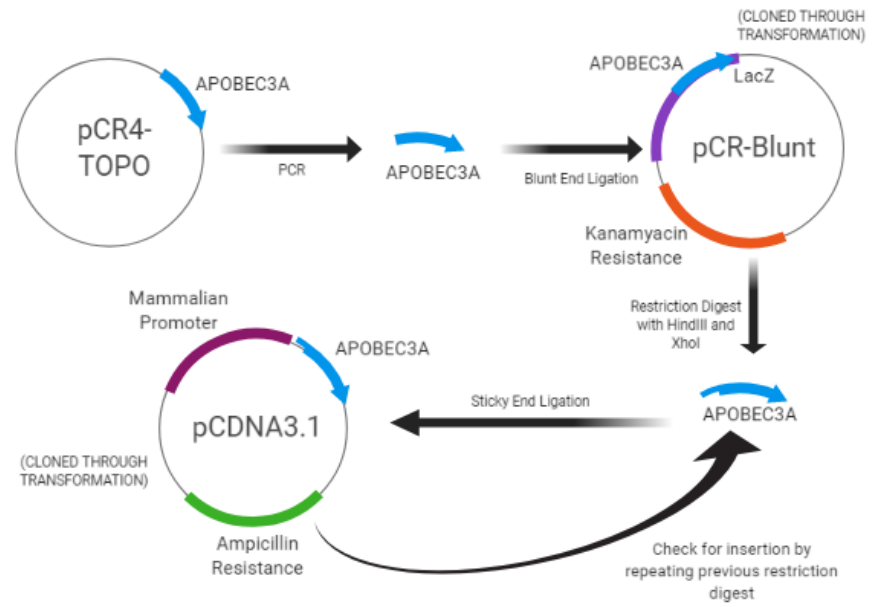
First, phylogenetic analysis was done on PYHIN proteins present in primate genomes in order to clarify exactly when the duplication event leading to the existence of both IFI16 and IFIX occurred, as doing so would provide better context for the types of selective pressures that could have driven both proteins to be retained by our ancestors. Following this, dual luciferase assay experiments were done to observe whether the repressive effect of APOBEC3A specifically on the LTR promoter sequence was mimicked by IFI16 *and* IFIX. Finally, as a follow-up to the protein-protein interaction experiment done previously with IFI16 and APOBEC3A, the physical interaction was probed between IFIX and APOBEC3A.

Methods

Cloning

The *APOBEC3A* and *IFIX* genes had to be inserted and cloned in plasmids with mammalian promoters in order to be expressible in HEK293 cells. *APOBEC3A* in the pCR4-TOPO vector was purchased from DharmaCon, and the gene was isolated from the plasmid through PCR. The forward primer was ATGGAAGCCAGCCCAG, and the reverse prier was GTTTCCCTGATTCTGGAGAATGG. PCR was done using 1X Q5 reaction buffer, 200 μM of dNTPs, 0.5 μM forward primer, μM reverse primer, 0.02

U/uL of Q5 High-Fidelity DNA Polymerase, and 5 ng plasmid DNA template. The reaction was performed in the thermocycler for an initial denaturation cycle of 98ºC for 30 seconds, then 40 cycles of the following: 98ºC denaturation for 10 seconds, 66ºC annealing for 30 seconds, and 72ºC extension for 15 seconds. A final extension was done at 72ºC for two minutes. The PCR product was then ligated to the pCR-Blunt vector through blunt end ligation, and the resulting plasmid was then used to transform *E. coli* (selective marker was Kanamycin resistance) in order to amplify the DNA. The DNA from the bacteria was purified through mini-prep, and the plasmid was cut with endonucleases XhoI and HindIII to isolate *APOBEC3A*, as was the plasmid vector pcDNA3.1, which, after ligation, created an *APOBEC3A* plasmid with the gene controlled by the CMV mammalian promoter present in pcDNA3.1. That plasmid was then amplified through transformation of *E. coli* (Figure 3). *IFIX* was also purchased from DharmaCon originally in a plasmid vector without a mammalian promoter. It was isolated from that plasmid through restriction digest with XhoI and BamHI endonucleases and ligated directly into the pcDNA3.1 plasmid. Successful ligation was checked through restriction digest with XhoI and BamHI (Figure 3).



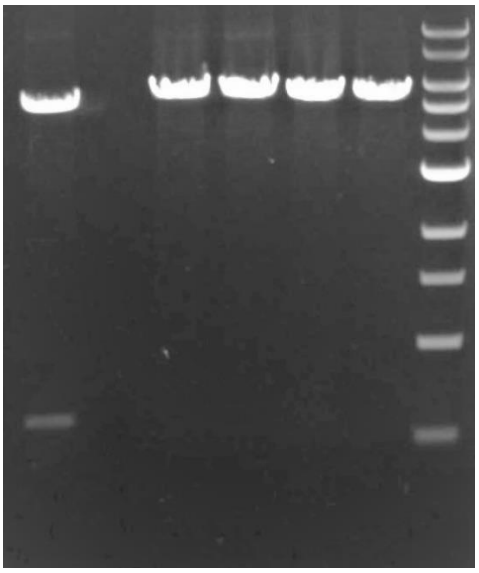


Figure 3: *APOBEC3A* Cloning A) Process of transferring *APOBEC3A* gene from original plasmid to plasmid with mammalian promoter sequence. B) Agarose gel electrophoresis confirmation of *APOBEC3A* insertion. Relevant lanes: Lane 1: Double digest of *APOBEC3A* plasmid with HindIII and XhoI restriction enzymes (3kb+600b), Lane 3: Plasmid digest with HindIII (3.6kb), Lane 4: Plasmid digest with XhoI (3.6kb), Lane 5: Undigested plasmid (3.6kb), Lane 7: NEB 1kb Ladder

Phylogenetics

Phylogenetic analyses were done as a way to investigate the evolutionary history of the *IFI16* and *IFIX* genes in primates. Previous studies had hypothesized that the two separate genes were encoded in the genome as a result of a duplication event in primates that conferred an evolutionary advantage, therefore investigating the evolutionary history of these sequences within primate genomes was a possible way to detect where the duplication event occurred (Cridland *et al.,* 2012). It would also help determine if the duplication events could have occurred multiple times as an example of convergent evolution, which could provide more evidence that IFI16 and IFIX both provided evolutionary advantages.

All primate PYHIN sequences were gathered through a BLASTn search of the human *IFI16* or *IFIX* cDNA sequence query. BLASTn queries nucleotide sequences and results display similar sequences, in this case those that showed homology to IFI16 and IFIX cDNA sequences in primates. From there, at least one sequence was gathered for each gene listed in the primate taxonomy and compiled into a FASTA file. Sequences were aligned using MEGA-X software CLUSTAL multiple sequence alignment algorithms. The gap opening penalty was 8, and the gap extension penalty was 0.2 (Kumar et al., 2018). Through automated color coding of amino acid residues based on electrochemical properties (charge/polarity, aromaticity, etc.) a visual overview of the sequence alignment indicated that the alignment was sound enough to continue to construction of phylogenetic trees. Phylogenetic trees are created through the computerized analysis of sequence alignments in order to reconstruct the most likely evolutionary history of the sequences. Maximum likelihood trees were constructed using

MEGA-X software using a bootstrap method with a gamma distributed change rate among sites, and four discrete gamma categories (Tamura et al., 2011). Maximum likelihood trees are constructed by using a mathematical model, in this case the Tamura-Nei model, to analyze different possible evolutionary progressions and choose the most likely one (Tamura and Nei, 1993). The Tamura-Nei model was utilized because of its accounting of factors which affect variation of substitution rates, and its known success in analyzing data specific for humans and chimpanzees. The bootstrap method was used to estimate probability as a measure of the number of times the specific branching event occurred out 100 unique constructions of phylogenetic trees, and a bootstrap number greater than or equal to 70 is considered statistically significant. The gamma distribution change rate is considered the standard probability distribution curve for maximum likelihood phylogenetic trees, and the four distinct gamma categories was the default set by the software to account for specific residues that are conserved throughout the evolutionary process (Tamura *et al.*, 2011).

Luciferase Assays

The purpose of the luciferase assays was to determine the effect of transfected *APOBEC3A*, *IFIX*, and *IFI16* on HIV-LTR promoter activity in HEK293 cells. HEK293 cells were cultured in D10 medium (DMEM media (Invitrogen), 10% fetal bovine serum (Invitrogen), 0.1% β-mercaptoethanol (Invitrogen), 1% non-essential amino acids (NEAA) (Invitrogen),0.1 Normocin^{TM} (Invitrogen), 1% penicillin-streptomycin-glutamine (Invitrogen), 1% Sodium Pyruvate (Invitrogen)).). The HEK293 cell line was established from human embryonic kidney epithelial cells and is commonly used for molecular biology experiments because they are very receptive to transfection, and are

easy to maintain in large quantities (Thomas and Smart, 2005). HEK293 cells were plated with $1.0*10^6$ cells in 1.0 mL per well in 24 well plates.

To perform transfection, Lipofectamine-2000 (Invitrogen) was incubated with Opti-MEM media (Invitrogen) at a 1:24 concentration in order for it to construct the lipid nanoparticles (Figure 4). The desired amount of DNA, diluted in Opti-MEM , was then mixed with the Lipofectamine-Opti-MEM mixture, and then dispensed over the cells in quantities of 200 μL per well. All cells were transfected with 10 ng RL-TK *Renilla* luciferase plasmid DNA and 100 ng HIV-LTR-Luc firefly luciferase with HIV-LTR promoter. RL-TK, or *Renilla* luciferase under the TK promoter, serves as a control for dual luciferase assays where luciferase will be expressed in a way that should be unaffected by the expression of added genes. HIV-LTR-Luc, or firefly luciferase with the HIV-LTR promoter, serves as the experimental plasmid, as HIV-LTR activity and thus luciferase expression is hypothesized to be affected by expression of added genes. Cells were transfected in triplicate with lipofectamine only as a negative control, or 50, 100, or 200 ng of plasmid DNA containing mammalian promoters driving expression of *IFI16*, *IFIX*, or *APOBEC3A*. Not including reporter plasmids, total transfected plasmid DNA always equaled 200 ng DNA and will be balanced by addition of *LacZ* expression plasmid. Because IFIX and IFI16 are both DNA sensors, it is important that the amount of DNA put into the cells is standardized to ensure any differences in data are not due to the presence of excess plasmid DNA. Plasmid DNA will be diluted in Opti-MEM and mixed with Lipofectamine 2000 diluted 1:24 in Opti-MEM. Cell cultures will then be dosed in the following concentrations in triplicate:

Negative control: Just Lipofectamine 2000

Positive control: 50, 100, 200 ng LacZ + 100 ng HIV-LTR-Luc, 10 ng RL-TK

IFIX: 500, 1000, 2000 ng + 100 ng HIV-LTR-Luc, 10 ng RL-TK

IFI16: 500, 1000, 2000 ng + 100 ng HIV-LTR-Luc, 10 ng RL-TK

APOBEC3A: 50, 100, 200 ng + 100 ng HIV-LTR-Luc, 10 ng RL-TK

The purpose of the negative control is to measure any background luciferase that is not a result of gene transfection. The purpose of the positive control is to provide a baseline value for the how much firefly and *Renilla* luciferase activity is recorded in the absence of added expressed genes without the proposed repression.

Using Promega^{TM} Dual Luciferase assay kit protocol (#E1910), cells were lysed and total firefly luciferase and *Renilla* luciferase activity will be assayed by introducing firefly luciferase substrate then *Renilla* beetle luciferase substrate to the cell lysate. The relative luminescence from each enzyme's activity was read on a Promega GloMax 20/20 luminometer. The ratio of the two will be calculated to represent the activity of the HIV-LTR. Greater firefly luciferase activity (alone or compared to *Renilla* luciferase activity) will be indicative of greater HIV-LTR promoter activity because it shows that more firefly luciferase was expressed. The experiments were all completed in triplicate, and average relative luminescence units were graphed. Significance was analyzed using a one-way ANOVA test, with post-hoc Tukey's pairwise comparisons being done on each possible pairing.

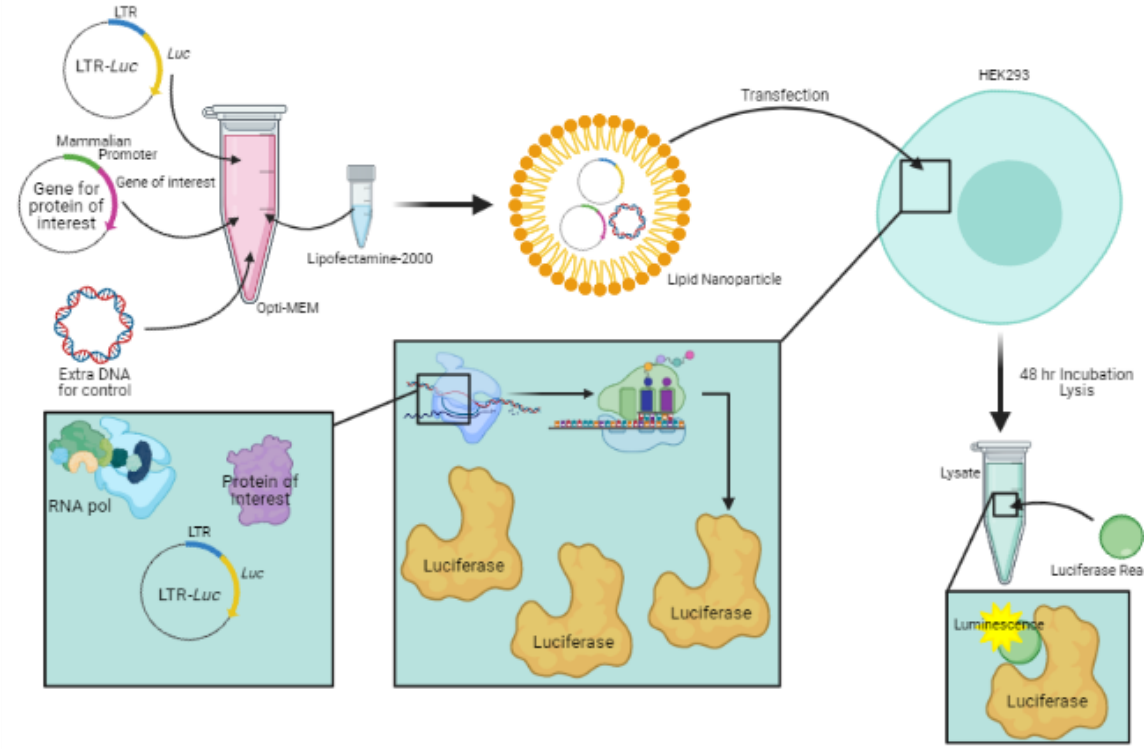


Figure 4: Luciferase Assay. The plasmid DNA was put into cells through transfection and incubated for 48 hours. Measurement of luminescence following exposure of cell lysate to luciferase reagent quantified relative expression of luciferase protein, which was controlled by the HIV-LTR.

Western Blots/IP

Western blots were done in order to observe physical interaction between IFIX and APOBEC3A. Previous data produced by Thomas Potts showed that IFI16 and APOBEC3A interact, therefore such an interaction between IFIX and APOBEC3A would further evidence the functional similarity between the two PYHIN proteins.

THP-1 cells were cultured in R10 medium (RPMI media (Invitrogen), 10% fetal bovine serum (Invitrogen), 0.1% β-mercaptoethanol (Invitrogen), 1% non-essential amino acids (NEAA) (Invitrogen),0.1 Normocin^{TM} (Invitrogen), 1% penicillin-streptomycin-glutamine (Invitrogen), 1% Sodium Pyruvate (Invitrogen)). The THP cell line is a model cell line for human monocytes, and can be stimulated to differentiate into model macrophages (Bosshart and Heinzelmann, 2016). Because IFIX is shown to be differentially expressed in macrophages, observing its activity in these model cells will allow for exploration into differential binding and expression activity in response to different stimuli. Of the six wells, five were dosed with PMA at a concentration of 5 ng/mL for 72 hours (Shannon *et al.*, 2018) (Figure 5). This stimulation catalyzed the maturation of THP-1 cells from monocyte to macrophage. One PMA-treated well was then transfected with empty Lipofectamine-2000 lipid particles as a control to observe possible effects of the transfection agent on protein interaction. Another PMA-treated well was stimulated with Poly I:C RNA. Because IFIX is not expected to respond to foreign RNA, this serves as a control for nucleic acid stimulation (Diner *et al.*, 2015). Two of the other PMA treated wells were stimulated with Vaccinia virus 70mer DNA, and interferon-stimulating DNA, both of which would serve as experimental conditions as IFIX is expected to respond nonspecifically to foreign DNA (Diner *et al.*, 2015).

Around 24 hours after stimulation, cells were lysed with NP-40 lysis buffer that had been mixed with a protease inhibitor and 750 units/mL Micrococcal Nuclease in order to prevent the immunoprecipitation from pulling down proteins connected by DNA as opposed to direct protein-protein binding. The lysis occurred for one hour at 4ºC. Each set of cells was lysed with 250 μL of solution, and 50 μL were separated to be used as "whole cell lysate" for the rest of the experiment. The rest of the cell lysate was then mixed with 20 μL Protein G and Protein A agarose beads and were agitated for one hour at 4ºC in order to bind any non-specific proteins. The solutions were then centrifuged at 4ºC for one minute at 14,000 RPM, and the supernatants were separated, and agitated overnight at 4ºC with 8.5 μL of anti-IFIX antibody Sigma HPA051224. Agarose beads (20 μL) were then added to the supernatant-antibody solution in order to bind to the anti-IFIX antibodies and were agitated at 4ºC for one hour. After centrifuging the solutions for 1 minute at 14,000 RPM and 4ºC, the supernatant was removed, and the beads were washed with 500 μL of lysis buffer for 5 minutes before being centrifuged as previously described. After 3 washes, the supernatant was removed and the immunoprecipitated beads and proteins (IP) were stored at -20ºC.

Protein samples (both from the IP and whole cell lysate (WCL)) were linearized and run onto a gel using sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE). SDS-PAGE allows proteins to be separated by sizes, which makes it easier to identify target proteins based on size once they are targeted by antibodies in a process known as western blotting. After the proteins have been run onto a gel, they are transferred to a nitrocellulose membrane and targeted by an antibody specific to a portion of their sequence, which is called a primary antibody. After allowing the primary

antibody to bind to the target protein, the secondary antibody then binds to the constant portion of the primary and triggers a luminescence reaction which can then be visualized.

The protein samples, 30 μL of WCL or IP, were mixed with 10 μL of Diothiothreotol (DDT) loading buffer and 4X Lammeli loading dye, which after boiling at 95ºC for 5 minutes allowed the protein samples to remain linearized and retain a negative charge so that they can be run through the SDS-PAGE. After consolidating the mixtures by centrifuging for 30 seconds at 14,000 RPM, the samples were loaded into wells of a 4-20% polyacrylamide gel (Bio Rad) and run with Tris-Glycine-SDS running buffer at 120 V. Broad Spectra Protein Ladder (10 μL) was also loaded into one well of each gel run in order to be able to approximate band sizes. Once the dye front reached the bottom of the gel, the gels were removed, and proteins were transferred to nitrocellulose membranes through iBlot. In order to prevent nonspecific binding of the antibody, membranes were rocked at room temperature for 30 minutes with a blocking solution of 5% (grams/mL) milk powder in Tris-Buffered-Saline w/ Tween (TBST). Membranes were then treated with 1:1,000 primary antibody anti-APOBEC3A Sigma HPA043237 to blocking solution overnight at 4ºC. After three washes in TBST for 5 minutes each, membranes were then treated with 1:10,000 secondary antibody Goat anti-Rabbit Antibody Santa Cruz sc-2030 to blocking solution for one hour at 4ºC and washed three more times. Membranes were developed using the procedures and reagents from the SuperSignal™ West Dura Kit (Thermo Scientific), then imaged using an Amersham Imager 600 at default chemiluminescence settings.

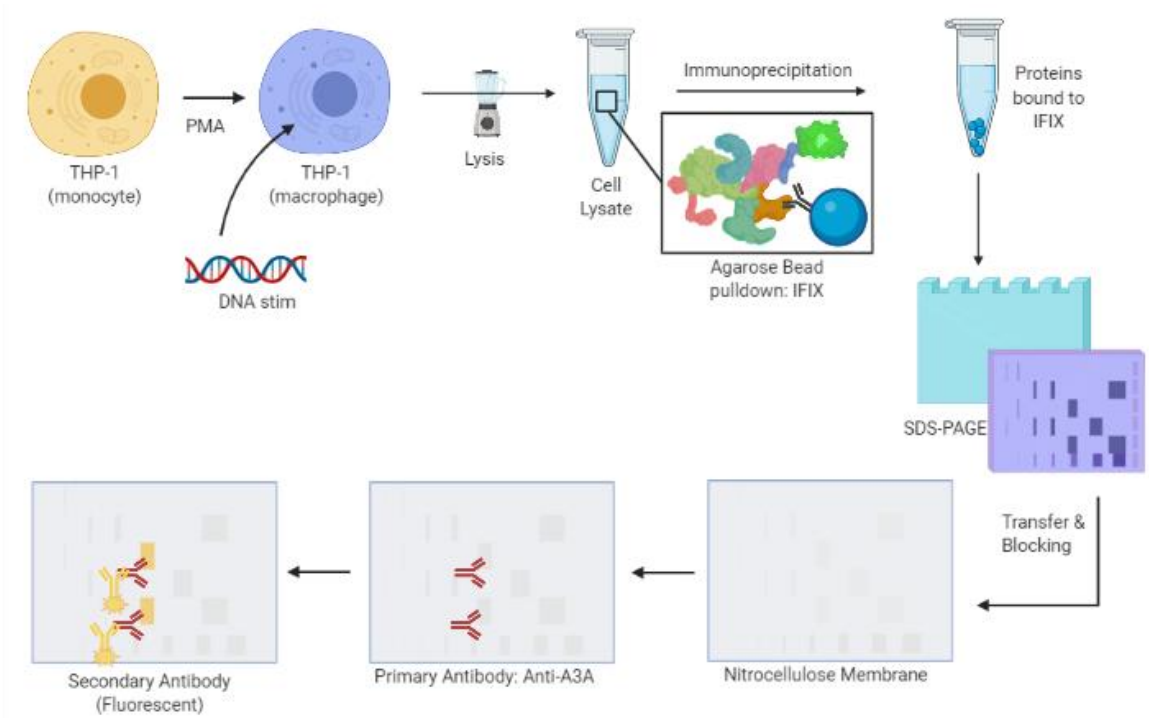


Figure 5: Immunoprecipitation/Immunoblot. IFIX and proteins interacting with it were isolated from THP-1 cell lysate through immunoprecipitation. Proteins were run on a gel through SDS-PAGE, and APOBEC3A was imaged using immunoblotting.

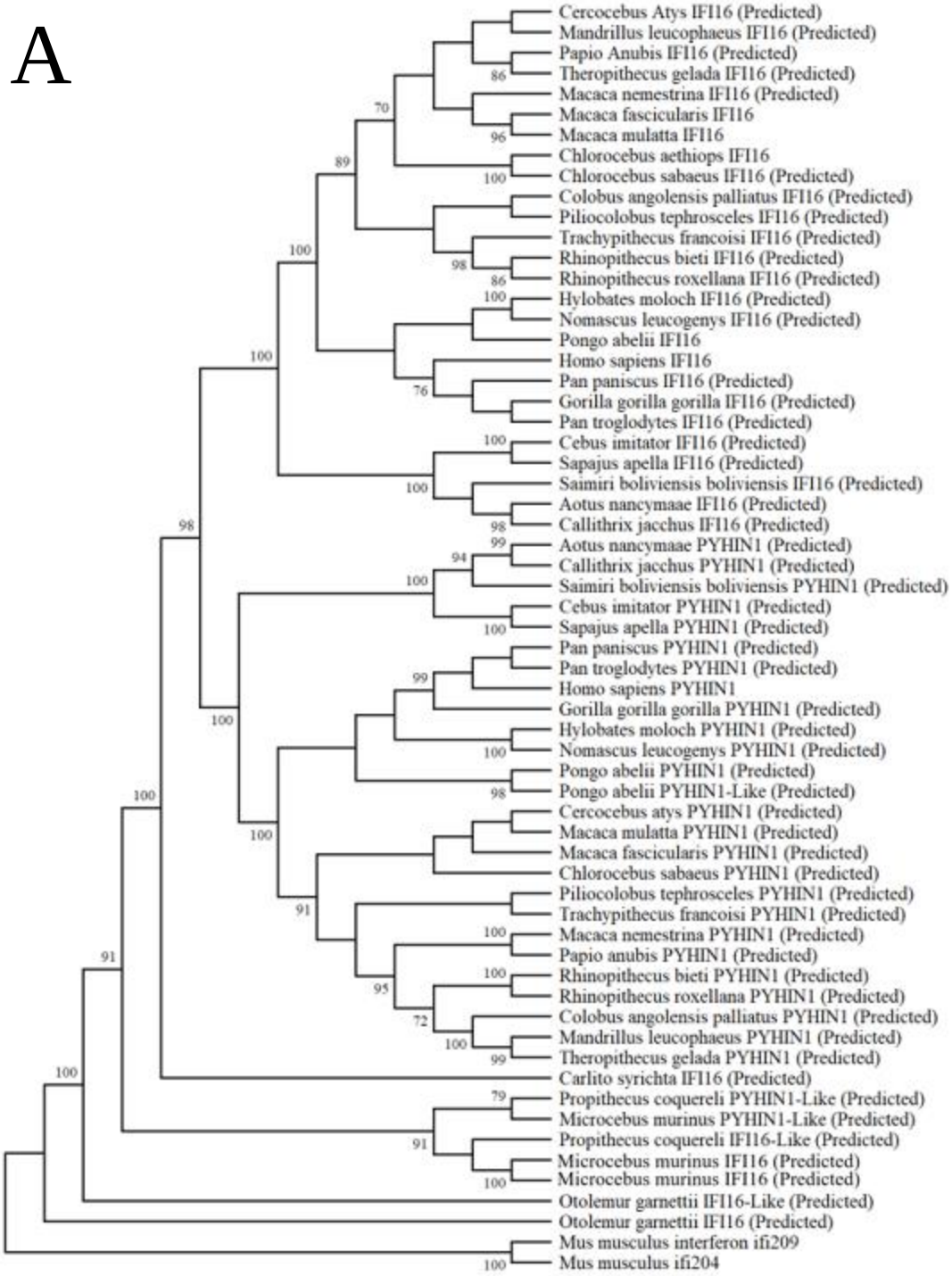
Results

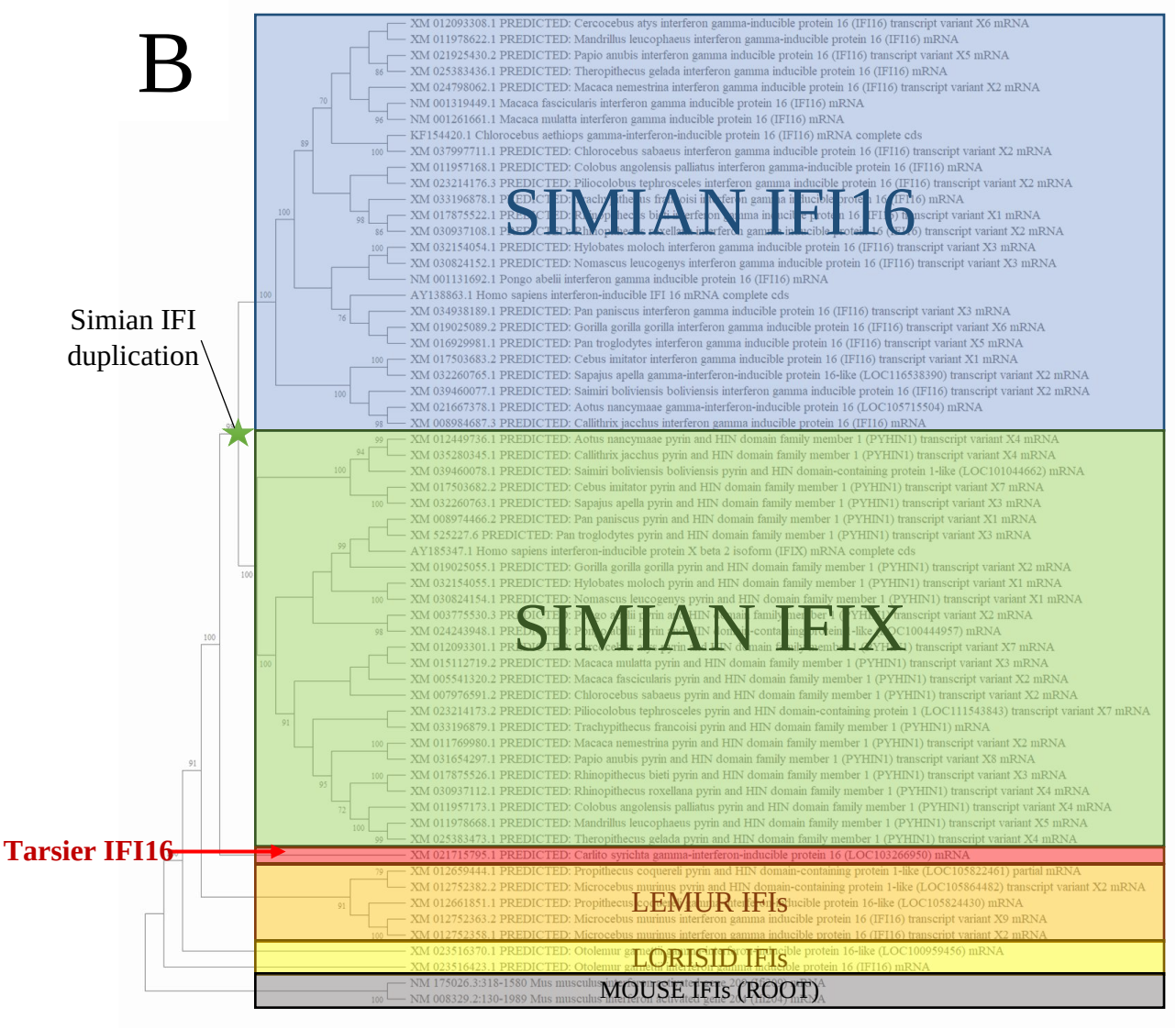
Phylogenetics

Before functional assays were to be done assessing similarities between IFI16 and IFIX proteins, we wanted to confirm literature hypotheses that the duplication event that led to the emergence of their two separate genes occurred in primates (Cridland *et al.*, 2012). To do this, 60 mRNA sequences of *IFI16, IFIX,* and other IFI-like PYHIN genes from 28 primate species were gathered through a BLASTn query of human IFIs in primates. These sequences were then codon-aligned through ClustalW and the phylogeny was analyzed through the construction of a phylogenetic gene tree (Figure 6A). Each node that had a statistical likelihood of greater than 70% was labeled and deemed significant, and as shown most of the major branching points were statistically significant. From this tree, the evolutionary progression of primate IFI PYHIN genes was established through comparison with the known primate taxonomy (Perelman et al., 2011) (Figure 6C). That general progression, depicted more broadly in Figure 6B, indicated not one IFI duplication in the primate lineage, but multiple. The oldest family of primates, the Lorisids, represented by *Otolemur garnettii,* experienced an isolated duplication event, as did the next-oldest Lemuriform infraorder. The representative species used for the tarsier family, *Carlito syrichta*, was the only primate to display only a singular IFI-like PYHIN gene (Figure 6A). This indicated that the previous duplication events did not affect the entire primate order. The most recent infraorder of primates to emerge were the simians, which consist of New World Monkeys, Old World Monkeys, and the Great Apes (including humans) (Figure 6C). The emergence of this infraorder directly coincided with the duplication of the IFIs into *IFIX* and *IFI16* (Figure 6A, 6B).

We have concluded that this duplication is the major duplication event hypothesized by Cridland and colleagues to have occurred at some point along the primate lineage. Conspicuously, the gene consistent in the primate order is *IFI16*, the only human PYHIN protein to have two HIN-200 domains. This means that *IFIX* is most likely the gene that emerged as the result of the duplication event, in this case a partial duplication of *IFI16*. Just as important as the initial simian duplication, however, is the fact that both IFIX and IFI16 were retained throughout the primate lineage, indicating that both play an important, and perhaps separate role, in simian survival.

A


Cercocebus Atys IFI16 (Predicted)
Mandrillus leucophaeus IFI16 (Predicted)
Papio Anubis IFI16 (Predicted)
Theropithecus gelada IFI16 (Predicted)
Macaca nemestrina IFI16 (Predicted)
Macaca fascicularis IFI16
Macaca mulatta IFI16
Chlorocebus aethiops IFI16
Chlorocebus sabaeus IFI16 (Predicted)
Colobus angolensis palliatus IFI16 (Predicted)
Piliocolobus tephrosceles IFI16 (Predicted)
Trachypithecus francoisi IFI16 (Predicted)
Rhinopithecus bieti IFI16 (Predicted)
Rhinopithecus roxellana IFI16 (Predicted)
Hylobates moloch IFI16 (Predicted)
Nomascus leucogenys IFI16 (Predicted)
Pongo abelii IFI16
Homo sapiens IFI16
Pan paniscus IFI16 (Predicted)
Gorilla gorilla gorilla IFI16 (Predicted)
Pan troglodytes IFI16 (Predicted)
Cebus imitator IFI16 (Predicted)
Sapajus apella IFI16 (Predicted)
Saimiri boliviensis boliviensis IFI16 (Predicted)
Aotus nancymaae IFI16 (Predicted)
Callithrix jacchus IFI16 (Predicted)
Aotus nancymaae PYHIN1 (Predicted)
Callithrix jacchus PYHIN1 (Predicted)
Saimiri boliviensis boliviensis PYHIN1 (Predicted)
Cebus imitator PYHIN1 (Predicted)
Sapajus apella PYHIN1 (Predicted)
Pan paniscus PYHIN1 (Predicted)
Pan troglodytes PYHIN1 (Predicted)
Homo sapiens PYHIN1
Gorilla gorilla gorilla PYHIN1 (Predicted)
Hylobates moloch PYHIN1 (Predicted)
Nomascus leucogenys PYHIN1 (Predicted)
Pongo abelii PYHIN1 (Predicted)
Pongo abelii PYHIN1-Like (Predicted)
Cercocebus atys PYHIN1 (Predicted)
Macaca mulatta PYHIN1 (Predicted)
Macaca fascicularis PYHIN1 (Predicted)
Chlorocebus sabaeus PYHIN1 (Predicted)
Piliocolobus tephrosceles PYHIN1 (Predicted)
Trachypithecus francoisi PYHIN1 (Predicted)
Macaca nemestrina PYHIN1 (Predicted)
Papio anubis PYHIN1 (Predicted)
Rhinopithecus bieti PYHIN1 (Predicted)
Rhinopithecus roxellana PYHIN1 (Predicted)
Colobus angolensis palliatus PYHIN1 (Predicted)
Mandrillus leucophaeus PYHIN1 (Predicted)
Theropithecus gelada PYHIN1 (Predicted)
Carlito syrichta IFI16 (Predicted)
Propithecus coquereli PYHIN1-Like (Predicted)
Microcebus murinus PYHIN1-Like (Predicted)
Propithecus coquereli IFI16-Like (Predicted)
Microcebus murinus IFI16 (Predicted)
Microcebus murinus IFI16 (Predicted)
Otolemur garnettii IFI16-Like (Predicted)
Otolemur garnettii IFI16 (Predicted)
Mus musculus interferon ifi209
Mus musculus ifi204


B
SIMIAN IFI16
SIMIAN IFIX
Simian IFI duplication
Tarsier IFI16
LEMUR IFIs
LORISID IFIs
MOUSE IFIs (ROOT)

C

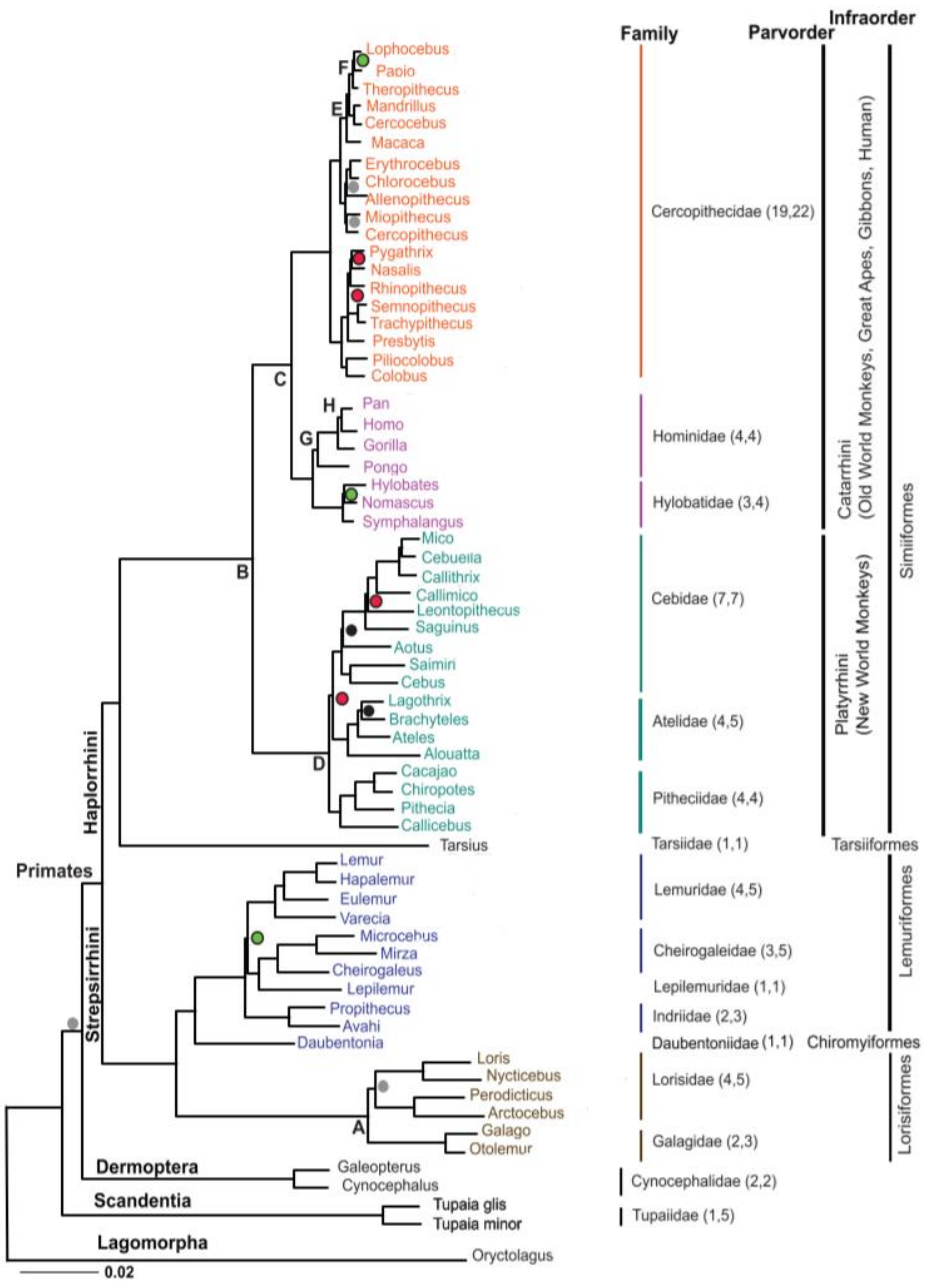


Figure 6: Phylogenetic analyses reveal duplication events leading to the emergence of IFI16, IFIX. A) Phylogenetic tree of all primate mRNA sequences available through NCBI nucleotide database. **B)** Annotated phylogenetic tree including official names of all sequences used, general categorization of subtrees, and green star at simian duplication. **C)** Primate phylogenetic tree constructed by Perelman and colleagues (Perelman *et al.*, 2011).

Luciferase Assays

The purpose of the luciferase assays was to observe the effect of the PYHIN proteins and APOBEC3A on the HIV-LTR promoter. We hypothesized that because literature data suggested both PYHIN proteins and APOBEC3A were shown to interact with the transcription factors and promoters respectively involved in HIV-1 transcription, both should have a similar effect on expression controlled by said promoter. This was done through the transfection of the genes of interest in plasmid form along with and luciferase reporter plasmids, and observation of expression of the luciferase gene controlled by the LTR promoter sequence through measurement of luminescence. Literature data, which showed that APOBEC3A inhibits the LTR promoter, was confirmed by the experiments, as an increasing dose of APOBEC3A was correlated with decreased firefly luminescence (Taura *et al.*, 2019) (Figure 7). This confirms that there is a dose-dependent effect of APOBEC3A on gene expression controlled by the LTR. These experiments not only served to confirm literature data, but also provided strong support for the experimental procedure that would next be used to assay the effect of human IFI expression on LTR promoter activity.

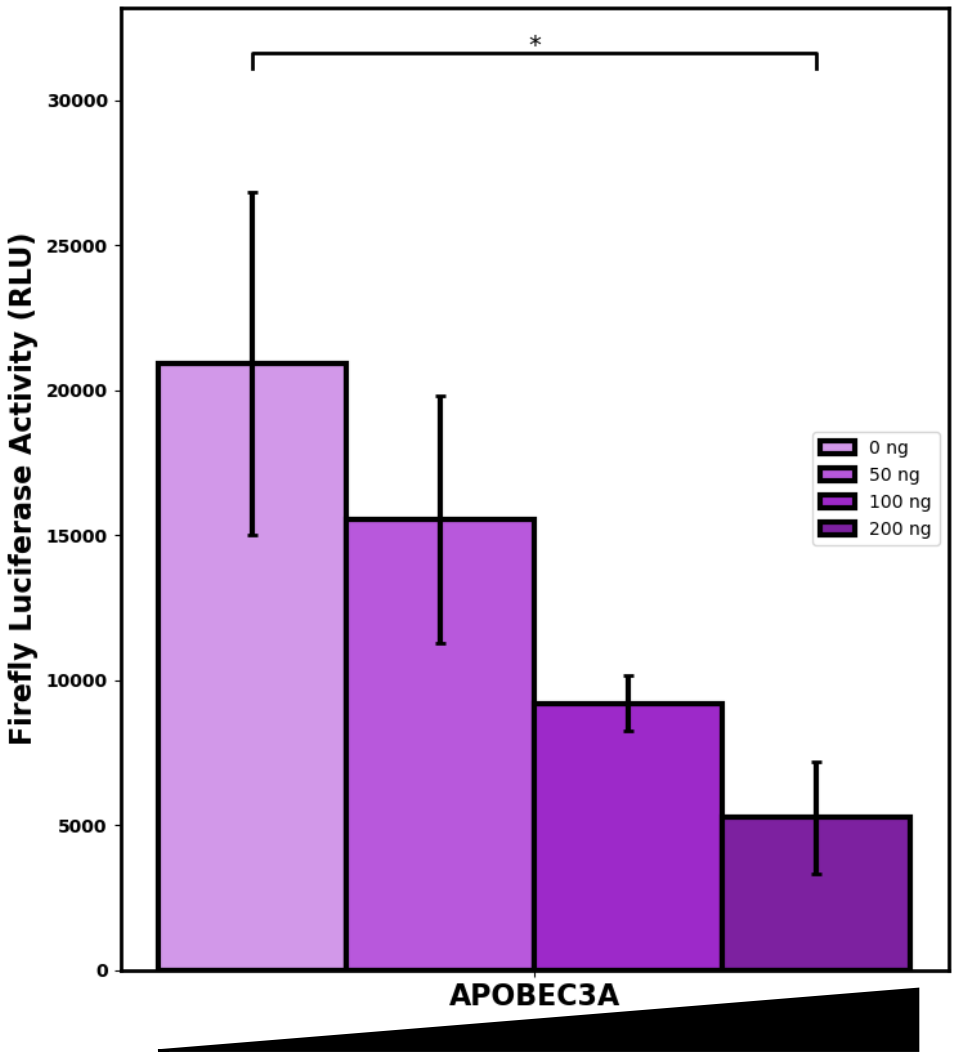


Figure 7: Increasing APOBEC3A doses inhibit the HIV-LTR promoter. HEK293 cells were transfected with amounts of APOBEC3A DNA shown in figure legend. All cells were transfected with equal amounts of plasmid encoding firefly luciferase with expression controlled by HIV-LTR promoter. Total transfected DNA was balanced using *LacZ* plasmid DNA. Relative luciferase activity was used to determine relative activity of the LTR promoter. Bars represent mean + standard error of mean. Data was statistically significant as analyzed through one-way ANOVA; bracketed bars with * indicate $p<0.05$ of post-hoc Tukey's test.

The same decrease in luminescence was noted with the dose-dependent response to PYHIN protein expression (Figure 8). Previous experiments had indicated that a larger dose of PYHIN proteins was necessary to elicit a response similar to the one seen with response to APOBEC3A, therefore the plasmid gene was transfected into the HEK293 cells at 10x the quantity that it was in APOBEC3A (Hotter *et al.*, 2019). Even at the lowest given dose of 500 ng of plasmid PYHIN, both IFI16 and IFIX showed at least a 60% decrease in luminescence, while at the highest dose of 2 μg of PYHIN plasmid, the luminescence was only 20-25% of the control (Figure 3). These data confirm the literature that suggests that IFI16 plays a role in silencing the LTR promoter, and also provides novel evidence that IFIX plays a similar role (Hotter *et al.*, 2019). The difference in data between IFI16 and IFIX suggest that there may be a clearer dose-dependent role in IFI16's inhibition of the LTR promoter sequence, as there is significance between the increasing doses as well as the control, while with IFIX it is only compared to the control. As previously noted, IFI16 and IFIX share two structural domains: a pyrin domain and a HIN-200a domain. These data therefore demonstrate that the portion of the PYHIN proteins that is involved in APOBEC3A-adjacent function is present in those domains and is less likely to be part of the HIN-200b domain function. As a whole, these results provide significant evidence that IFIX and IFI16 both play a role in the silencing of HIV expression alongside APOBEC3A.

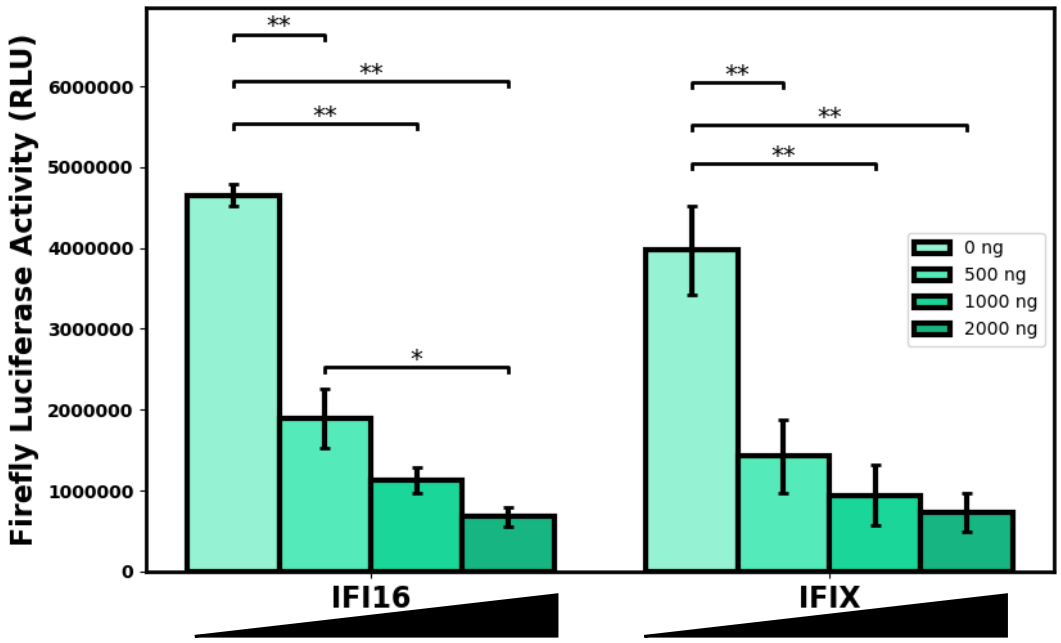


Figure 8: PYHIN proteins inhibit the HIV-LTR promoter. HEK293 cells were transfected with amounts of IFIX or IFI16 plasmid DNA shown in figure legend. All cells were transfected with equal amounts of plasmid encoding firefly luciferase with expression controlled by HIV-LTR promoter. Total transfected DNA was balanced using *LacZ* plasmid DNA. Relative luciferase activity was used to determine relative activity of the LTR promoter. Bars represent mean + standard error of mean. Data was statistically significant as analyzed through one-way ANOVA; bracketed bars with * indicate $p < 0.05$, ** indicate $p < 0.01$ of post-hoc Tukey's test.

Western Blots

Following evidence suggesting a similarity in function and mechanism between the PYHIN proteins and APOBEC3A, we probed physical interaction between the two proteins. To do this, a western blot was done for APOBEC3A on both the whole cell lysate and a sample immunoprecipitated for IFIX-bound proteins (Figure 9). The image for the western blot of the whole cell lysate came out blank, which we hypothesize is because there was not enough APOBEC3A present in the whole cell lysate to yield a powerful enough signal for the imaging machine to read. Through the image of the immunoprecipitated sample, however, three bands are clear across all of the samples. The thickest and highest band is estimated to represent proteins around 50 kDa in mass, which is generally representative of the heavy chain of an antibody. Relatedly, the bottom-most band is approximated to represent the ~20 kDa light chains of the antibodies. We hypothesize that the reason the antibodies were imaged is because the antibodies used in the precipitation were from rabbits, and the secondary antibody was anti-rabbit, meaning it was specific to the constant portion of the precipitation antibody, which is made up of the heavy chain and a portion of the light chain. Therefore, since the secondary antibody was able to bind to the precipitation antibody, the light and heavy chains were marked by luminescence. The middle band, however, is approximately 30 kDa, which is the expected size for APOBEC3A. This indicates that the primary antibody showed that APOBEC3A was present in the immunoprecipitation. This means that it is likely APOBEC3A physically interacts with IFIX. This result was expected because it was shown that the interaction between APOBEC3s and IFI16 occurred with IFI16's pyrin domain, which is very similar to the pyrin domain of IFIX.

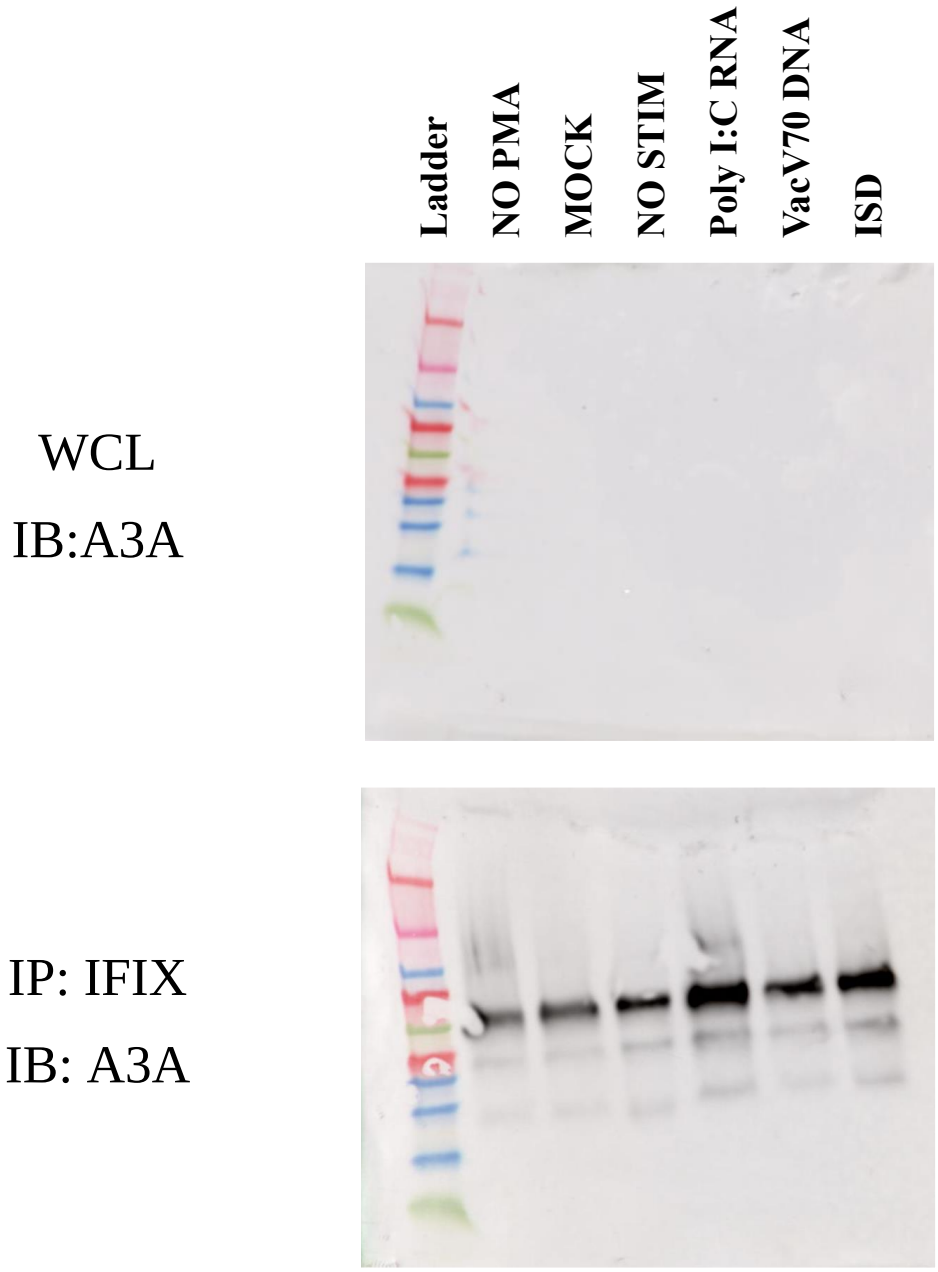


Figure 9: Western blot (immunoblot) of whole THP-1 lysates (top) and THP-1 lysates with IFIX immunoprecipitated from them (bottom). From left to right, the black bands are lysates from THP-1 cells stimulated with: nothing, PMA, PMA + Lipofectamine 2000, PMA + transfected Poly I:C RNA, PMA + transfected *Vaccinia* virus 70mer DNA, and PMA + transfected *Herpes simplexvirus 60mer DNA*

Discussion

The purpose of these experiments was to elucidate how shared structural characteristics between closely related PYHIN proteins IFI16 and IFIX correlate to shared functional characteristics. Through phylogenetic analysis, it was confirmed that the two genes have been conserved throughout primates, and may have even duplicated in two divergent events, one in Old World primates and one in New World primates. Then, through dual-luciferase assays, we observed the effect of IFI16, IFIX, and APOBEC3A on LTR promoter activity in order to explore the noncanonical function o the proteins (functions outside of its role as a sensor of foreign DNA). It was confirmed that both IFI16 and APOBEC3A have an inhibitory role on the HIV-LTR promoter sequence (Hotter *et al.*, 2019; Taura *et al.*, 2019). Evidence was also provided that IFIX has a similar, if not almost identical, effect on the LTR promoter activity as IFI16, suggesting that the structural region of the proteins which is involved in this function is a shared one. Finally, in order to further confirm the relationship between IFIX and APOBEC3A, as well as the similarities between IFIX and IFI16, an immunoprecipitation and western blot was done in order to determine if there was physical binding between the two proteins, as was shown by a previous lab member was the case between IFI16 and APOBEC3A. It was determined that, as predicted, the proteins do physically interact. Ultimately, these experiments were successful in not only reconfirming that the PYHIN protein family has a far broader set of functions than originally described, but also providing evidence for novel functions of IFIX that indicate a similarity between its biological importance and that of IFI16.

Phylogenetic Analysis:

Construction of a phylogenetic gene tree for IFI16 and IFIX using sequences pulled from a BLASTn of human IFI16 showed the progression of IFI-like PYHIN genes in the primate order. It was indicated that from the *IFI16* predecessor there were multiple duplication events that led to the emergence of *IFIX* or *IFIX-like* genes separately in lemurs and simians, as well as a duplication in primate lineages which emerged prior to lemurs which resulted in a separate *IFI16-like* gene in *Otolemur garnettii.* As a whole, these multiple duplication events make it apparent that there is selective pressure in primates for the diversification of PYHIN genes, and specifically, there may be selection for partial duplications which resulted in the separate emergence of a PYHIN gene coding for one pyrin domain and one HIN-200 domain. This conclusion alone makes it apparent that there is a selective advantage to having both IFIX and IFI16, especially in simians given how early the duplication event occurred and was retained throughout the lineage. There are a number of possible selective pressures that could have led to the retainment of both IFI-like PYHINs. It may have been a possible exercise in redundancy, so that when one IFI-like DNA sensor was rendered inactivated, perhaps by random mutation, the other could make up for the loss. This explanation alone, however, seems unlikely because there are other DNA sensing PRRs such as cGAS which could be performing a similar function (Orzalli et al., 2015). The scenario in which this would be important, however, is if an IFI-dependent and STING/cGAS independent pathway such as that proposed by our lab is essential to the full function of the immune system. The other possibility, which I hypothesize is more likely, is that there are independent

functions of IFI16 and IFIX in the intrinsic immune system which make both of them equally essential to immune defense from viruses. So far, it has been demonstrated that IFI16 plays a possible role in a number of intrinsic immune functions related to cellular stress responses, antiviral defense, and control of gene expression (Diner *et al.*, 2016). IFIX has been implicated in a number of similar functions, however as previously stated there remain differences between the two proteins that ought to be further explored.

The phylogenetic analyses done in this study also provide important context for the way these proteins are studied in the lab. It has been alluded to throughout my explanations that IFIX and IFI16 are often studied in mouse analogs, and conclusions are even often drawn about IFI16 based off of its activity in mouse cells or the activity of the mouse IFI p209, which has a similar primary structure to IFI16. This is extremely apparent in the study done by Gray and colleagues in 2012, which concluded based off of the elimination of ALRs in mice cells and knockdown of IFI16 in human cells that IFIs are "dispensable" for the interferon response to cellular DNA (Gray *et al.*, 2016). The abundance of evidence presented in this paper analyzing the DNA sensing pathway(s) of IFI16 already contradicts, this, as does the fact that if IFIX was not knocked out, there was in fact an intact IFI-like DNA sensor in the human cells that produced an immune response. The paper nonetheless exemplifies why it is important to understand that the evolutionary history and current role of IFI-like PYHIN proteins in intrinsic immunity is different in primates and mice. It is clear that the divergence patterns of primate IFIs is very different from that described by The more in-depth understanding of IFI16 and IFIX's evolutionary history that comes from this study implies that it may be more

preferable to use simian-derived primary cells instead of mouse derived primary cells when characterizing PYHIN proteins using nonhuman models.

The completeness of the phylogenetic tree was guided by the availability of genomic data from NCBI's nucleotide database. Although this database had various simian species' genomes sequenced and annotated, the diversity of non-simian primates was extremely lacking. The only representative species of tarsier was *Carlito syrichta*, and the only representative species for the pre-lemur primate family of Lorisids was *Otolemur garnettii*. Although the *IFI* genes identified in these species fit within the story imagined for the gene family's emergence in primates, it is possible that these species are an exception for their respective taxonomical subgroups rather than the norm. In the future, as the diversity of annotated primate genomes becomes more extensive, it will be beneficial to update the sequences listed in Appendix A to better reflect most recent data.

Luciferase Assays and Western Blots

The luciferase assays were done in order to determine the effect of IFI16, IFIX, and APOBEC3A on HIV-LTR promoter activity. Through this assay, a decrease in luminescence was observed in a dose dependent response to all three of the proteins of interest. This was hypothesized to be the result of the experiment, as literature has previously described both APOBEC3A and IFI16 as restricting HIV transcription through the same mechanism: binding of the Sp-1 transcription factor thereby inhibiting the HIV-LTR promoter (Hotter *et al.*, 2019; Taura *et al.*, 2019). Our novel data, which connects structural similarities between IFI16 and IFIX to similar function in HIV-LTR inhibition *and* in physical interaction with APOBEC3A implies the two PYHIN proteins may function through a similar mechanism. Our data showed further evidence for this

hypothesis when the western blot data showed physical interaction between IFIX and APOBEC3A, just like Thomas Potts had shown to occur between IFI16 and APOBEC3A. These results were also expected, because as stated in Diner, the binding interaction between IFI16 and APOBEC3 was suggested to be in the pyrin domain (Diner *et al.*, 2015; Taura *et al.*, 2019). Although the primary structure of the pyrin domains between human IFI16 and IFIX is extremely similar, this still provides evidence that can help further pinpoint the structural residues responsible for the binding event, because now it is apparent that it is more likely to be in the region of shared amino acid residues for the two proteins (Cridland *et al.*, 2012).

Overall, this series of experiments provides an example of PYHIN proteins' functional characteristics that have broader reaching implications. It is clear that IFI16 and IFIX both play a role similar to, if not in conjunction with, APOBEC3A, in the silencing of HIV through their impact on the LTR promoter. Other literature has described antiviral activity of both IFI16 and IFIX through other, different mechanisms, such as the repression of HSV through possible recruitment of or role in proteasome complexes (Diner *et al.*, 2015). Separate literature has also described the role of IFIX and IFI16's pyrin domain in PML bodies, which, as previously described, are involved in a host of antiviral functions (Diner *et al.*, 2016). Such evidence of diverse mechanisms being centralized around these proteins contributes to our lab's theory that IFIX and IFI16 may play central roles in the innate immune response to viral infection and DNA damage by bringing together proteins that play differing but cooperative roles. This would explain the broad binding capabilities and diverse set of functions associated with

PYHIN proteins, as well as why they are targets for viruses such as HSV during infection.

Future Work

The phylogenetic analyses done in this experiment are but the groundwork future investigations of the important structural characteristics of PYHIN proteins. It remains clear that PYHIN proteins may play differing roles across animal immune systems. Despite their recent emergence in the mammalian lineage, there is substantial variation in the expression characteristics of the proteins across species. While mice express a diverse set of 13 PYHIN proteins, bats, which have been shown to be reservoirs for all kinds of diseases, many of which have undergone zoonosis and jumped to humans, show no evidence of PYHIN proteins in *any* of their genomes, which is something quite curious for an order of animals which make up 20% of all mammals (Clayton and Munir, 2020; Unterholzner *et al.*, 2010). Taken together, this illustrates that there is an applicable benefit to understanding the evolutionary history of PYHIN proteins more than we do already, and by doing so we may gain a better understanding of the role, or rather roles, they play in different animals' immune systems, including our own.

Using the structural data gathered in order to complete phylogenetic analyses, finding conserved motifs throughout the primate lineage may also provide useful targets for mutagenesis experiments within the pyrin domain. These could include point-mutation studies or whole-domain deletion studies. Repeating the immunoprecipitation/immunoblot experiments with mutated IFI16 or IFIX proteins would further specify which specific residues are responsible for the actual binding event taking place between the PYHIN proteins and APOBEC3A. Identifying specific

differences in the functions of IFI16 and IFIX will also likely inform our molecular understanding of their mechanisms. Functions attributed to IFI16 but not IFIX could be correlated to the HIN-200b domain present in only the former of the two proteins. his molecular understanding of the mechanism is important for a number of reasons, namely better characterizing a component of HIV infection known as the "latent reservoir." When HIV infects a cell, it uses an enzyme called reverse transcriptase to transcribe its RNA genome into a DNA genome, which is then integrated into the host cell's genome. Depending on various factors at the time of integration, the "provirus," or viral genome integrated into cellular DNA, can remain unexpressed for up to decades. The cells in which this is the case make up the latent reservoir, where since the virus is unexpressed, it cannot be fought by the immune system or drug treatments. Some scientists believe that the key to curing HIV infection will come in the form of "shocking" the silent proviruses out of latency, and then being able to eradicate the virus from the body. This theoretical treatment strategy is known as the "shock-and-kill method."

There also is much more to investigate regarding the varied roles of IFIX and IFI16 in viral infection. Their intrinsic immune function in HIV-1 infection represents but a fraction of the numerous intrinsic and innate immune functions these proteins have. In the future, a more comprehensive characterization of IFI16 and IFIX's antiviral functions will be essential for us to better understand what their overall role in the immune system is. This knowledge would also better contextualize the phylogenetic data constructed in this study, better indicating what possible selective pressures drove the duplication which led to the emergence of these two similar proteins.

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Appendix A: Primate PYHIN Sequences

>AY138863.1_Homo_sapiens_interferon-inducible_IFI_16_mRNA_complete_cds

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