

**UNITED STATES
SECURITIES AND EXCHANGE COMMISSION**
Washington, D.C. 20549

SCHEDULE 14A INFORMATION

Proxy Statement Pursuant to Section 14(a) of the
Securities Exchange Act of 1934
(Amendment No.)

Filed by the Registrant

Filed by a Party other than the Registrant

Check the appropriate box:

- Preliminary Proxy Statement
- Confidential, for Use of the Commission Only (as permitted by Rule 14a-6(e)(2))**
- Definitive Proxy Statement
- Definitive Additional Materials
- Soliciting Material under §240.14a-12

ATYR PHARMA, INC.

(Name of Registrant as Specified In Its Charter)

(Name of Person(s) Filing Proxy Statement, if other than the Registrant)

Payment of Filing Fee (Check the appropriate box):

- No fee required.
- Fee computed on table below per Exchange Act Rules 14a-6(i)(1) and 0-11.
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 - (3) Filing Party: _____
 - (4) Date Filed: _____

aTyr Pharma, Inc.
3545 John Hopkins Court, Suite #250
San Diego, CA 92121

NOTICE OF ANNUAL MEETING OF STOCKHOLDERS

To Be Held On May 6, 2020

Dear Stockholder:

You are cordially invited to attend the 2020 Annual Meeting of Stockholders of aTyr Pharma, Inc., a Delaware corporation (the "Company"). The meeting will be held virtually via live webcast on Wednesday, May 6, 2020 at 8:30 a.m. Pacific Time. The meeting is being held for the following purposes:

1. To elect two Class II directors, as nominated by the Company's Board of Directors (the "Board of Directors"), to hold office until the 2023 Annual Meeting of Stockholders or until their successors are duly elected and qualified.
2. To ratify the appointment of Ernst & Young LLP as the independent registered public accounting firm of the Company for its fiscal year ending December 31, 2020.
3. To approve an amendment to the aTyr Pharma, Inc. 2015 Stock Option and Incentive Plan to increase the number of shares of common stock reserved for issuance thereunder by 350,000 shares.
4. To approve an amendment to the Company's Restated Certificate of Incorporation to increase the authorized number of shares of common stock from 10,714,286 to 21,425,000 shares.
5. To approve the authorization to adjourn the 2020 Annual Meeting of Stockholders, if necessary, to solicit additional proxies if there are not sufficient votes in favor of Proposal 3 or Proposal 4.
6. To transact such other business as may properly come before the meeting or any adjournment or postponement thereof.

These items of business are more fully described in the Proxy Statement accompanying this Notice.

Proposal 1 relates solely to the election of two Class II directors nominated by the Board of Directors and does not include any other matters relating to the election of directors, including without limitation, the election of directors nominated by any stockholder of the Company.

The Board of Directors has fixed the close of business on Monday, March 16, 2020 as the record date for the determination of stockholders entitled to notice of, and to vote at, the 2020 Annual Meeting of Stockholders, or at any adjournments of the 2020 Annual Meeting of Stockholders.

In order to ensure your representation at the 2020 Annual Meeting of Stockholders, please vote over the Internet, by telephone or by completing and returning the enclosed proxy card promptly in the enclosed envelope. The 2020 Annual Meeting of Stockholders will be a completely virtual meeting. There will be no physical meeting location. The meeting will only be conducted via live webcast. In order to attend, you must register in advance at www.proxydocs.com/LIFE prior to the deadline of Monday 4, 2020 at 2:00 p.m. Pacific Time. Upon completing your registration, you will receive further instructions via email, including your unique link that will allow you access to the meeting and you will have the ability to submit questions. Please be sure to follow the instructions on the enclosed proxy card and/or voting instruction form and subsequent instructions that will be delivered to you via email. If you attend the 2020 Annual Meeting of Stockholders virtually, you may submit an electronic ballot during the meeting.

All stockholders are cordially invited to attend the 2020 Annual Meeting of Stockholders.

Important Notice Regarding the Availability of Proxy Materials for the 2020 Annual Meeting of Stockholders to be Held Virtually on May 6, 2020 via Live Webcast.

By Order of the Board of Directors

aTyr Pharma, Inc.



Sanjay S. Shukla, M.D., M.S.
President and Chief Executive Officer

San Diego, California
April 2, 2020

This Proxy Statement and the Annual Report are available electronically at www.proxydocs.com/LIFE. The website contains instructions as to how to vote by internet or over the telephone.

Your vote is important, whether or not you expect to attend the 2020 Annual Meeting of Stockholders via live webcast. You are urged to vote either via the Internet or telephone, or by marking, dating and signing the enclosed proxy card and returning it as promptly as possible in the enclosed envelope. Voting promptly will help avoid the additional expense of further solicitation to assure a quorum at the meeting.

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ATYR PHARMA, INC.

PROXY STATEMENT
FOR THE 2020 ANNUAL MEETING OF STOCKHOLDERS
May 6, 2020

INFORMATION CONCERNING SOLICITATION AND VOTING

General

This proxy statement ("Proxy Statement") is furnished in connection with the solicitation of proxies for use prior to or at the 2020 Annual Meeting of Stockholders (the "Annual Meeting") of aTyr Pharma, Inc., a Delaware corporation, to be held at 8:30 a.m. Pacific Time on Wednesday, May 6, 2020 and at any adjournments or postponements thereof for the following purposes:

1. To elect two Class II directors, as nominated by the Company's Board of Directors ("Board of Directors"), to hold office until the 2023 Annual Meeting of Stockholders or until their successors are duly elected and qualified;
2. To ratify the appointment of Ernst & Young LLP as the independent registered public accounting firm of the Company for its fiscal year ending December 31, 2020;
3. To approve an amendment to the aTyr Pharma, Inc. 2015 Stock Option and Incentive Plan (the "2015 Stock Plan") to increase the number of shares of common stock reserved for issuance thereunder by 350,000 shares;
4. To approve an amendment to the Company's Restated Certificate of Incorporation to increase the authorized number of shares of common stock from 10,714,286 to 21,425,000 shares;
5. To approve the authorization to adjourn the Annual Meeting, if necessary, to solicit additional proxies if there are not sufficient votes in favor of Proposal 3 or Proposal 4; and
6. To transact such other business as may properly come before the Annual Meeting or any adjournment or postponement thereof.

Virtual Annual Meeting

The Annual Meeting will be a completely virtual meeting. There will be no physical meeting location. The meeting will only be conducted via live webcast. In order to attend, you must register in advance at www.proxydocs.com/LIFE prior to the deadline of Monday, May 4, 2020 at 2:00 p.m. Pacific Time. Please be sure to follow the instructions on the enclosed proxy card and/or voting instruction form and subsequent instructions that will be delivered to you via email.

Upon completing your registration, you will receive further instructions via email, including your unique link that will allow you access to the Annual Meeting and you will have the ability to submit questions. This year's stockholders question and answer session will include questions submitted in advance of and during the Annual Meeting. You may submit a question in advance of the meeting at www.proxydocs.com/LIFE after logging in with your control number. We do not place restrictions on the type or form of questions that may be asked; however, we reserve the right to edit or reject redundant questions or questions that we deem profane or otherwise inappropriate. During the live question and answer session of the Annual Meeting, we will answer questions as they come in and address those asked in advance, as time permits.

The virtual meeting platform is fully supported across browsers and devices running the most updated version of applicable software and plugins. Participants should ensure that they have a strong internet connection wherever they intend to participate in the Annual Meeting. We will have technicians ready to assist you with any technical difficulties you may have accessing the Annual Meeting. If you have registered for the Annual Meeting, you will receive an email with information about technical support.

On or about April 2, 2020, we mailed to all stockholders entitled to vote at the Annual Meeting a Notice of Annual Meeting of Stockholders, this Proxy Statement and our 2019 Annual Report, including our annual report on Form 10-K ("Annual Report").

Solicitation

This solicitation is made by the Board of Directors on behalf of the Company. We will bear the costs of preparing, mailing, online processing and other costs of the proxy solicitation made by our Board of Directors. In addition, we have engaged Alliance Advisors, LLC (“Alliance Advisors”) to assist us with the solicitation of proxies. We will pay Alliance Advisors a service fee, plus out-of-pocket expenses and additional fees based upon work performed at our request, which is not expected to exceed \$20,000. In addition to solicitations by mail, Alliance Advisors may solicit proxies by telephone and e-mail. **IF YOU NEED ASSISTANCE WITH THE VOTING OF YOUR SHARES, YOU MAY CONTACT ALLIANCE ADVISORS TOLL-FREE AT (844) 866-9428.** Copies of solicitation materials may be furnished to brokers, custodians, nominees and other fiduciaries for forwarding to beneficial owners of shares of our common stock, and normal handling charges may be paid for such forwarding service. Officers and other Company employees, who will receive no additional compensation for their services, may solicit proxies by mail, e-mail, via the Internet, personal interview or telephone.

Voting Rights and Outstanding Shares

Only holders of record of our common stock as of the close of business on March 16, 2020 are entitled to receive notice of, and to vote at, the Annual Meeting. Each holder of common stock will be entitled to one vote for each share held on all matters to be voted upon at the Annual Meeting. At the close of business on March 16, 2020, there were 9,352,498 shares of our common stock issued and outstanding.

A quorum of stockholders is necessary to take action at the Annual Meeting. Stockholders representing a majority of the outstanding shares of our common stock (present online at the Annual Meeting or represented by proxy) will constitute a quorum. We will appoint an inspector of elections for the meeting to determine whether or not a quorum is present and to tabulate votes cast by proxy or online at the Annual Meeting. Abstentions, withheld votes and broker non-votes (which occur when a broker, bank or other nominee holding shares for a beneficial owner does not vote on a particular matter because such broker, bank or other nominee does not have discretionary authority to vote on that matter and has not received voting instructions from the beneficial owner) are counted as present for purposes of determining the presence of a quorum for the transaction of business at the Annual Meeting.

Votes Required for Each Proposal

To elect our directors and approve the other proposals being considered at the Annual Meeting, the voting requirements are as follows:

| <u>Proposal</u> | <u>Vote Required</u> | <u>Discretionary Voting Permitted?</u> |
|---|----------------------|--|
| Election of Directors | Plurality | No |
| Ratification of Ernst & Young LLP | Majority Cast | Yes ⁽¹⁾ |
| Approval of Amendment to 2015 Stock Plan | Majority Cast | No |
| Approval of Increase in Authorized Common Stock | Majority Outstanding | Yes ⁽¹⁾ |
| Approval of the Authorization to Adjourn the Annual Meeting, if necessary | Majority Cast | Yes ⁽¹⁾ |

- (1) The New York Stock Exchange (“NYSE”) has advised us that this proposal is considered to be a “routine” matter under NYSE rules. Accordingly, if you hold your shares in street name and do not provide voting instructions to your broker, bank or other agent that holds your shares, your broker, bank or other agent has discretionary authority under NYSE rules to vote your shares on this proposal.

“*Discretionary Voting Permitted*” means that brokers will have discretionary voting authority with respect to shares held in street name for their clients, even if the broker does not receive voting instructions from their client.

“*Majority Cast*” means a majority of the votes properly cast for or against such matter.

“*Majority Outstanding*” means a majority of the shares of common stock outstanding and entitled to vote on the Record Date.

“*Plurality*” means a plurality of the votes properly cast on such matter. For the election of directors, the two nominees receiving the most votes will be elected as directors.

The vote required and method of calculation for the proposals to be considered at the Annual Meeting are as follows:

Proposal 1—Election of Directors. If a quorum is present, the director nominees receiving the highest number of votes, at the meeting or by proxy, will be elected as directors. You may vote “FOR” all nominees, “WITHHOLD” for all nominees, or “WITHHOLD” for any nominee by specifying the name of the nominee on your proxy card. The NYSE has advised us that Proposal 1 is not considered to be a discretionary item, so if you do not instruct your broker how to vote with respect to this proposal, your broker may not vote on this proposal, and those votes will be counted as broker “non-votes.” Withheld votes and broker non-votes will have no effect on the outcome of the election of the directors.

Proposal 2—Ratification of Ernst & Young LLP as Independent Registered Public Accountants. Approval of this proposal requires the affirmative vote of a majority of the votes properly cast for and against such matter. You may vote “FOR,” “AGAINST” or “ABSTAIN” from voting on this proposal. If you abstain from voting on this matter, your shares will not be counted as “votes cast” with respect to such matter, and the abstention will have no effect on the proposal. Broker non-votes will not be counted as “votes cast” and will therefore have no effect on the proposal. The NYSE has advised us that Proposal 2 is considered to be a discretionary item, and your broker will be able to vote on this proposal even if it does not receive instructions from you, so we do not anticipate any broker non-votes in connection with Proposal 2.

Proposal 3—Approval of Amendment to the 2015 Stock Plan. Approval of this proposal requires the affirmative vote of a majority of the votes properly cast for and against such matter. You may vote “FOR,” “AGAINST” or “ABSTAIN” from voting on this proposal. If you abstain from voting on this matter, your shares will not be counted as “votes cast” with respect to such matter, and the abstention will have no effect on the proposal. Broker non-votes will not be counted as “votes cast” and will therefore have no effect on the proposal.

Proposal 4—Approval of Increase in Authorized Common Stock. Approval of this proposal requires the affirmative vote of a majority of the shares of common stock outstanding and entitled to vote on the Record Date. You may vote “FOR,” “AGAINST” or “ABSTAIN” from voting on this proposal. If you abstain from voting on this matter, it will have the same effect as a vote “AGAINST” the proposal. The NYSE has advised us that Proposal 4 is considered to be a discretionary item, and your broker will be able to vote on this proposal even if it does not receive instructions from you, so we do not anticipate any broker non-votes in connection with Proposal 4.

Proposal 5—Approval of the Authorization to Adjourn the Annual Meeting, if Necessary. Approval of this proposal requires the affirmative vote of a majority of the votes properly cast for and against such matter. You may vote “FOR,” “AGAINST” or “ABSTAIN” from voting on this proposal. If you abstain from voting on this matter, your shares will not be counted as “votes cast” with respect to such matter, and the abstention will have no effect on the proposal. Broker non-votes will not be counted as “votes cast” and will therefore have no effect on the proposal.

We request that you vote your shares by proxy by mail, over the Internet, or by telephone. If you choose to vote by mail, your shares will be voted in accordance with your voting instructions if the proxy card is received prior to the Annual Meeting. If you sign and return your proxy card but do not give voting instructions, your shares will be voted FOR: (i) the election of each of the Company’s two nominees as directors; (ii) the ratification of the appointment of Ernst & Young LLP as the independent registered public accounting firm for the Company for the fiscal year ending December 31, 2020; (iii) an amendment to the 2015 Stock Plan to increase the number of shares of common stock reserved for issuance thereunder by 350,000 shares; (iv) the increase in the authorized shares of common stock from 10,714,286 to 21,425,000 shares; (v) the adjournment of the Annual Meeting, if necessary; and (vi) as the proxy holders deem advisable, in their discretion, on other matters that may properly come before the Annual Meeting.

How to Place your Vote

Stockholders who vote by proxy over the Internet or by telephone need not return a proxy card or voting instruction form by mail, but may incur costs, such as usage charges, from telephone companies or Internet service providers.

Voting by Internet. Registered stockholders can vote via the Internet at www.proxypush.com/LIFE. You will need to use the control number appearing on your proxy card to vote via the Internet. You can use the Internet to transmit your voting instructions up until 8:30 a.m. Pacific Time on May 6, 2020. Internet voting is available 24 hours a day. If you vote via the Internet, you do not need to return a proxy card.

Voting by Telephone. Registered stockholders can vote by telephone by calling the toll-free telephone number 1-866-284-6674. You will need to use the control number appearing on your proxy card to vote via by telephone. You may transmit your voting instructions by any touch-tone telephone up until 8:30 a.m. Pacific Time on May 6, 2020. Telephone voting is available 24 hours a day. If you vote by telephone, you do not need to return a proxy card.

Voting by Mail. If you are a registered stockholder and received a printed proxy card, you can vote by marking, dating and signing it, and returning it in the postage-paid envelope provided. Please promptly mail your proxy card to ensure that it is received prior to the start of the Annual Meeting.

Vote at the Meeting. The Annual Meeting will be a completely virtual meeting. There will be no physical meeting location. The meeting will only be conducted via live webcast. In order to attend, you must register in advance at www.proxydocs.com/LIFE prior to the deadline of Monday, May 4, 2020 at 2:00 p.m. Pacific Time. Upon completing your registration, you will receive further instructions via email, including your unique link that will allow you access to the meeting and you will have the ability to submit questions in advance of and during the Annual Meeting. Please be sure to follow the instructions on the enclosed proxy card and/or voting instruction form and subsequent instructions that will be delivered to you via email. If your shares are registered directly in your name, you are considered a stockholder of record and you have the right to vote online at the Annual Meeting. If your shares are held in the name of your broker, bank or other nominee, you are considered the beneficial owner of shares held in street name. As a beneficial owner, if you wish to vote online at the Annual Meeting, you will need a legal proxy from your broker, bank or other nominee authorizing you to vote those shares.

If your shares are held in street name, the voting instruction form sent to you by your broker, bank or other nominee should indicate whether the institution has a process for beneficial holders to provide voting instructions over the Internet or by telephone. A number of banks and brokerage firms participate in a program that also permits stockholders whose shares are held in street name to direct their vote over the Internet or by telephone. If your bank or brokerage firm gives you this opportunity, the voting instructions from the bank or brokerage firm that accompany this Proxy Statement will tell you how to use the Internet or telephone to direct the vote of shares held in your account. If your voting instruction form does not include Internet or telephone information, please complete and return the voting instruction form in the self-addressed, postage-paid envelope provided by your broker.

Revocability of Proxies

Any proxy may be revoked at any time before the final vote at the Annual Meeting by filing an instrument revoking it with the Company's Secretary or by submitting a duly executed proxy bearing a later date prior to the time of the Annual Meeting. Stockholders who have voted by proxy over the Internet or by telephone or have executed and returned a proxy and who then attend the Annual Meeting and desire to vote at the Annual Meeting are requested to notify the Secretary in writing prior to the time of the Annual Meeting. We request that all such written notices of revocation to the Company be addressed to Nancy Denyes, Secretary, c/o aTyr Pharma, Inc., at the address of our principal executive offices at 3545 John Hopkins Court, Suite #250, San Diego, CA 92121. Stockholders may also revoke their proxy by entering a new vote over the Internet or by telephone prior to the deadlines described above. If your shares are held by your broker, bank or other nominee, you should follow the instructions provided by your broker, bank or other nominee. In each case, your most current proxy card or telephone or internet proxy is the one that is counted.

Stockholder Proposals to be Presented at the Next Annual Meeting

Any stockholder who meets the requirements of the proxy rules under the Securities Exchange Act of 1934, as amended (the "Exchange Act"), may submit proposals to the Board of Directors to be presented at the 2021 annual meeting. Such proposals must comply with the requirements of Rule 14a-8 under the Exchange Act and be submitted in writing by notice delivered or mailed by first-class United States mail, postage prepaid, to our Secretary at our principal executive offices at the address set forth above no later than December 3, 2020 in order to be considered for inclusion in the proxy materials to be disseminated by the Board of Directors for such annual meeting. If the date of the 2021 annual meeting is moved by more than 30 days from the date contemplated at the time of the previous year's proxy statement, then notice must be received within a reasonable time before we begin to print and send proxy materials. If that happens, we will publicly announce the deadline for submitting a proposal in a press release or in a document filed with the Securities and Exchange Commission ("SEC"). A proposal submitted outside the requirements of Rule 14a-8 under the Exchange Act will be considered untimely for consideration at the annual meeting if received after February 16, 2021.

Our Amended and Restated Bylaws ("Bylaws") also provide for separate notice procedures to recommend a person for nomination as a director or to propose business to be considered by stockholders at a meeting. To be considered timely under these provisions, the stockholder's notice must be received by our Secretary at our principal executive offices at the address set forth above no earlier than January 6, 2021 and no later than February 5, 2021. Our Bylaws also specify requirements as to the form and content of a stockholder's notice.

The Board of Directors, a designated committee thereof or the chairman of the meeting may refuse to acknowledge the introduction of any stockholder proposal if it is not made in compliance with the applicable notice provisions.

PROPOSAL 1

ELECTION OF DIRECTORS

General

Our Restated Certificate of Incorporation provides for a board of directors that is divided into three classes. The term for each class is three years, staggered over time. This year, the term of the directors in Class II expires. Two of our Class II directors will each stand for re-election at the Annual Meeting and one will be retiring from our Board of Directors at the end of his term. Our Board of Directors is currently comprised of eight members, and effective as of our Annual Meeting, our Board will consist of seven members. If the Class II director nominees are elected at the Annual Meeting, the composition of our Board of Directors will be as follows: Class I— Mr. John K. Clarke and Dr. Paul Schimmel; Class II— Mr. Timothy P. Coughlin and Dr. Jane A. Gross; and Class III— Dr. Sanjay S. Shukla, Mr. Jeffrey S. Hatfield and Dr. Svetlana Lucas. Dr. James C. Blair is retiring from the Board of Directors at the Annual Meeting. Dr. Blair has served on our Board of Directors since 2010, and we thank him for his years of service.

In the absence of instructions to the contrary, the persons named as proxy holders in the accompanying proxy intend to vote in favor of the election of the nominees designated below to serve until the 2023 Annual Meeting of Stockholders and until their successors shall have been duly elected and qualified. Each nominee is currently a director. The Board of Directors expects that each nominee will be available to serve as a director, but if any such nominee should become unavailable or unwilling to stand for election, it is intended that the shares represented by the proxy will be voted for such substitute nominee as may be designated by the Board of Directors. The biographies of our directors and their ages as of March 16, 2020 are set forth below.

| Name | Age | Position |
|------------------------------|-----|---|
| Sanjay S. Shukla, M.D., M.S. | 48 | President, Chief Executive Officer and Director |
| John K. Clarke (1)(2)(3) | 66 | Chairman of the Board |
| James C. Blair, Ph.D. (2)(3) | 80 | Director |
| Timothy P. Coughlin (1)(2) | 53 | Director |
| Jane A. Gross, Ph.D. | 63 | Director |
| Jeffrey S. Hatfield (1)(3) | 62 | Director |
| Svetlana Lucas, Ph.D. | 48 | Director |
| Paul Schimmel, Ph.D. | 79 | Director |

- (1) Member of the Audit Committee.
- (2) Member of the Compensation Committee.
- (3) Member of the Nominating and Corporate Governance Committee.

Nominees for Director

Class II:

The two individuals listed below are nominated for election as Class II directors to serve a three-year term ending at the 2023 Annual Meeting of Stockholders and until their successors are elected and qualified. Mr. Coughlin was previously elected by the stockholders. Dr. Gross joined the Board of Directors in June 2019 and was recommended for nomination to the Board of Directors by the Nominating and Corporate Governance Committee.

The Board of Directors recommends that you vote FOR the following nominees.

Timothy P. Coughlin has served as a director since April 2017. Mr. Coughlin is the former Chief Financial Officer of Neurocrine Biosciences, Inc. Neurocrine, a biopharmaceutical company that has received U.S. Food and Drug Administration approval for INGREZZA (valbenazine) and ORILISSA (elagolix), both of which were discovered and developed during his tenure at Neurocrine from 2002 to 2018. Prior to joining Neurocrine, he was with Catholic Health Initiatives, a nationwide integrated healthcare delivery system, where he served as Vice President, Financial Services. Mr. Coughlin also served as a Senior Manager in the Health Sciences practice of Ernst & Young LLP and its predecessors from 1989 to 1999. Mr. Coughlin serves on the board of directors of Retrophin, Inc. and Fate Therapeutics, Inc., both biotechnology companies. He also served on the board of directors of Peloton Therapeutics prior to its sale to Merck & Co in 2019. Mr. Coughlin holds a master's degree in international business from San Diego State University and a bachelor's degree in accounting from Temple University. Mr. Coughlin is a certified public accountant in both California and Pennsylvania. Our Board of Directors believes that

Mr. Coughlin is qualified to serve on our Board of Directors due to his extensive background in financial and accounting matters for public companies, his experience in the life science industry and his years of business and leadership experience.

Jane A. Gross, Ph.D. has served as a director since June 2019. Dr. Gross currently serves as Chief Scientific Officer, Senior Vice President, Research and Development of Aptevo Therapeutics Inc. (Aptevo), a position she has held since September 2016. In this role, Dr. Gross led the discovery of novel protein therapeutics based on the ADAPTIR platform in immuno-oncology, leading research efforts in molecular biology and protein engineering, immunology, protein and cell sciences, pharmacology and translational research. Prior to joining Aptevo, Dr. Gross served as Vice President, Applied Research and Non-Clinical Development at Emergent BioSolutions Inc. and Vice President, Immunology Research at ZymoGenetics, Inc., where she led efforts in discovery and development of therapeutics from novel genes. Dr. Gross holds a Ph.D. in Immunology from the University of California, Berkeley under Jim Allison (2018 recipient of the Nobel Prize in Physiology and Medicine) and a Post-Doctoral Fellowship from the University of Washington in Immunology. Our Board of Directors believes that Dr. Gross is qualified to serve on our Board of Directors due to her extensive experience in the biotherapeutics industry and her expertise in immunology and oncology.

Continuing Directors:

Class III: Currently Serving Until the 2021 Annual Meeting

Jeffrey S. Hatfield has served as a director since April 2017. Mr. Hatfield currently serves as Chief Executive Officer and a member of the board of directors at Zafgen, a biopharmaceutical company dedicated to significantly improving the health and well-being of patients affected by metabolic diseases. Previously, Mr. Hatfield served as President, Chief Executive Officer and a member of the board of directors of Vitae Pharmaceuticals from 2004 to 2016. As CEO, Mr. Hatfield successfully transitioned Vitae from a novel platform technology start-up to a thriving product-focused company with a robust pipeline of multiple first-in-class clinical stage and pre-clinical stage assets generated from the company's internal discovery engine. Mr. Hatfield took the company public in 2014, and in October 2016, Vitae Pharmaceuticals was acquired by Allergan plc for approximately \$639.0 million in cash. Prior to joining Vitae Pharmaceuticals, Mr. Hatfield worked at Bristol-Myers Squibb in a variety of executive positions, including: Senior Vice President of BMS's Immunology and Virology Divisions, where he was responsible for all aspects of the \$1.0 billion business; President and General Manager, Canada; and, Vice President, U.S. Managed Health Care. He previously served as a board member of Ambit Biosciences before its acquisition by Daiichi-Sankyo in 2015, and as a member of the board of directors of the Biotechnology Industry Organization (BIO), serving on the Executive Company Section. Mr. Hatfield currently serves as Chairman of the Board of Miragen Therapeutics, a biotherapeutic company, and as an Adjunct Professor and member of the Dean's Advisory Committee for Purdue University's College of Pharmacy, where he is a Distinguished Alumnus. Mr. Hatfield holds an M.B.A. from The Wharton School, University of Pennsylvania and a bachelor's degree in pharmacy from Purdue University. Our Board of Directors believes Mr. Hatfield is qualified to serve on our Board of Directors due to his extensive experience within the field of drug discovery and development and his broad leadership experience.

Svetlana Lucas, Ph.D. has served as a director since June 2019. Dr. Lucas currently serves as Chief Business Officer at Scribe Therapeutics, a private biotechnology company. Prior to her current role, she served as Senior Vice President, Business Development at Tizona Therapeutics, Inc. (Tizona), a clinical stage immunotherapy company, where she was responsible for the company's business development strategy and transactions, including a global strategic collaboration with AbbVie Inc. (AbbVie). Before joining Tizona, Dr. Lucas was Head of Oncology and Inflammation External R&D at Amgen Inc. (Amgen), where she oversaw business development activities, including Amgen's strategic cancer immunotherapy research collaboration and licensing agreement with Kite Pharma, and collaborated with Amgen Ventures on several investments in oncology and inflammation. Dr. Lucas joined Amgen following the acquisition of Onyx Pharmaceuticals, Inc. (Onyx), where she spearheaded the company's oncology partnering strategy and due diligence of new opportunities. Prior to Onyx, she held positions of increasing responsibility in strategy, business development and strategic marketing at Amgen, PDL BioPharma/Facet Biotech (acquired by AbbVie), and XOMA Corporation. She began her career as a strategy consultant in the Life Sciences practice of McKinsey & Company, Inc. Dr. Lucas received her Ph.D. in Molecular Biology and Biochemistry from California Institute of Technology, and an undergraduate degree in Biology from Moscow State University. Our Board of Directors believes that Dr. Lucas is qualified to serve on our Board of Directors due to her extensive business development experience in the biotherapeutics industry.

Sanjay S. Shukla, M.D., M.S. has served as our President and Chief Executive Officer and as a director since November 2017. Dr. Shukla served as our Chief Medical Officer from March 2016 to November 2017. From April 2015 to March 2016, Dr. Shukla worked in an advisory capacity for a number of companies, including as a consultant to our company from January 2016 to March 2016. Prior to that, from October 2012 to April 2015, Dr. Shukla served as Vice President and Global Head of Integrated Medical Services for Novartis, a biopharmaceutical company, where he led global medical affairs operations, with oversight for all pharma general medicines therapies, both inline and in development. Dr. Shukla served as Chief Executive Officer of RXMD, a clinical development consultancy that assisted in advancing proof of concept for early

stage drug candidates, from April 2009 to September 2012. Prior to that, Dr. Shukla served in a variety of clinical development, data analytics and drug safety roles at Vifor Pharma, a biopharmaceutical company, and Aspreva Pharmaceuticals (acquired by Vifor Pharma). Dr. Shukla received his M.D. from Howard University College of Medicine and his Bachelors of Science in microbiology and Master of Science in epidemiology and biostatistics from the University of Maryland. Our Board of Directors believes that Dr. Shukla is qualified to serve on our Board of Directors due to his experience as our Chief Executive Officer and previously as our Chief Medical Officer, as well as his medical background, experience in the life science industry and his leadership experience.

Class I: Currently Serving Until the 2022 Annual Meeting

John K. Clarke has served as Chairman of our Board of Directors since September 2005. Mr. Clarke is Managing Partner of Cardinal Partners, a venture capital firm focused on healthcare investing. He co-founded Cardinal Partners in 1997 and has served as President of CHP Management, Inc. since that time. He currently serves as a director on the boards of various privately held biotechnology companies, including Vividion Therapeutics, Inc. and Ivenix Corporation. He has also served as a director for several biotechnology and biopharmaceutical companies including Alnylam Pharmaceuticals, Inc., Momenta Pharmaceuticals, Inc., Verastem, Inc. and Sirtris Pharmaceuticals, Inc. (acquired by GlaxoSmithKline); healthcare information technology companies, including TechRx Technology Services Corporation (acquired by NDCHealth) and Visicu, Inc. (acquired by Phillips Electronics); and a privately held biopharmaceutical company, Rib-X Pharmaceuticals Inc. Mr. Clarke holds an A.B. in economics and biology from Harvard University and an M.B.A. from the Wharton School at the University of Pennsylvania. Our Board of Directors believes Mr. Clarke is qualified to serve on our Board of Directors due to his extensive experience within the field of drug discovery and development and his broad leadership experience on various public and private company boards.

Paul Schimmel, Ph.D. has served as a director since September 2005. Dr. Schimmel is currently a director of Alnylam Pharmaceuticals, Inc. (“Alnylam”), a biopharmaceutical company (from which he is retiring at Alnylam’s 2020 Annual Meeting of Stockholders), as well as a director of several private companies. He was a cofounder of Repligen Corporation, Alkermes, Inc. Cubist Pharmaceuticals, Sirtris Pharmaceuticals, and Alnylam, and a founding Director of Momenta, Inc. Dr. Schimmel is an Ernest and Jean Hahn Professor of Molecular Medicine and of Chemistry at Scripps Research. He was formerly the John D. and Catherine T. MacArthur Professor of Biochemistry and Biophysics in the Department of Biology at the Massachusetts Institute of Technology. Dr. Schimmel holds a B.A. from Ohio Wesleyan University and a Ph.D. in biochemistry and biophysics from the Massachusetts Institute of Technology. He is an elected member of the National Academy of Sciences, the National Academy of Medicine, the National Academy of Inventors, the American Philosophical Society and the American Academy of Arts and Sciences. Our Board of Directors believes Dr. Schimmel is qualified to serve on our Board of Directors due to his role as one of our scientific founders and his discoveries and scientific leadership in the field of tRNA synthetase biology and other areas important to the development of therapeutics.

Retiring Class II Director:

The person listed below is retiring from the Board of Directors as of the Annual Meeting date and is not nominated for re-election at the Annual Meeting.

James C. Blair, Ph.D. has served as a director since December 2010. Dr. Blair has been a Partner of Domain Associates, a venture capital firm with a focus on life sciences, since the company’s founding in 1985. Present Board memberships include Clovis Oncology, Inc., a biopharmaceutical company, as well as numerous private company boards. Dr. Blair currently serves on the Board of Directors of the Prostate Cancer Foundation and the Sanford Burnham Prebys Medical Discovery Institute. He is also on the advisory board of the Department of Molecular Biology at Princeton University. Dr. Blair holds a B.S.E. in electrical engineering from Princeton University and an M.S.E. and Ph.D. in electrical engineering from the University of Pennsylvania. Our Board of Directors believes that Dr. Blair is qualified to serve on our Board of Directors due to his experience in the life science industry and his years of business and leadership experience.

Board of Directors’ Role in Risk Management

Risk is inherent with every business, and how well a business manages risk can ultimately determine its success. We face a number of risks, including risks relating to our financial condition, development and commercialization activities, operations and intellectual property. Management is responsible for the day-to-day management of risks we face, while our Board of Directors, as a whole and through its committees, has responsibility for the oversight of risk management. In its risk oversight role, our Board of Directors has the responsibility to satisfy itself that the risk management processes designed and implemented by management are adequate and functioning as designed.

The role of our Board of Directors in overseeing the management of our risks is conducted primarily through committees of the Board of Directors, as disclosed in the descriptions of each of the committees below and in the charters of each of the committees. The full Board of Directors (or the appropriate board committee in the case of risks that are under the

purview of a particular committee) discusses with management our major risk exposures, their potential impact on our company, and the steps we take to manage them. When a board committee is responsible for evaluating and overseeing the management of a particular risk or risks, the chairman of the relevant committee reports on the discussion to the full Board of Directors during the committee reports portion of the next board meeting. This enables our Board of Directors and its committees to coordinate the risk oversight role, particularly with respect to interrelated risks.

Compensation Risk Assessment

We believe that although a portion of the compensation provided to our executive officers and other employees is performance-based, our executive compensation program does not encourage excessive or unnecessary risk taking. This is primarily due to the fact that our compensation programs are designed to encourage our executive officers and other employees to remain focused on both short-term and long-term strategic goals, in particular in connection with our pay-for-performance compensation philosophy. As a result, we do not believe that our compensation programs are reasonably likely to have a material adverse effect on our company.

Board of Directors and Committees of the Board of Directors

During 2019, the Board of Directors held a total of ten meetings. All directors attended at least 75% of the total number of Board meetings and of the total number of meetings of committees of the Board of Directors on which the director served during the time he or she served on the Board of Directors or such committees, except for Dr. Schimmel who attended seven of ten Board meetings.

Our Board of Directors has determined that all of our directors, except for Dr. Shukla, are independent, as determined in accordance with the rules of the Nasdaq Stock Market ("Nasdaq") and the SEC. In making such independence determination, the Board of Directors considered the relationships that each non-employee director has with us and all other facts and circumstances that the Board of Directors deemed relevant in determining their independence, including the beneficial ownership of our capital stock by each non-employee director. In considering the independence of the directors listed above, our Board of Directors considered the association of our directors with the holders of more than 5% of our common stock. There are no family relationships among any of our directors or executive officers.

The Board of Directors has a standing Audit Committee, Compensation Committee and Nominating and Corporate Governance Committee. Each of our Audit Committee, Compensation Committee and Nominating and Corporate Governance Committee is composed entirely of independent directors in accordance with current Nasdaq Marketplace Rules. Furthermore, our Audit Committee meets the enhanced independence standards established by the Sarbanes-Oxley Act of 2002 ("Sarbanes-Oxley Act") and related rulemaking of the SEC. Copies of our Audit Committee, Compensation Committee and Nominating and Corporate Governance Committee charters and our corporate governance guidelines are available, free of charge, on our website at <http://www.atyrpharma.com>, under the "Investors/Corporate Governance" link.

Audit Committee

Mr. Clarke, Mr. Coughlin and Mr. Hatfield currently serve on the Audit Committee, which is chaired by Mr. Coughlin. Our Board of Directors has determined that Mr. Coughlin qualifies as an "Audit Committee financial expert," as defined under the applicable rules of the SEC. We believe that the composition and functioning of our Audit Committee complies with all applicable requirements of the Sarbanes-Oxley Act, and all applicable SEC and Nasdaq rules and regulations. The Audit Committee's responsibilities include:

- appointing, approving the compensation of, and assessing the independence of our independent registered public accounting firm;
- approving auditing and permissible non-audit services, and the terms of such services, to be provided by our independent registered public accounting firm;
- reviewing the internal audit plan with the independent registered public accounting firm and members of management responsible for preparing our financial statements;
- reviewing and discussing with management and the independent registered public accounting firm our annual and quarterly financial statements and related disclosures as well as critical accounting policies and practices used by us;
- reviewing the adequacy of our internal control over financial reporting;

- establishing policies and procedures for the receipt and retention of accounting-related complaints and concerns;
- recommending, based upon the Audit Committee's review and discussions with management and the independent registered public accounting firm, whether our audited financial statements shall be included in our Annual Report on Form 10-K;
- monitoring the integrity of our financial statements and our compliance with legal and regulatory requirements as they relate to our financial statements and accounting matters;
- preparing the Audit Committee report required by SEC rules to be included in our annual proxy statement;
- reviewing all related party transactions for potential conflict of interest situations and approving all such transactions; and
- reviewing quarterly earnings releases.

During 2019, the Audit Committee held four meetings. Mr. Hatfield was appointed as a member of the Audit Committee on May 8, 2019.

Compensation Committee

Dr. Blair, Mr. Clarke and Mr. Coughlin currently serve on the Compensation Committee, which is chaired by Dr. Blair. We believe that the composition and functioning of our Compensation Committee complies with all applicable requirements of the Sarbanes-Oxley Act, and all applicable SEC and Nasdaq rules and regulations. The Compensation Committee's responsibilities include:

- annually reviewing and approving corporate goals and objectives relevant to the compensation of our Chief Executive Officer;
- evaluating the performance of our Chief Executive Officer in light of such corporate goals and objectives and recommending the compensation of our Chief Executive Officer to the Board of Directors for approval;
- reviewing and approving the compensation of our other officers;
- reviewing and establishing our overall management and employee compensation, philosophy and policy;
- overseeing and administering our compensation and similar plans;
- evaluating and assessing potential and current compensation advisors in accordance with the independence standards identified in the applicable Nasdaq Stock Market and SEC rules;
- retaining and approving the compensation of any compensation advisors;
- reviewing and approving our policies and procedures for the grant of equity-based awards;
- reviewing and making recommendations to our Board of Directors with respect to director compensation;
- preparing the compensation committee report required by the SEC rules to be included in our annual proxy statement;
- reviewing and discussing with management the compensation discussion and analysis to be included in our annual proxy statement or Annual Report on Form 10-K; and
- reviewing and discussing with our Board of Directors corporate succession plans for the Chief Executive Officer and other key officers.

Pursuant to its charter, the Compensation Committee has the authority to retain compensation consultants to assist in its evaluation of executive and director compensation. Our Compensation Committee may retain one or more third-party compensation advisors to provide information and advice in future years for consideration in establishing overall compensation for our executives and directors.

During 2019, the Compensation Committee held two meetings.

Nominating and Corporate Governance Committee

Dr. Blair, Mr. Clarke and Mr. Hatfield currently serve on the Nominating and Corporate Governance Committee, which is chaired by Mr. Clarke. We believe that the composition and functioning of our Nominating and Corporate Governance Committee complies with all applicable requirements of the Sarbanes-Oxley Act, and all applicable SEC and Nasdaq rules and regulations. The Nominating and Corporate Governance Committee's responsibilities include:

- developing and recommending to the Board of Directors criteria for board and committee membership;
- establishing procedures for identifying and evaluating Board of Director candidates, including nominees recommended by stockholders;
- identifying individuals qualified to become members of the Board of Directors;
- recommending to the Board of Directors the persons to be nominated for election as directors and to each of the Board's committees;
- developing and recommending to the Board of Directors a set of corporate governance guidelines; and
- overseeing the evaluation of the Board of Directors.

During 2019, the Nominating and Corporate Governance Committee held three meetings.

Board Leadership

The positions of our Chairman of the Board and Chief Executive Officer are presently separated. Separating these positions allows our Chief Executive Officer to focus on our day-to-day business, while allowing the Chairman of the Board to lead our Board of Directors in its fundamental role of providing advice to and independent oversight of management. Our Board of Directors recognizes the time, effort and energy that the Chief Executive Officer must devote to his position in the current business environment, as well as the commitment required to serve as our Chairman of the Board, particularly as our Board of Directors' oversight responsibilities continue to grow. Our Board of Directors also believes that this structure ensures a greater role for the independent directors in the oversight of our company and active participation of the independent directors in setting agendas and establishing priorities and procedures for the work of our Board of Directors.

While our Bylaws and corporate governance guidelines do not require that our Chairman of the Board and Chief Executive Officer positions be separate, our Board of Directors believes that having separate positions and having an independent outside director serve as Chairman of the Board is the appropriate leadership structure for us at this time and demonstrates our commitment to good corporate governance. Our separated Chairman of the Board and Chief Executive Officer positions are augmented by the independence of seven of our eight directors, and our three entirely independent Board committees that provide appropriate oversight in the areas described above. At executive sessions of independent directors, these directors speak candidly on any matter of interest, without the Chief Executive Officer or other executives present. The independent directors met three times in 2019 without management present. We believe this structure provides consistent and effective oversight of our management and our company.

Director Nominations

The director qualifications developed to date focus on what our Board of Directors believes to be essential competencies to effectively serve on the Board of Directors. The Nominating and Corporate Governance Committee must reassess such criteria from time to time and submit any proposed changes to the Board of Directors for approval. Presently, at a minimum, the Nominating and Corporate Governance Committee must be satisfied that each nominee it recommends: (i) has experience at a strategic or policymaking level in a business, government, non-profit or academic organization of high standing, (ii) is highly accomplished in his or her respective field, with superior credentials and recognition, (iii) is well regarded in the community and has a long-term reputation for high ethical and moral standards, (iv) has sufficient time and availability to devote to the affairs of the Company, particularly in light of the number of boards of directors on which such nominee may serve, and (v) to the extent such nominee serves or has previously served on other boards, the nominee has a demonstrated history of actively contributing at board meetings.

In addition to those minimum qualifications, the Nominating and Corporate Governance Committee recommends that our Board of Directors select persons for nomination to help ensure that:

- a majority of our Board of Directors is "independent" in accordance with Nasdaq standards;
- each of the Audit Committee, Compensation Committee and Nominating and Corporate Governance Committee be comprised entirely of independent directors; and
- at least one member of the Audit Committee shall have the experience, education and other qualifications necessary to qualify as an "Audit Committee financial expert" as defined by the rules of the SEC.

In addition to other standards the Nominating and Corporate Governance Committee may deem appropriate from time to time for the overall structure and compensation of the Board of Directors, the Nominating and Corporate Governance Committee may consider the following factors when recommending that our Board of Directors select persons for nomination:

- whether a nominee has direct experience in the biotechnology or pharmaceuticals industry or in the markets in which the Company operates; and
- whether the nominee, if elected, assists in achieving a mix of directors that represents a diversity of background and experience.

Although the Nominating and Corporate Governance Committee may consider whether nominees assist in achieving a mix of directors that represents a diversity of background and experience, which is not only limited to race, gender or national origin, we have no formal policy regarding director diversity.

The Nominating and Corporate Governance Committee adheres to the following process for identifying and evaluating nominees for the Board of Directors. First, it solicits recommendations for nominees from non-employee directors, our Chief Executive Officer, other executive officers, third-party search firms or any other source it deems appropriate. The Nominating and Corporate Governance Committee then reviews and evaluates the qualifications of proposed nominees and conducts inquiries it deems appropriate; all proposed nominees are evaluated in the same manner, regardless of who initially recommended such nominee. In reviewing and evaluating proposed nominees, the Nominating and Corporate Governance Committee may consider, in addition to the minimum qualifications and other criteria for directorship approved by our Board of Directors from time to time, all facts and circumstances that it deems appropriate or advisable, including, among other things, the skills of the proposed nominee, his or her depth and breadth of business experience or other background characteristics, his or her independence and the needs of the Board of Directors.

If the Nominating and Corporate Governance Committee decides to retain a third-party search firm to identify proposed nominees, it has sole authority to retain and terminate such firm and to approve any such firm's fees and other retention terms.

Each nominee for election as director at the Annual Meeting is recommended by the Nominating and Corporate Governance Committee and is presently a director and stands for re-election by the stockholders. From time to time, the Company may pay fees to third-party search firms to assist in identifying and evaluating potential nominees, although no such fees have been paid in connection with nominations to be acted upon at the Annual Meeting.

Pursuant to our Bylaws, stockholders who wish to nominate persons for election to the Board of Directors at an annual meeting must be a stockholder of record at the time of giving the notice, entitled to vote at the meeting, present (themselves or by proxy) at the meeting and must comply with the notice procedures in our Bylaws. A stockholder's notice of nomination to be made at an annual meeting must be delivered to our principal executive offices not less than 90 days nor more than 120 days before the anniversary date of the immediately preceding annual meeting. However, if an annual meeting is more than 30 days before or more than 60 days after such anniversary date, the notice must be delivered no later than the later of the 90th day prior to such annual meeting or the 10th day following the day on which the first public announcement of the date of such annual meeting was made. A stockholder's notice of nomination may not be made at a special meeting unless such special meeting is held in lieu of an annual meeting. The stockholder's notice must include the following information for the person making the nomination:

- name and address;
- the class and number of shares of the Company owned beneficially or of record;
- disclosure regarding any derivative, swap or other transactions which give the nominating person economic risk similar to ownership of shares of the Company or provide the opportunity to profit from an increase in the price of value of shares of the Company;
- any proxy (other than a revocable proxy given in response to a public proxy solicitation made pursuant to, and in accordance with, the Exchange Act), agreement, arrangement, understanding or relationship that confers a right to vote any shares of the Company;
- any agreement, arrangement, understanding or relationship engaged in for the purpose of acquiring, holding, disposing or voting of any shares of any class or series of capital stock of the Company;
- any rights to dividends or other distributions on the shares that are separate from the underlying shares;

- any performance-related fees that the nominating person is entitled to based on any increase or decrease in the value of any shares of the Company;
- a description of all agreements, arrangements or understandings by and between the proposing stockholder and another person relating to the proposed business (including an identification of each party to such agreement, arrangement or understanding and the names, addresses and class and number of shares owned beneficially or of record of other stockholders known by the proposing stockholder support such proposed business);
- a statement whether or not the proposing stockholder will deliver a proxy statement and form of proxy to holders of, in the case of a business proposal, at least the percentage of voting power of all shares of capital stock required to approve the proposal or, in the case of director nominations, at least the percentage of voting power of all of the shares of capital stock reasonably believed by the proposing stockholder to be sufficient to elect the nominee; and
- any other information relating to the nominating person that would be required to be disclosed in a proxy statement filed with the SEC.

With respect to proposed director nominees, the stockholder's notice must include all information required to be disclosed in a proxy statement in connection with a contested election of directors or otherwise required pursuant to Regulation 14A under the Exchange Act (including such person's written consent to being named in the proxy statement as a nominee and to serving as a director if elected).

For matters other than the election of directors, the stockholder's notice must also include a brief description of the business desired to be brought before the meeting, the reasons for conducting such business at the meeting and any material interest in such business of the stockholder(s) proposing the business.

The stockholder's notice must be updated and supplemented, if necessary, so that the information required to be provided in the notice is true and correct as of the record date for the meeting and as of the date that is ten business days prior to the meeting.

The Board of Directors, a designated committee thereof or the chairman of the meeting will determine if the procedures in our Bylaws have been followed, and if not, declare that the proposal or nomination will be disregarded. The nominee must be willing to provide any other information reasonably requested by the Nominating and Corporate Governance Committee in connection with its evaluation of the nominee's independence. There have been no material changes to the process by which stockholders may recommend nominees to our Board of Directors.

Stockholder Communications with the Board of Directors

The Board of Directors has adopted a process for stockholders to send communications to the Board of Directors. Stockholders may send correspondence to the Board of Directors, c/o the Chairman of the Board, at our principal executive offices at the address set forth above. We will forward all correspondence addressed to the Board of Directors or any individual director.

Director Attendance at Annual Meetings

Directors are encouraged to attend the Annual Meeting. Six of our directors attended the 2019 Annual Meeting of Stockholders, in person or by phone.

Compensation Committee Interlocks and Insider Participation

None of the members of the Compensation Committee is, or has at any time during the past fiscal year been, an officer or employee of the Company or had any relationship requiring disclosure under Item 404 of Regulation S-K. None of the members of the Compensation Committee has formerly been an officer of the Company. None of our executive officers serve, or in the past fiscal year, have served as a member of the Board of Directors or Compensation Committee of any other entity that has one or more executive officers serving as a member of our Board of Directors or Compensation Committee.

Director Compensation

In April 2015, our Board of Directors adopted a non-employee director compensation policy, which became effective upon the completion of our initial public offering in May 2015, that is designed to provide a total compensation package that enables us to attract and retain, on a long-term basis, high-caliber non-employee directors. In January 2016 and February 2017,

our Board of Directors adopted amendments to the policy with respect to the cash and equity component of compensation to our non-employee directors. Under this policy, as amended to date, all non-employee directors are paid cash compensation for service on the Board of Directors and committees of the Board of Directors as set forth below, prorated based on days of service during a calendar year.

| | Annual Retainer |
|---|-----------------|
| Board of Directors | |
| All non-employee members | \$ 37,500 |
| Additional retainer for Chairperson | \$ 35,000 |
| Audit Committee: | |
| Chairperson | \$ 25,000 |
| Non-Chairperson members | \$ 8,000 |
| Compensation Committee: | |
| Chairperson | \$ 10,000 |
| Non-Chairperson members | \$ 5,000 |
| Nominating and Corporate Governance Committee: | |
| Chairperson | \$ 7,500 |
| Non-Chairperson members | \$ 4,000 |

In addition, under the policy, each new non-employee director who is initially appointed or elected to our Board of Directors will receive an option grant to purchase up to 2,285 shares of common stock, which will vest in equal monthly installments during the 36 months following the grant date, subject to the director's continued service on our Board of Directors. Thereafter, on the date of each annual meeting of stockholders, each continuing non-employee director will be eligible to receive an annual option grant to purchase up to 1,428 shares of common stock, which will vest in full upon the earlier of the first anniversary of the date of grant or the date of the following annual meeting of stockholders, subject to the director's continued service on our Board of Directors. All of the foregoing options will be granted with an exercise price equal to the fair market value of our common stock on the date of grant.

We have agreed to reimburse all reasonable out-of-pocket expenses incurred by non-employee directors in attending Board and committee meetings.

Director Compensation Table—2019

The following table sets forth information with respect to the compensation earned by our non-employee directors during the fiscal year ended December 31, 2019. During 2019, Dr. Shukla did not receive compensation for his service on the Board of Directors. The compensation paid to Dr. Shukla as an employee of our company is set forth under the heading "Compensation of Executive Officers—Summary Compensation Table" below.

| Name | Fees Earned or Paid in Cash | Option Awards ⁽¹⁾ | Total |
|--|-----------------------------|------------------------------|------------|
| John K. Clarke (Chairman) ⁽²⁾ | \$ 93,000 | \$ 8,936 | \$ 101,936 |
| James C. Blair, Ph.D. ⁽³⁾ | \$ 51,500 | \$ 8,936 | \$ 60,436 |
| Timothy P. Coughlin ⁽⁴⁾ | \$ 67,500 | \$ 8,936 | \$ 76,436 |
| Jane A. Gross, Ph.D. ⁽⁵⁾ | \$ 19,059 | \$ 9,216 | \$ 28,275 |
| Jeffrey S. Hatfield ⁽⁶⁾ | \$ 46,665 ⁽⁷⁾ | \$ 8,936 | \$ 55,601 |
| Svetlana Lucas, Ph.D. ⁽⁸⁾ | \$ 19,059 | \$ 9,216 | \$ 28,275 |
| John D. Mendlein, Ph.D. ⁽⁹⁾ | \$ 18,750 | \$ — | \$ 18,750 |
| Amir H. Nashat, Sc.D. ⁽¹⁰⁾ | \$ 16,125 | \$ — | \$ 16,125 |
| Paul Schimmel, Ph.D. ⁽¹¹⁾ | \$ 37,500 | \$ 8,936 | \$ 46,436 |

(1) In accordance with SEC rules, this column reflects the aggregate grant date fair value of the option awards granted during 2019 computed in accordance with Financing Accounting Standards Board Accounting Standards Codification Topic 718 ("FASB ASC Topic 718"). For additional information on the valuation assumptions underlying the value of these options, see Part II, Item 8 "Financial Statements and Supplementary Data" of our Annual Report in the Notes to Consolidated Financial Statements, Note 6, "Stockholders Equity". These amounts do not reflect the actual economic value that may be realized by the directors upon the vesting of the stock options, the exercise of the stock options or the sale of the common stock underlying such stock options. Our non-employee directors will only realize compensation to the extent the trading price of our common stock is greater than the exercise price of such stock options.

(2) Mr. Clarke held stock options to purchase an aggregate of 7,405 shares of common stock as of December 31, 2019.

(3) Dr. Blair held stock options to purchase an aggregate of 7,405 shares of common stock as of December 31, 2019.

(4) Mr. Coughlin held stock options to purchase an aggregate of 6,569 shares of common stock as of December 31, 2019.

(5) Dr. Gross held stock options to purchase an aggregate of 2,285 shares of common stock as of December 31, 2019.

- (6) Mr. Hatfield held stock options to purchase an aggregate of 6,569 shares of common stock as of December 31, 2019.
- (7) Includes \$5,165 and \$4,000 earned in 2019 and paid in 2020 for services on the Audit Committee and on the Nominating and Corporate Governance Committee in 2019, respectively.
- (8) Dr. Lucas held stock options to purchase an aggregate of 2,285 shares of common stock as of December 31, 2019.
- (9) Dr. Mendlein resigned from our Board of Directors effective as of June 28, 2019. During 2019, Dr. Mendlein also received fees of \$90,000 pursuant to a Strategic Advisor Agreement. Dr. Mendlein held stock options to purchase an aggregate of 38,053 shares of common stock as of December 31, 2019.
- (10) Dr. Nashat completed his service on our Board of Directors as of our 2019 Annual Meeting of Stockholders on May 8, 2019 and therefore has not served on our Board of Directors since that date and did not receive the annual option grant on May 8, 2019. Dr. Nashat held stock options to purchase an aggregate of 5,977 shares of common stock as of December 31, 2019.
- (11) Dr. Schimmel held stock options to purchase an aggregate of 7,907 shares of common as of December 31, 2019.

Required Vote

The nominees receiving the highest number of affirmative votes of all the votes properly cast shall be elected as Class II directors to serve until the 2023 Annual Meeting of Stockholders or until their successors have been duly elected and qualified.

Recommendation of the Board of Directors

The Board of Directors unanimously recommends that the stockholders vote FOR the election of the nominees listed above.

PROPOSAL 2

RATIFICATION OF INDEPENDENT REGISTERED PUBLIC ACCOUNTING FIRM

The Audit Committee has appointed Ernst & Young LLP as the Company's independent registered public accounting firm for its fiscal year ending December 31, 2020. Ernst & Young LLP has audited the Company's financial statements since 2008. Representatives of Ernst & Young LLP will attend the Annual Meeting and will have the opportunity to make a statement if they desire to do so. They will also be available to respond to appropriate questions.

The Company's organizational documents do not require that the stockholders ratify the selection of Ernst & Young LLP as the Company's independent registered public accounting firm, and stockholder ratification is not binding on the Company, the Board of Directors or the Audit Committee. The Company requests such ratification, however, as a matter of good corporate practice. The ratification of the selection of Ernst & Young LLP requires the affirmative vote of a majority of the votes cast on the proposal at the Annual Meeting. Our Board of Directors, including our Audit Committee, values the opinions of our stockholders and, to the extent there is any significant vote against the ratification of the selection of Ernst & Young LLP as disclosed in this Proxy Statement, we will consider our stockholders' concerns and evaluate what actions may be appropriate to address those concerns, although the Audit Committee, in its discretion, may still retain Ernst & Young LLP.

Principal Accountant Fees and Services

The following table shows information about fees billed to the Company by Ernst & Young LLP for the fiscal years ended December 31, 2019 and 2018:

| Fees billed by Ernst & Young LLP | Fiscal Year Ended | |
|----------------------------------|-------------------|------------|
| | 2019 | 2018 |
| Audit Fees ⁽¹⁾ | \$ 300,152 | \$ 349,966 |
| Audit-Related Fees | — | — |
| Tax Fees | — | — |
| All Other Fees | — | — |
| Total | \$ 300,152 | \$ 349,966 |

(1) Includes fees associated with the annual audit of our financial statements, the reviews of our interim financial statements and the issuance of consent and comfort letters in connection with certain financing transactions and registration statements.

Audit Committee Pre-Approval Policies

The Audit Committee is directly responsible for the appointment, retention and termination, and for determining the compensation, of our independent registered public accounting firm. The Audit Committee is required to pre-approve all auditing services and the terms thereof and non-audit services (other than non-audit services prohibited under Section 10A(g) of the Exchange Act or the applicable rules of the SEC or the Public Company Accounting Oversight Board), except that pre-approval is not required for the provision of non-audit services if the "de minimus" provisions of Section 10A(i)(1)(B) of the Exchange Act are satisfied. The Audit Committee may delegate to the chairperson of the Audit Committee the authority to grant pre-approvals for audit and non-audit services, provided such approvals are presented to the Audit Committee at its next scheduled meeting. All services provided by Ernst & Young LLP during fiscal year 2019 and 2018 were pre-approved by the Audit Committee in accordance with the pre-approval policy described above.

Required Vote

The ratification of the selection of Ernst & Young LLP requires the affirmative vote of a majority of the votes cast on the proposal at the Annual Meeting (meaning the number of shares voted "for" the proposal must exceed the number of shares voted "against" the proposal). Abstentions are not considered votes cast for the foregoing purpose, and will have no effect on the vote for this proposal.

Recommendation of the Board of Directors

The Board of Directors unanimously recommends that the stockholders vote FOR the ratification of the appointment of Ernst & Young LLP as the independent registered public accounting firm of the Company for its fiscal year ending December 31, 2020.

PROPOSAL 3

APPROVAL OF AN AMENDMENT TO THE 2015 STOCK PLAN

The Board of Directors believes that stock-based incentive awards can play an important role in our success by encouraging and enabling our employees, officers, non-employee directors and consultants and those of our subsidiaries upon whose judgment, initiative and efforts we largely depend for the successful conduct of our business to acquire a proprietary interest in our company. The Board of Directors believes that providing such persons with a direct stake in our company assures a closer identification of the interests of such individuals with those of our company and our stockholders, thereby stimulating their efforts on our behalf and strengthening their desire to remain with our company.

On March 16, 2020, the Board of Directors approved an amendment to the 2015 Stock Plan, subject to stockholder approval, to increase the aggregate number of shares authorized for issuance under the 2015 Stock Plan by 350,000 shares to 951,945 shares of common stock. This amendment was designed to enhance the flexibility of the Compensation Committee in granting stock options and other awards to our officers, employees, non-employee directors and other key persons and to ensure that we can continue to grant stock options and other awards to such persons at levels determined to be appropriate by the Compensation Committee. A copy of the 2015 Stock Plan (as amended by the proposed amendment) is attached as Annex A to this Proxy Statement and is incorporated herein by reference.

Based solely on the closing price of our common stock as reported on Nasdaq on March 27, 2020, the maximum aggregate market value of the additional shares of common stock that could potentially be issued under the 2015 Stock Plan is \$1,134,000.

Summary of Material Features of the 2015 Stock Plan

The material features of the 2015 Stock Plan are:

- The maximum number of shares of common stock to be issued under the 2015 Stock Plan is 601,945, previously increased (i) on January 1, 2016 and on each January 1 thereafter until January 1, 2019 by the lesser of an amount as determined by the Compensation Committee or 4% of the number of shares of stock issued and outstanding on the immediately preceding December 31, and (ii) by 71,428 shares in an amendment to the plan approved by the Board of Directors in March 2019 and by our stockholders at the 2019 Annual Meeting of Stockholders;
- Following January 1, 2019, there were no longer any automatic annual evergreen increases;
- The award of stock options (both incentive and non-qualified options), stock appreciation rights, restricted stock, restricted stock units, unrestricted stock, cash-based awards, performance share awards and dividend equivalent rights is permitted;
- Shares reacquired on the open market will not be added to the reserved pool under the 2015 Stock Plan;
- Stock options and stock appreciation rights will not be repriced in any manner without stockholder approval;
- Without stockholder approval, the exercise price of stock options and stock appreciation rights will not be reduced and stock options and stock appreciation rights will not be otherwise repriced through cancellation in exchange for cash, other awards or stock options or stock appreciation rights with a lower exercise price;
- Any material amendment to the 2015 Stock Plan is subject to approval by our stockholders; and
- The term of the 2015 Stock Plan will expire on May 6, 2025.

Based solely on the closing price of our common stock as reported by Nasdaq on March 27, 2020 and the maximum number of shares that would have been available for awards as of such date under the 2015 Stock Plan, the maximum aggregate market value of the common stock that could potentially be issued under the 2015 Stock Plan is \$430,029. The shares of common stock underlying any awards that are forfeited, canceled or otherwise terminated, other than by exercise, under the 2015 Stock Plan and our 2014 Stock Plan, as amended (the "2014 Stock Plan"), will be added back to the shares of common stock available for issuance under the 2015 Stock Plan. Shares of common stock repurchased on the open market will not be added back to the shares of common stock available for issuance under the 2015 Stock Plan.

Rationale for Share Increase

The 2015 Stock Plan is critical to our ongoing effort to build stockholder value. Equity incentive awards are an important component of our executive and non-executive employees' compensation. Our Compensation Committee and the Board of Directors believe that we must continue to offer a competitive equity compensation program in order to attract, retain and motivate the talented and qualified employees necessary for our continued growth and success.

We manage our long-term stockholder dilution by limiting the number of equity incentive awards granted annually. The Compensation Committee carefully monitors our annual net burn rate, total dilution and equity expense in order to maximize stockholder value by granting only the number of equity incentive awards that it believes are necessary and appropriate to attract, reward and retain our employees. Our compensation philosophy reflects broad-based eligibility for equity incentive awards for high performing employees. By doing so, we link the interests of those employees with those of our stockholders and motivate our employees to act as owners of the business.

Our Board of Directors determined the size of reserved pool under the 2015 Stock Plan based on projected equity awards to anticipated new hires, projected annual equity awards to existing employees and an assessment of the magnitude of increase that our institutional investors and the firms that advise them would likely find acceptable.

Our Board of Directors also considered the amount of underwater options and overhang in the determination of the proposed share increase under the 2015 Stock Plan. All of our outstanding employee stock options are "underwater," meaning the exercise price of each of those options is greater than our current stock price as of March 16, 2020. Overhang is another measure of the dilutive impact of equity programs. Our overhang is equal to the number of shares subject to outstanding equity compensation awards (i.e., unexercised options, excluding outstanding inducement awards, and unvested stock awards) plus the number of shares available for the grant of future awards under the 2015 Stock Plan, divided by the total number of outstanding shares of common stock. As of December 31, 2019, our overhang was 15.7%. In February 2020, we completed an underwritten follow-on public offering of 4,235,294 shares of our common stock at a price to the public of \$4.25 per share. In March 2020, the underwriters fully exercised their over-allotment option resulting in the issuance of an additional 635,294 shares of common stock. As a result, as of March 16, 2020, our overhang decreased to 6.5%. The 350,000 share increase under the 2015 Stock Plan being proposed in this Proposal 3 would result in an increase to our overhang from March 16, 2020 to approximately 10.2%.

Summary of the 2015 Stock Plan

The following description of certain features of the 2015 Stock Plan is intended to be a summary only. The summary is qualified in its entirety by the full text of the 2015 Stock Plan (as amended by the plan amendment), which is attached hereto as Annex A.

Administration. The 2015 Stock Plan will be administered by the Administrator, as defined in the 2015 Stock Plan. The Administrator has full power to select, from among the individuals eligible for awards, the individuals to whom awards will be granted, to make any combination of awards to participants, and to determine the specific terms and conditions of each award, subject to the provisions of the 2015 Stock Plan. The Administrator may delegate to our Chief Executive Officer the authority to grant awards to employees who are not subject to the reporting and other provisions of Section 16 of the Exchange Act, subject to certain limitations and guidelines.

Eligibility; Plan Limits. All full-time and part-time officers, employees, non-employee directors and consultants are eligible to participate in the 2015 Stock Plan, subject to the discretion of the Administrator. As of March 16, 2020, approximately 81 individuals are currently eligible to participate in the 2015 Stock Plan, which includes 6 officers, 31 employees who are not officers, 7 non-employee directors and 37 consultants. There are certain limits on the number of awards that may be granted under the 2015 Stock Plan. For example, no more than 112,469 shares of common stock (subject to adjustment for stock splits and similar events) may be granted in the form of stock options or stock appreciation rights to any one individual for any calendar year period. Furthermore, the shares of common stock underlying any awards that are forfeited, canceled or otherwise terminated, other than by exercise, under the 2015 Stock Plan and the Company's 2014 Stock Plan, will be added back to the shares of common stock available for issuance under the 2015 Stock Plan. Shares of common stock repurchased on the open market will not be added back to the shares of common stock available for issuance under the 2015 Stock Plan.

Stock Options. The 2015 Stock Plan permits the granting of (1) options to purchase common stock intended to qualify as incentive stock options under Section 422 of the Internal Revenue Code of 1986, as amended (the "Code") and (2) options that do not so qualify. Options granted under the 2015 Stock Plan will be non-qualified options if they fail to qualify as incentive

options or exceed the annual limit on incentive stock options. Incentive stock options may only be granted to employees of the Company and its subsidiaries. Non-qualified options may be granted to any persons eligible to receive incentive options and to non-employee directors and consultants. The option exercise price of each option will be determined by the Administrator but may not be less than 100% of the fair market value of the common stock on the date of grant. Fair market value for this purpose will be the last reported sale price of the shares of common stock on Nasdaq on the date immediately preceding the grant date. The exercise price of an option may not be reduced after the date of the option grant, other than to appropriately reflect changes in our capital structure.

The term of each option will be fixed by the Administrator and may not exceed ten years from the date of grant. The Administrator will determine at what time or times each option may be exercised. Options may be made exercisable in installments and the exercisability of options may be accelerated by the Administrator in circumstances involving the optionee's death, disability, retirement or termination of employment, or a change in control. In general, unless otherwise permitted by the Administrator, no option granted under the 2015 Stock Plan is transferable by the optionee other than by will or by the laws of descent and distribution or pursuant to a domestic relations order, and options may be exercised during the optionee's lifetime only by the optionee, or by the optionee's legal representative or guardian in the case of the optionee's incapacity.

Upon exercise of options, the option exercise price must be paid in full either in cash, by certified or bank check or other instrument acceptable to the Administrator or by delivery (or attestation to the ownership) of shares of common stock that are beneficially owned by the optionee and that are not subject to risk of forfeiture. Subject to applicable law, the exercise price may also be delivered to the Company by a broker pursuant to irrevocable instructions to the broker from the optionee. In addition, the Administrator may permit non-qualified options to be exercised using a net exercise feature which reduces the number of shares issued to the optionee by the number of shares with a fair market value equal to the exercise price.

To qualify as incentive options, options must meet additional federal tax requirements, including a \$100,000 limit on the value of shares subject to incentive options that first become exercisable by a participant in any one calendar year.

Stock Appreciation Rights. The Administrator may award stock appreciation rights subject to such conditions and restrictions as the Administrator may determine. Stock appreciation rights entitle the recipient to shares of common stock equal to the value of the appreciation in the stock price over the exercise price. The exercise price is the fair market value of the common stock on the date of grant. The term of a stock appreciation right may not exceed ten years.

Restricted Stock. The Administrator may award shares of common stock to participants subject to such conditions and restrictions as the Administrator may determine. These conditions and restrictions may include the achievement of certain performance goals and/or continued employment with us through a specified restricted period. During the vesting period, restricted stock awards may be credited with dividend equivalent rights (but dividend equivalents payable with respect to restricted stock awards with vesting tied to the attainment of performance criteria shall not be paid unless and until such performance conditions are attained with respect to the restricted stock award).

Restricted Stock Units. The Administrator may award restricted stock units to participants. Restricted stock units are ultimately payable in the form of shares of common stock subject to such conditions and restrictions as the Administrator may determine. These conditions and restrictions may include the achievement of certain performance goals and/or continued employment with the Company through a specified vesting period. In the Administrator's sole discretion, it may permit a participant to make an advance election to receive a portion of his or her future cash compensation otherwise due in the form of a restricted stock unit award, subject to the participant's compliance with the procedures established by the Administrator and requirements of Section 409A of the Code. During the deferral period, the deferred stock awards may be credited with dividend equivalent rights.

Unrestricted Stock Awards. The Administrator may also grant shares of common stock which are free from any restrictions under the 2015 Stock Plan. Unrestricted stock may be granted to any participant in recognition of past services or other valid consideration and may be issued in lieu of cash compensation due to such participant.

Dividend Equivalent Rights. The Administrator may grant dividend equivalent rights to participants, which entitle the recipient to receive credits for dividends that would be paid if the recipient had held specified shares of common stock. Dividend equivalent rights granted as a component of another award (other than a stock option or stock appreciation right) may be paid only if the related award becomes vested. Dividend equivalent rights may be settled in cash, shares of common stock or a combination thereof, in a single installment or installments, as specified in the award.

Cash-Based Awards. The Administrator may grant cash bonuses under the 2015 Stock Plan to participants. The cash bonuses may be subject to the achievement of certain performance goals.

Performance Share Awards. The Administrator may grant performance share awards to any participant which entitle the recipient to receive shares of common stock upon the achievement of certain performance goals and such other conditions as the Administrator shall determine. Subject to the Administrator's discretion to accelerate in the case of retirement, death, disability or a change in control, these awards granted to employees will have a vesting period of at least one year except in the case of a "sale event," as defined in the 2015 Stock Plan, and such other limitations and conditions as the Administrator shall determine.

Change of Control Provisions. The 2015 Stock Plan provides that upon the effectiveness of a "sale event," as defined in the 2015 Stock Plan, except as otherwise provided by the Compensation Committee in the award agreement, all stock options, stock appreciation rights and other awards will be assumed or continued by the successor entity and adjusted accordingly to take into account the impact of the transaction. To the extent, however, that the parties to such sale event do not agree that all stock options, stock appreciation rights or any other awards shall be assumed or continued, then such stock options and stock appreciation rights shall terminate at the effective time of such sale event. In addition, the Company may make or provide for payment, in cash or in kind, to participants holding options and stock appreciation rights equal to the difference between the per share cash consideration and the exercise price of the options or stock appreciation rights. The Administrator shall also have the option to make or provide for a payment, in cash or in kind, to grantees holding other awards in an amount equal to the per share cash consideration multiplied by the number of vested shares under such awards. All awards will terminate in connection with a sale event unless they are assumed by the successor entity.

Adjustments for Stock Dividends, Stock Splits, Etc. The 2015 Stock Plan requires the Administrator to make appropriate adjustments to the number of shares of common stock that are subject to the 2015 Stock Plan, to certain limits in the 2015 Stock Plan, and to any outstanding awards to reflect stock dividends, stock splits, extraordinary cash dividends and similar events.

Tax Withholding. Participants in the 2015 Stock Plan are responsible for the payment of any federal, state or local taxes that the Company is required by law to withhold upon the exercise of options or stock appreciation rights or vesting of other awards. Subject to approval by the Administrator, participants may elect to have their tax withholding obligations satisfied by authorizing the Company to withhold shares of common stock to be issued pursuant to exercise or vesting. The Administrator may also require awards to be subject to mandatory share withholding up to the required withholding amount.

Amendments and Termination. The Board of Directors may at any time amend or discontinue the 2015 Stock Plan and the Administrator may at any time amend or cancel any outstanding award for the purpose of satisfying changes in the law or for any other lawful purpose. However, no such action may adversely affect any rights under any outstanding award without the holder's consent. To the extent required under the rules of Nasdaq, any amendments that materially change the terms of the 2015 Stock Plan will be subject to approval by our stockholders. Amendments shall also be subject to approval by our stockholders if and to the extent determined by the Administrator to be required by the Code to preserve the qualified status of incentive options.

Effective Date of Plan. The 2015 Stock Plan was approved by our Board of Directors on April 25, 2015. Awards of incentive options may be granted under the 2015 Stock Plan until April 25, 2025. No other awards may be granted under the 2015 Stock Plan after the date that is ten years from the date the 2015 Stock Plan was effective.

New Plan Benefits

Because the grant of awards under the 2015 Stock Plan is within the discretion of the Administrator, we cannot determine the dollar value or number of shares of common stock that will in the future be received by or allocated to any participant in the 2015 Stock Plan, except with respect to non-employee directors. Under our non-employee director compensation policy, each continuing non-employee director will be eligible to receive an annual option grant to purchase up to 1,428 shares of common stock. On and after the date of the Annual Meeting, any such stock options will be granted under the 2015 Stock Plan if this Proposal 3 is approved by our stockholders. For additional information regarding our current compensation program for non-employee directors, please see "Director Compensation" above.

| Name and Position | Number of Shares Subject to Awards (#) |
|---|---|
| All current directors who are not executive officers as a group (7 persons) | 9,996 per calendar year |

Awards Granted under the 2015 Stock Plan

The following table shows, for each of the individuals and the various groups indicated, the number of shares subject to awards that have been granted (even if not currently outstanding) under the 2015 Stock Plan since its approval by our stockholders as of March 16, 2020.

| Name and Position | Number of Shares Subject to Awards (#) |
|--|--|
| Sanjay S. Shukla, M.D., M.S., <i>President and Chief Executive Officer</i> | 129,001 |
| Jill M. Broadfoot, Chief Financial Officer | 28,715 |
| Nancy E. Denyes, General Counsel | 40,010 |
| All current executive officers, as a group | 197,726 |
| All current directors who are not executive officers, as a group | 39,923 |
| Each nominee for election as a director: | |
| Timothy P. Coughlin | 6,569 |
| Jane A. Gross, Ph.D. | 2,285 |
| Each associate of any executive officers, current directors or director nominees | — |
| Each other persons who received or is to receive 5% of awards | — |
| All employees, including all current officers who are not executive officers, as a group | 212,347 |

Tax Aspects Under the Code

The following is a summary of the principal federal income tax consequences of certain transactions under the 2015 Stock Plan. It does not describe all federal tax consequences under the 2015 Stock Plan, nor does it describe state or local tax consequences.

Incentive Options. No taxable income is generally realized by the optionee upon the grant or exercise of an incentive option. If shares of common stock issued to an optionee pursuant to the exercise of an incentive option are sold or transferred after two years from the date of grant and after one year from the date of exercise, then (i) upon sale of such shares, any amount realized in excess of the option price (the amount paid for the shares) will be taxed to the optionee as a long-term capital gain, and any loss sustained will be a long-term capital loss, and (ii) the Company will not be entitled to any deduction for federal income tax purposes. The exercise of an incentive option will give rise to an item of tax preference that may result in alternative minimum tax liability for the optionee.

If shares of common stock acquired upon the exercise of an incentive option are disposed of prior to the expiration of the two-year and one-year holding periods described above (a "disqualifying disposition"), generally (i) the optionee will realize ordinary income in the year of disposition in an amount equal to the excess (if any) of the fair market value of the shares of common stock at exercise (or, if less, the amount realized on a sale of such shares of common stock) over the option price thereof, and (ii) we will be entitled to deduct such amount. Special rules will apply where all or a portion of the exercise price of the incentive option is paid by tendering shares of common stock.

If an incentive option is exercised at a time when it no longer qualifies for the tax treatment described above, the option is treated as a non-qualified option. Generally, an incentive option will not be eligible for the tax treatment described above if it is exercised more than three months following termination of employment (or one year in the case of termination of employment by reason of disability). In the case of termination of employment by reason of death, the three-month rule does not apply.

Non-Qualified Options. No income is realized by the optionee at the time a non-qualified option is granted. Generally (i) at exercise, ordinary income is realized by the optionee in an amount equal to the difference between the option price and the fair market value of the shares of common stock on the date of exercise, and we receive a tax deduction for the same amount, and (ii) at disposition, appreciation or depreciation after the date of exercise is treated as either short-term or long-term capital gain or loss depending on how long the shares of common stock have been held. Special rules will apply where all or a portion of the exercise price of the non-qualified option is paid by tendering shares of common stock. Upon exercise, the optionee will also be subject to Social Security taxes on the excess of the fair market value over the exercise price of the option.

Other Awards. The Company generally will be entitled to a tax deduction in connection with other awards under the 2015 Stock Plan in an amount equal to the ordinary income realized by the participant at the time the participant recognizes such income. Participants typically are subject to income tax and recognize such tax at the time that an award is exercised, vests or becomes non-forfeitable, unless the award provides for a further deferral.

Parachute Payments. The vesting of any portion of an award that is accelerated due to the occurrence of a change in control (such as a sale event) may cause a portion of the payments with respect to such accelerated awards to be treated as "parachute payments" as defined in the Code. Any such parachute payments may be non-deductible to the Company, in whole or in part, and may subject the recipient to a non-deductible 20% federal excise tax on all or a portion of such payment (in addition to other taxes ordinarily payable).

Limitation on Deductions. Under Section 162(m) of the Code, compensation paid to any publicly held corporation's "covered employees" (as defined under Section 162(m) of the Code) that exceeds \$1 million per taxable year for any covered employee is generally non-deductible. Prior to the enactment of the Tax Cuts and Jobs Act, compensation that qualified as "performance-based compensation" under Section 162(m) of the Code was not subject to this deduction limitation. Pursuant to the Tax Cuts and Jobs Act, this exception for "performance-based compensation" under Section 162(m) of the Code was repealed with respect to taxable years beginning after December 31, 2017, except that certain transition relief is provided for remuneration provided pursuant to a written binding contract which was in effect on November 2, 2017 and which was not modified in any material respect on or after such date. As a result, compensation paid to any of our "covered employees" in excess of \$1 million per taxable year generally will not be deductible unless, among other requirements, it is intended to qualify, and is eligible to qualify, as "performance-based compensation" under Section 162(m) of the Code pursuant to the transition relief described above. Because of certain ambiguities and uncertainties as to the application and interpretation of Section 162(m) of the Code, as well as other factors beyond the control of the Compensation Committee, no assurance can be given that any award granted under the 2015 Stock Plan will be eligible for such transition relief and, therefore, eligible for the "performance-based compensation" exception under Section 162(m) of the Code.

Equity Compensation Plan Information

The following table provides information as of December 31, 2019 regarding shares of common stock that may be issued under our equity compensation plans, consisting of our 2015 Stock Plan, our 2015 Employee Stock Purchase Plan (the "ESPP"), and our 2014 Stock Plan.

| Plan Category | Equity Compensation Plan Information | | |
|---|--|---|--|
| | Number of Securities to be Issued upon Exercise of Outstanding Options, Warrants and Rights (a)(1) | Weighted Average Exercise Price of Outstanding Options, Warrants and Rights (b) (2) | Number of Securities Remaining Available for Future Issuance under Equity Compensation Plan (Excluding Securities Reflected in Column (a)) (c) |
| Equity compensation plans approved by security holders: 2014 Stock Plan, 2015 Stock Plan and ESPP (3) | 349,268 | \$ 53.04 (4) | 339,696 |
| Equity compensation plans not approved by security holders: Inducement option grants (5) | 14,285 | \$ 11.41 | — |
| Total | 363,553 | | 339,696 |

(1) Includes 351,078 shares subject to outstanding stock options and 12,475 shares subject to outstanding restricted stock unit ("RSU") awards.

(2) The weighted-average exercise price is calculated based solely on outstanding stock options and does not reflect the shares that will be issued upon the vesting and settlement of outstanding awards of RSUs, which have no exercise price.

(3) The number of shares of stock available for issuance under the 2015 Stock Plan was automatically increased each January 1, from January 1, 2016 until January 1, 2019, by the lesser of (i) 1,840,000 shares of common stock, (ii) 4% of the outstanding number of shares of the Company's common stock on the immediately preceding December 31, and (iii) an amount as determined by the Compensation Committee of the Board of Directors. The number of shares of stock available for issuance under the ESPP was automatically increased each January 1, 2016 until January 1, 2019, by the lesser of 1% of the outstanding number of shares of common stock on the immediately preceding December 31 or such lesser amount of shares as determined by the Compensation Committee of the Board of Directors. We no longer grant new awards under our 2014 Stock Plan, and any awards previously granted under such plan prior to our initial public offering that are forfeited, canceled, reacquired by us prior to vesting satisfied without the issuance of stock or otherwise terminated (other than by exercise) are added to shares available for issuance under the 2015 Stock Plan.

(4) Does not include purchase rights accruing under the ESPP because the purchase right (and therefore the number of shares to be purchased) will not be determined until the end of the purchase period.

(5) In July 2018, we granted a non-qualified stock option as an inducement award in connection with the hiring of Ms. Broadfoot. This option grant was an inducement grant issued outside of our 2015 Stock Plan in accordance with Nasdaq Listing Rule 5635(c)(4). The option grant was granted pursuant to a form of non-qualified stock option agreement non-plan inducement grant previously approved by the Board of Directors. Certain terms of the option are governed by the terms and conditions of the 2015 Stock Plan (other than those applicable to the share reserve) as if it had actually been issued under the 2015 Stock Plan.

Vote Required

The approval of the amendment to the 2015 Stock Plan requires the affirmative vote of a majority of the votes cast on the proposal at the Annual Meeting (meaning the number of shares voted "for" the proposal must exceed the number of shares voted "against" the proposal). Abstentions and broker non-votes are not considered votes cast for the foregoing purpose, and will have no effect on the vote for this proposal.

Recommendation of the Board of Directors

The Board of Directors unanimously recommends that the stockholders vote FOR the approval of the amendment to the 2015 Stock Plan.

PROPOSAL 4

APPROVAL OF INCREASE IN NUMBER OF AUTHORIZED SHARES OF COMMON STOCK

Our Board of Directors is recommending that the stockholders approve an amendment to the Company's Restated Certificate of Incorporation (the "Charter") to increase the Company's authorized number of shares of common stock from 10,714,286 to 21,425,000 shares. The form of the proposed Certificate of Amendment is attached to this proxy statement as Annex B.

As of March 16, 2020, there were: (i) 9,352,498 shares of common stock outstanding; (ii) 13,904 shares of common stock reserved for future issuance upon exercise of warrants; (iii) 489,148 shares of common stock reserved for issuance upon exercise or vesting and settlement of outstanding stock options and RSUs; (iv) 132,725 shares available for additional grants under our 2015 Stock Plan (not including the increase set forth in Proposal 3); and (v) 78,697 shares of common stock reserved for issuance under our ESPP. Thus, as of March 16, 2020, we had 647,314 unissued and unreserved authorized shares of common stock (not including the increase of shares requested pursuant to Proposal 3).

Rationale for the Increase in Authorized Shares

Our Board of Directors believes it is in the best interest of our company to increase the number of authorized shares of common stock to give our company greater flexibility in considering and planning for future potential business needs. The increase in the authorized shares of common stock to 21,425,000 shares is expected to create capital liquidity to permit and enhance opportunities for growth. Unless further stockholder approval is required for a proposed issuance of additional shares by the rules of the Nasdaq Stock Market or other applicable laws or regulations, the additional shares may be used for various purposes without further stockholder approval. These purposes may include: raising capital; establishing strategic relationships or licensing arrangements with other companies; expanding our business through the acquisition of other businesses, products or technologies; providing equity incentives to employees, officers and directors; and other purposes.

As of the date of this Proxy Statement, the Board of Directors has not approved any plans or proposals to issue any of the additional shares of our common stock that would become authorized for issuance if this proposal is approved, other than pursuant to our various employee and director equity plans and pursuant to our Sales Agreement with H.C. Wainwright & Co., LLC, under which we may elect to issue and sell shares of our common stock having an aggregate offering price of up to approximately \$10,000,000, of which \$3,318,990 had sold as of the date of this Proxy Statement. The Board of Directors desires to have the shares available to provide additional flexibility to use our common stock for financing and business purposes in the future. From our inception through December 31, 2019, we have financed our operations primarily through the sale of equity securities and debt financings. To date, we have not derived any revenue from product sales. We expect our expenses to increase in connection with our ongoing activities, particularly as we continue to advance our lead product candidate, ATY1923, in clinical development, continue our research and development activities with respect to potential product candidates based on tRNA synthetase biology and Neuropilin-2 biology, and seek marketing approval for products that we may develop. In addition, if we obtain marketing approval for any of our product candidates, we expect to incur significant commercialization expenses related to product sales, marketing, manufacturing and distribution. Until we can generate sufficient product revenues, if ever, we expect to finance our cash needs through a combination of equity offerings, grant funding, collaborations, strategic partnerships and/or licensing arrangements, and when we are closer to commercialization of our product candidates potentially through debt financings. We may use some of the additional authorized shares for a capital raising transaction if we have an appropriate opportunity. If the authorization of an increase in the available common stock is postponed until the foregoing specific needs arise, the delay and expense incident to obtaining approval of the stockholders at that time could impair our ability to meet our objectives.

If this proposal is not approved by our stockholders, our financing alternatives will likely be limited by the lack of sufficient unissued and unreserved authorized shares of common stock, and stockholder value may be harmed by this limitation. In addition, our future success depends upon our ability to attract, retain and motivate highly-skilled scientific, commercial and managerial employees, and if this proposal is not approved by our stockholders, the lack of sufficient unissued and unreserved authorized shares of common stock to provide future equity incentive opportunities as our Board of Directors or the Compensation Committee deems appropriate could adversely impact our ability to achieve these goals. In short, if our stockholders do not approve this proposal, we may not be able to access the capital markets, complete corporate collaborations, partnerships or other strategic transactions, attract, retain and motivate employees, and pursue other business opportunities integral to our growth and success.

Effects of the Increase in Authorized Shares

The additional common stock to be authorized by adoption of the amendment would have rights identical to our currently outstanding common stock. Adoption of the proposed amendment and issuance of the common stock would not affect the rights of the holders of our currently outstanding common stock, except for, with respect to the issuance of additional shares, effects incidental to increasing the number of shares of our common stock outstanding, such as dilution of earnings per share, if any, and voting rights of current holders of our common stock.

The additional shares of common stock that would become available for issuance if the proposal is adopted could also be used by us to oppose a hostile takeover attempt or to delay or prevent changes in control or management of our company. For example, without further stockholder approval, the Board of Directors could strategically sell shares of common stock in a private transaction to purchasers who would oppose a takeover or favor the current Board of Directors. Although this proposal to increase the authorized common stock has been prompted by business and financial considerations and not by the threat of any hostile takeover attempt (nor is our Board of Directors currently aware of any such attempts directed at our company), stockholders should be aware that approval of the proposal could facilitate future efforts by us to deter or prevent changes in control of our company, including transactions in which our stockholders might otherwise receive a premium for their shares over then current market prices.

Timing of the Proposed Charter Amendment

If the authorized share increase is approved, as soon as practicable after the Annual Meeting, we will file the Certificate of Amendment with the office of the Secretary of State of Delaware to implement the increase in the authorized shares of our common stock. Upon approval and following such filing with the Secretary of State of Delaware, the Certificate of Amendment will become effective on the date it is filed.

Vote Required

Assuming a quorum is present, the affirmative vote of a majority of outstanding shares of stock entitled to vote as of the record date is required to approve the amendment of the Charter to increase the authorized number of shares of common stock from 10,714,286 to 21,425,000 shares. You may vote "for", "against", or "abstain" from voting on this proposal. For purposes of determining whether this proposal has passed, abstentions will have the effect of a vote "against" the increase in authorized shares of common stock.

Recommendation of the Board of Directors

The Board of Directors unanimously recommends that stockholders vote FOR the amendment to the Charter to increase the Company's authorized number of shares of common stock from 10,714,286 to 21,425,000 shares.

PROPOSAL 5

AUTHORIZATION TO ADJOURN THE ANNUAL MEETING

General

If the Annual Meeting is convened and a quorum is present, but there are not sufficient votes to approve Proposal 3 or Proposal 4, our proxy holders may move to adjourn the Annual Meeting at that time in order to enable our Board of Directors to solicit additional proxies.

In this proposal, we are asking our stockholders to authorize the holder of any proxy solicited by our Board of Directors to vote in favor of granting discretionary authority to the proxy holders, and each of them individually, to adjourn the Annual Meeting to another time and place, if necessary, to solicit additional proxies in the event that there are not sufficient votes to approve Proposal 3 or Proposal 4. If our stockholders approve this proposal, we could adjourn the Annual Meeting and any adjourned session of the Annual Meeting and use the additional time to solicit additional proxies, including the solicitation of proxies from our stockholders that have previously voted. Among other things, approval of this proposal could mean that, even if we had received proxies representing a sufficient number of votes to defeat Proposal 3 or Proposal 4, we could adjourn the Annual Meeting without a vote on such proposals and seek to convince our stockholders to change their votes in favor of such proposals.

If it is necessary to adjourn the Annual Meeting, no notice of the adjourned meeting is required to be given to our stockholders, other than an announcement at the Annual Meeting of the time and place to which the Annual Meeting is adjourned, so long as the meeting is adjourned for 30 days or less and no new record date is fixed for the adjourned meeting. At the adjourned meeting, we may transact any business which might have been transacted at the original meeting.

Vote Required

Approval of this Proposal 5 requires the affirmative vote of the majority of the votes cast (meaning the number of shares voted "for" the proposal must exceed the number of shares voted "against" the proposal). Abstentions and broker non-votes are not considered votes cast for the foregoing purpose, and will have no effect on the vote for this proposal.

Recommendation of the Board of Directors

The Board of Directors unanimously recommends that stockholders vote FOR this proposal to authorize the adjournment of the Annual Meeting.

EXECUTIVE OFFICERS

The following table sets forth certain information about our executive officers as of the date of this proxy:

| Name | Age | Position |
|------------------------------|-----|---|
| Sanjay S. Shukla, M.D., M.S. | 48 | President, Chief Executive Officer and Director |
| Jill M. Broadfoot | 58 | Chief Financial Officer |
| Nancy E. Denyes | 52 | General Counsel and Corporate Secretary |

Executive Officers

Sanjay S. Shukla, M.D., M.S. has served as our President and Chief Executive Officer and as a director since November 2017. Dr. Shukla served as our Chief Medical Officer from March 2016 to November 2017. From April 2015 to March 2016, Dr. Shukla worked in an advisory capacity for a number of companies, including as a consultant to our company from January 2016 to March 2016. Prior to that, from October 2012 to April 2015, Dr. Shukla served as Vice President and Global Head of Integrated Medical Services for Novartis, a biopharmaceutical company, where he led global medical affairs operations, with oversight for all pharma general medicines therapies, both inline and in development. Dr. Shukla served as Chief Executive Officer of RXMD, a clinical development consultancy that assisted in advancing proof of concept for early stage drug candidates, from April 2009 to September 2012. Prior to that, Dr. Shukla served in a variety of clinical development, data analytics and drug safety roles at Vifor Pharma, a biopharmaceutical company, and Aspreva Pharmaceuticals (acquired by Vifor Pharma). Dr. Shukla received his M.D. from Howard University College of Medicine and his Bachelors of Science in microbiology and Master of Science in epidemiology and biostatistics from the University of Maryland. Our Board of Directors believes that Dr. Shukla is qualified to serve on our Board of Directors due to his experience as our Chief Executive Officer and previously as our Chief Medical Officer, as well as his medical background, experience in the life science industry and his leadership experience.

Jill M. Broadfoot has served as our Chief Financial Officer since July 2018. From January 2017 to July 2018, Ms. Broadfoot served as Chief Financial Officer of Emerald Health Pharmaceuticals Inc. and Emerald Health Bioceticals Inc., where she was responsible for establishing operations for the U.S.-based pharmaceutical and biocetrical entities as well as the establishment of operations, corporate governance, finance and accounting and investor relations functions, among others. Prior to Emerald Health, Ms. Broadfoot served as Vice President, U.S. Corporate Controller at GW Pharmaceuticals, from May 2016 to January 2017. While at GW Pharmaceuticals, her responsibilities included establishing U.S. commercial operations and implementing U.S. public company financial and accounting standards in connection with the transfer of corporate operations from the U.K. to the U.S. Prior to joining GW Pharmaceuticals, Ms. Broadfoot served as Chief Financial Officer of Vical Inc., from October 2004 to March 2013, where she had oversight of finance, investor relations, manufacturing, information technology, human resources, and business development. Prior to that, Ms. Broadfoot held various positions at DJO Global, Inc., most recently as Vice President of Finance, and served as an audit manager at Ernst & Young LLP. Ms. Broadfoot holds a B.S. in business administration and accounting from San Diego State University and is a Certified Public Accountant.

Nancy E. Denyes has served as our General Counsel since February 2019 and as our Corporate Secretary since January 2015. Ms. Denyes served as our Vice President, Legal Affairs from October 2014 to February 2019, and provided consulting services to us from 2013 to 2014. Ms. Denyes practiced law in the corporate department at Cooley LLP and was named partner in 2000. Her practice at Cooley was focused on securities and corporate matters, including private financings, public offerings, mergers and acquisitions and corporate governance and disclosure issues. Ms. Denyes holds a J.D. from the University of California, Berkeley School of Law and a B.A. in economics and business from the University of California, Los Angeles.

COMPENSATION OF EXECUTIVE OFFICERS

The following table presents information regarding the total compensation earned by each individual who served as our chief executive officer at any time during the fiscal year ended December 31, 2019, and our two other most highly compensated executive officers who were serving as executive officers as of December 31, 2019. We refer to these officers in this Proxy Statement as our named executive officers. The following table also sets forth information regarding total compensation earned by each of our named executive officers during the fiscal year ending December 31, 2019 and 2018.

SUMMARY COMPENSATION TABLE

The following table presents all of the compensation awarded to or earned by or paid to our named executive officers during the fiscal years indicated below.

| Name and Principal Position | Year | Salary (\$) | Stocks Awards (\$) ⁽¹⁾ | Option Awards (\$) ⁽¹⁾ | Non-Equity Incentive Plan Compensation (\$) ⁽²⁾ | All Other Compensation (\$) ⁽³⁾ | Total (\$) |
|--|------|-------------|-----------------------------------|-----------------------------------|--|--|------------|
| Sanjay S. Shukla, M.D., M.S. <i>President and Chief Executive Officer</i> | 2019 | 450,000 | 25,860 | 82,400 | 95,625 | 10,076 | 663,961 |
| | 2018 | 450,000 | — | 780,000 | 140,549 | 9,916 | 1,380,465 |
| Jill M. Broadfoot ⁽⁴⁾ <i>Chief Financial Officer</i> | 2019 | 350,000 | 12,930 | 20,600 | 59,500 | 11,594 | 454,624 |
| | 2018 | 148,526 | — | 121,880 | 58,324 | 5,393 | 334,123 |
| Nancy E. Denyes ⁽⁵⁾ <i>General Counsel</i> | 2019 | 335,000 | — | 51,500 | 49,831 | 12,932 | 449,263 |

- (1) Amounts shown reflect aggregate full grant date fair value of equity-based awards granted during the year in accordance with FASB ASC Topic 718. Pursuant to FASB ASC Topic 718, the amounts shown exclude the impact of estimated forfeitures related to service-based vesting conditions.
- (2) The amounts reported for 2018 reflect the cash bonus determined by our Compensation Committee (for the named executive officers other than Dr. Shukla), and by our Board of Directors upon recommendation of our Compensation Committee (for Dr. Shukla), based on certain performance goals and achievement of certain developmental, clinical or regulatory milestones as specified by our Board of Directors upon recommendation of our Compensation Committee. The amounts reported for 2019 represent bonuses awarded by our Board of Directors on February 25, 2020 based upon recommendation of our Compensation Committee, and based on certain performance goals and achievement of certain developmental, clinical or regulatory milestones as specified by our Board of Directors upon recommendation of the Compensation Committee.
- (3) The amounts reported in 2019 in this column include: (i) 401(k) employer match of \$9,500 and life insurance premium of \$576 to Dr. Shukla; (ii) 401(k) employer match of \$11,018 and life insurance premium of \$576 to Ms. Broadfoot; and (iii) HSA employee contribution of \$3,900, 401(k) employer match of \$8,456 and life insurance premium of \$576 to Ms. Denyes.
- (4) Ms. Broadfoot joined our company and was appointed as our Chief Financial Officer on July 30, 2018.
- (5) Ms. Denyes was promoted to General Counsel on February 6, 2019 and did not serve as an executive officer in 2018.

Base Salaries. Our Compensation Committee reviews the base salaries of our executive officers, including our named executive officers, from time to time and makes adjustments as it determines to be reasonable and necessary to reflect the scope of an executive officer's performance, contributions, responsibilities, experience, prior salary level, position (in the case of a promotion) and market conditions.

Bonuses. In January 2016, the Board of Directors adopted our Senior Executive Cash Incentive Bonus Plan ("Bonus Plan"), which applies to certain key executives ("Executives"), that are recommended by the Compensation Committee and selected by the Board of Directors. The Bonus Plan provides for bonus payments based upon the attainment of performance targets established by the Compensation Committee and related to operational and financial metrics with respect to our company or any of our subsidiaries ("Performance Goals"), which may include achievement of specified research and development, publication, clinical and/or regulatory milestones, total shareholder return, earnings before interest, taxes, depreciation and amortization, net income (loss) (either before or after interest, taxes, depreciation, stock compensation expense, restructuring charges and/or amortization), changes in the market price of our common stock, economic value-added, funds from operations or similar measure, sales or revenue, acquisitions or strategic transactions, operating income (loss), cash flow (including, but not limited to, operating cash flow and free cash flow), return on capital, assets, equity, or investment, return on sales, gross or net profit levels, productivity, expense, margins, operating efficiency, customer satisfaction, working capital, earnings (loss) per share of our common stock, sales or market shares and number of customers. Any bonuses paid under the Bonus Plan will be based upon objectively determinable bonus formulas that tie such bonuses to one or more performance targets relating to the Performance Goals. The bonus formulas will be adopted in each performance period by the Compensation Committee and communicated to each Executive. No bonuses will be paid under the Bonus Plan unless and until the Compensation Committee makes a determination with respect to the attainment of the performance objectives. Notwithstanding the foregoing, the Compensation Committee may adjust bonuses payable under the Bonus Plan based on achievement of individual performance goals or pay bonuses (including, without limitation, discretionary bonuses) to Executives under the Bonus Plan based upon such other terms and conditions as the Compensation Committee may in its discretion determine.

Equity Incentive Compensation. We generally grant stock options to our employees, including our named executive officers, in connection with their initial employment with us. We also have historically granted stock options on an annual basis as part of annual performance reviews of our employees.

Outstanding Equity Awards at Fiscal Year-End

The following table sets forth certain information with respect to outstanding equity awards held by each of our named executive officers as of December 31, 2019:

| Name | Vesting Commencement Date | Option Awards | | | | Option Exercise Price (\$) | Option Expiration Date | Stock Awards | | Market Value of Shares that have not Vested (\$) |
|------------------------------|---------------------------|---|---|--|--|----------------------------|------------------------|--|--------|--|
| | | Number of Securities Underlying Unexercised Options (#) Exercisable | Number of Securities Underlying Unexercised Options (#) Unexercisable | Equity Incentive Plan Awards: Number of Securities Underlying Unexercised Unearned Options (#) | Number of Shares of Stock that have Vested (#) | | | Number of Shares of Stock that have not Vested (#) | | |
| Sanjay S. Shukla, M.D., M.S. | 3/30/2016 | 10,914 (1) | 728 (1) | — | 68.04 | 3/30/2026 | | | | |
| | 9/13/2016 | 1,596 (2) | 368 (2) | — | 42.84 | 9/13/2026 | | | | |
| | 2/7/2017 | 3,288 (2) | 1,354 (2) | — | 46.20 | 2/7/2027 | | | | |
| | 11/1/2017 | 16,741 (2) | 15,401 (2) | — | 56.00 | 11/1/2027 | | | | |
| | 2/6/2018 | 9,821 (2) | 11,607 (2) | — | 46.20 | 2/6/2028 | | | | |
| | 2/6/2019 | 2,976 (2) | 11,309 (2) | — | 7.24 | 2/6/2029 | | | | |
| Jill M. Broadfoot | 7/30/2018 | 5,060 (1) | 9,225 (1) | — | 11.41 | 7/30/2028 | | | | |
| | 2/6/2019 | 744 (2) | 2,827 (2) | — | 7.24 | 2/6/2029 | | | | |
| | 2/6/2019 | — | — | — | — | — | — | 3,571 (3) | 14,891 | |
| Nancy E. Denyes | 10/10/2014 | 2,542 (1) | — | — | 248.36 | 10/10/2024 | | | | |
| | 4/17/2015 | 448 (2) | — | — | 128.10 | 4/17/2025 | | | | |
| | 5/6/2015 | 628 (2) | — | — | 196.00 | 5/6/2025 | | | | |
| | 10/1/2015 | 1,214 (2) | — | — | 143.36 | 10/1/2025 | | | | |
| | 1/27/2016 | 1,398 (2) | 30 (2) | — | 85.96 | 1/27/2026 | | | | |
| | 9/13/2016 | 2,119 (2) | 488 (2) | — | 42.84 | 9/13/2026 | | | | |
| | 2/7/2017 | 1,771 (2) | 729 (2) | — | 46.20 | 2/7/2027 | | | | |
| | 2/6/2018 | 1,637 (2) | 1,934 (2) | — | 46.20 | 2/6/2028 | | | | |
| | 5/16/2018 | 1,885 (2) | 1,686 (2) | — | 11.90 | 5/16/2028 | | | | |
| | 5/16/2018 | — | — | — | — | — | 893 | 892 (3) | 3,720 | |
| | 2/6/2019 | 1,860 | 7,068 | — | 7.24 | 2/6/2029 | | | | |

- (1) 1/4th of the shares subject to the option vest one year from Vesting Commencement Date and the remaining shares subject to the option vest in 36 equal monthly installments following the one-year anniversary of the Vesting Commencement Date. The option is subject to full acceleration in the event the employee is terminated by our company without Cause or resigns for Good Reason within the period commencing two months prior to and ending 12 months following a Change in Control or Sale Event (as such capitalized terms are defined in the 2015 Stock Plan, as applicable or the respective stock option agreements evidencing such stock option).
- (2) 1/48th of the total shares subject to the option vest monthly from the Vesting Commencement Date set forth in the table above. The option is subject to full acceleration in the event the employee is terminated by our company without Cause or resigns for Good Reason within the period commencing two months prior to and ending 12 months following a Change in Control or Sale Event (as such capitalized terms are defined in the 2015 Stock Plan, as applicable or the respective stock option agreements evidencing such stock option).
- (3) Vests in two equal annual installments from Vesting Commencement Date set forth in the table above. The award is subject to accelerated vesting upon termination without cause upon a Change of Control.

401(k) Savings Plan and Other Benefits. We maintain a tax-qualified retirement plan (“401(k) Plan”), that provides eligible U.S. employees with an opportunity to save for retirement on a tax advantaged basis. Eligible employees are able to defer eligible compensation subject to applicable annual Code limits. Employees’ pre-tax contributions are allocated to each participant’s individual account and are then invested in selected investment alternatives according to the participants’ directions. Employees are immediately and fully vested in their contributions. Our 401(k) Plan is intended to be qualified under Section 401(a) of the Code with our 401(k) Plan’s related trust intended to be tax exempt under Section 501(a) of the Code. As a tax-qualified retirement plan, contributions to our 401(k) Plan and earnings on those contributions are not taxable to the

employees until distributed from our 401(k) Plan. We match employee contributions under the 401(k) Plan in an amount up to 3% of each applicable employee's compensation (equivalent to a 50% match with respect to up to 6% of such employee's compensation). We also pay, on behalf of our employees, a significant portion of premiums for health, life and disability insurance.

Employment Arrangements with Our Named Executive Officers

We consider it essential to the best interests of our stockholders to attract high quality executives and foster the continuous employment of our key management personnel. In this regard, we believe some severance arrangements are necessary. We also recognize that the possibility of a change in control may exist and that the uncertainty and questions that it may raise among management could result in the departure or distraction of management personnel to the detriment of our company and our stockholders. In order to reinforce and encourage the continued attention and dedication of certain key members of management, on December 21, 2015, the Compensation Committee approved the Executive Severance and Change in Control Policy ("Policy"). The purpose of the Policy is to provide certain of our senior management employees with compensation and benefits in the event of a termination of employment without Cause or for Good Reason (as such terms are defined in the Policy).

The post-termination compensation and benefits under the Policy include the (i) acceleration of time-based vesting provisions of outstanding equity awards that would have vested within 12 months of the termination, (ii) severance in the amount of 12 months of base salary, and (iii) payment of the employer portion of group health care benefits under COBRA for up to 12 months after termination.

In addition, if the termination occurs within two months prior to or one year after the closing of a Sale Event (as defined in the Policy), then, in lieu of the benefits described above, such eligible employee is entitled to (i) full acceleration of time-based vesting provisions of all outstanding equity awards, (ii) severance in the amount of 12 months of base salary, (iii) payment of the employee's bonus target for the calendar year in which the termination occurred, and (iv) payment of the employer portion of group health care benefits under COBRA for up to 12 months after termination.

In each case, receipt of any compensation or benefits under the Policy is subject to the eligible employee's execution of a severance agreement and release.

To the extent Section 280G of the Code is applicable with respect to payments to an eligible employee, such eligible employee shall be entitled to receive either: (a) payment of the full amounts set forth above to which the eligible employee is entitled or (b) payment of such lesser amount that does not trigger excise taxes under Section 4999 of the Code, whichever results in the employee receiving a higher amount after taking into account all federal, state, and local income, excise and employment taxes.

Employees who are party to an agreement or an arrangement with us that provides greater benefits in the aggregate than set forth in the Policy are not eligible to receive any payments or benefits under the Policy.

In addition, we have also entered into a written employment agreement with our President and Chief Executive Officer that provides for payments in connection with the resignation, retirement or other termination of such named executive officer, or a change in control, as described below.

Sanjay S. Shukla, M.D., M.S.

Dr. Shukla entered into an at-will employment offer letter with us on March 30, 2016 to serve as our Chief Medical Officer, which provided for an initial base salary of \$375,000, subject to adjustments as determined by us in our sole discretion. Pursuant to the terms of his employment offer letter, Dr. Shukla was considered annually for a bonus target, in an amount of up to 40% of his then-current base salary, as determined by our Board of Directors based on corporate achievements of goals and achievement of Dr. Shukla's individual goals.

On November 1, 2017, we announced a leadership transition whereby Dr. Shukla, our then-current Chief Medical Officer, succeeded Dr. Mendlein, our then-current Chief Executive Officer, as our President, Chief Executive Officer, and principal executive officer effective as of November 1, 2017 ("CEO Transition").

Under the terms of an employment agreement with Dr. Shukla entered November 1, 2017 (CEO Employment Agreement), Dr. Shukla is entitled to an initial annual base salary of \$450,000, subject to annual review and increase as determined by the Compensation Committee. In addition, Dr. Shukla is eligible for an annual bonus target, in the amount of

45% of his then-current base salary for the rest of 2017, and then in an amount of 50% of his then-current base salary for subsequent calendar years, as determined by the Compensation Committee. Dr. Shukla was granted an option to purchase 32,142 shares of our common stock, effective as of November 1, 2017, pursuant to the 2015 Plan.

Dr. Shukla's employment is at-will. In the event that Dr. Shukla's employment is terminated by Dr. Shukla for Good Reason or by us without Cause (as such terms are defined below), Dr. Shukla will be entitled to receive (i) the amount of his accrued but unpaid salary and unpaid expense reimbursements and any accrued but unused vacation as of the date of termination, (ii) any vested benefits Dr. Shukla may have under any employee benefit plan, which shall be paid in accordance with the terms of such employee benefit plans, as of the date of termination, (iii) any earned but unpaid incentive compensation from the prior calendar year, (iv) an amount equal to Dr. Shukla's current annual base salary plus his annual target incentive compensation in the year of termination, (v) acceleration of the time-based vesting provisions of all stock options or other stock-based awards that would have vested within 12 months of the termination, and (vi) payment of the amount that would reasonably be required to obtain equivalent health insurance coverage for up to 12 months after termination, in the case of each of (iv), (v) and (vi), subject to the execution of a separation agreement and release.

In the event that Dr. Shukla's employment is terminated by us without Cause or by Dr. Shukla for Good Reason within two months prior and 12 months after any Change in Control, as such terms are defined below, Dr. Shukla is entitled to (i) a cash payment equal to his then-current base salary plus his annual target incentive compensation in the year of termination, (ii) full acceleration of the time-based vesting provisions of all outstanding stock options or other stock-based awards, and (iii) payment of the amount that would reasonably be required to obtain equivalent health insurance coverage for up to 12 months after termination.

Under the CEO Employment Agreement, the terms below are generally defined as follows:

"Cause" means (i) conduct by the employee constituting a material act of willful misconduct in connection with the performance of his duties; (ii) the employee's conviction of, or the entry of a pleading of guilty or nolo contendere by the employee to, any crime involving (A) fraud or embezzlement in either case that results in material damage to us or any of our subsidiaries or affiliates or (B) any felony; (iii) willful and repeated failure by the employee to substantially perform the duties, functions and responsibilities of his positions that result in material damage to us or any of our subsidiaries and affiliates, that continues after he has received prior written notice from the Board of Directors of such purported repeated failure, which notice details the grounds of such purported repeated failure and requests its cure, and the employee has been given a reasonable opportunity to cure which will not be less than 30 days; or (iv) a material breach by the employee of any of the material provisions contained in the CEO Employment Agreement which has continued for more than 30 days following written notice of such purported breach; and

"Change in Control" means (i) any "person", as such term is used in Sections 13(d) and 14(d) of the Exchange Act (other than our company, any of our subsidiaries, or any trustee, fiduciary or other person or entity holding securities under any employee benefit plan or trust of our company or any of our subsidiaries), together with all "affiliates" and "associates" (as such terms are defined in Rule 12b-2 under the Exchange Act) of such person, shall become the "beneficial owner" (as such term is defined in Rule 13d-3 under the Exchange Act), directly or indirectly, of securities of our company representing 50 percent or more of the combined voting power of our then outstanding securities having the right to vote in an election of the Board (Voting Securities) (in such case other than as a result of an acquisition of securities directly from us); (ii) the date a majority of the members of the Board of Directors is replaced during any 12-month period by directors whose appointment or election is not endorsed by a majority of the members of the Board of Directors before the date of the appointment or election; or (iii) the consummation of (A) any consolidation or merger of our company or any subsidiary of our company where the stockholders of our company, immediately prior to the consolidation or merger, would not, immediately after the consolidation or merger, beneficially own (as such term is defined in Rule 13d-3 under the Exchange Act), directly or indirectly, shares representing in the aggregate more than 50 percent of the voting shares of our company issuing cash or securities in the consolidation or merger (or of its ultimate parent corporation, if any), or (B) any sale or other transfer (in one transaction or a series of transactions contemplated or arranged by any party as a single plan) of all or substantially all of the assets of our company; provided, however, that with respect to clause (A) above and as approved by the Board of Directors, a Change of Control shall be deemed to have occurred upon the consummation of a transaction whereby shares representing in the aggregate of more than 30 percent but less than 50 percent of the voting shares of our company are beneficially owned by the acquiring party or parties and such transaction includes a contingent right for the acquiring party or parties to acquire additional voting shares of our company that would represent more than 50 percent of our company's voting shares in the aggregate.

“Good Reason” means (i) a material diminution in the Executive’s responsibilities, authority or duties; (ii) a material diminution in the Executive’s Base Salary except for across-the-board salary reductions based on our company’s financial performance similarly affecting all or substantially all senior management employees of our company; or (iii) relocation of our executive headquarters to a location more than 50 miles from San Diego, California.

Jill M. Broadfoot

Ms. Broadfoot entered into an at-will employment offer letter with us on July 16, 2018, which provided for an initial base salary of \$350,000, subject to adjustments as determined by us in our sole discretion. Pursuant to the terms of her employment offer letter, Ms. Broadfoot is eligible for an annual bonus, currently in a target amount of up to 40% of her then-current base salary, as determined by our Board of Directors based on corporate achievements of goals and achievement of Ms. Broadfoot’s individual goals.

Ms. Broadfoot is also eligible to receive certain post-termination compensation and benefits in accordance with the Policy described above.

Nancy E. Denyes

Ms. Denyes entered into an at-will employment offer letter with us on October 7, 2014, which provided for an initial base salary of \$240,000, subject to adjustments as determined by us in our sole discretion.

Ms. Denyes is also eligible to receive certain post-termination compensation and benefits in accordance with the Policy described above.

CERTAIN RELATIONSHIPS AND RELATED TRANSACTIONS

Other than the compensation agreements and other arrangements described under “Compensation of Executive Officers” and the transactions described below, since January 1, 2018, there has not been and there is not currently proposed, any transaction or series of similar transactions to which we were, or will be, a party in which the amount involved exceeded, or will exceed the lesser of \$120,000 or 1% of the average of our total assets at year end for the last two completed fiscal years and in which any director, executive officer, holder of five percent or more of any class of our capital stock or any member of the immediate family of, or entities affiliated with, any of the foregoing persons, had, or will have, a direct or indirect material interest.

Payments to The Scripps Research Institute

We provided funding to The Scripps Research Institute (TSRI) under an amended and restated research funding and option agreement, as amended (the “Research Funding and Option Agreement”). In May 2018, we terminated the Research Funding and Option Agreement, effective as of November 10, 2018. From January 1, 2017 to November 10, 2018, we paid \$3.4 million to TSRI under the Research Funding and Option Agreement. Paul Schimmel, Ph.D., one of our directors, is a faculty member at TSRI and such payments funded a portion of his research activities conducted at TSRI.

Executive Officer and Director Compensation

Employment Agreements

We have entered into offer letters or employment agreements with each of our named executive officers. For more information regarding these arrangements, see “Compensation of Officers—Employment Arrangements with Our Named Executive Officers.”

Stock Option Awards

For information regarding stock option awards and other equity incentive awards granted to our named executive officers and directors, see “Election of Directors—Director Compensation” and “Compensation of Executive Officers.”

John D. Mendlein, Ph.D. – Strategic Advisor Agreement

Dr. Mendlein served as a strategic advisor to us pursuant to the terms of an advisor agreement entered with Dr. Mendlein in November 2017 (the Strategic Advisor Agreement). In June 2019, Dr. Mendlein resigned from our Board of Directors and, in August 2019, we gave notice to terminate the Strategic Advisor Agreement effective September 2019. Pursuant to the terms of the Strategic Advisor Agreement, we agreed to: (i) pay Dr. Mendlein as a strategic advisor to us for a period of up to four years, at a monthly rate of \$42,500 for the first year and \$7,500 per month for the rest of the term (which amount totaled \$600,000); (ii) as part of our annual review of compensation, pay Dr. Mendlein a to-be-determined cash bonus in February 2018 with respect to 2017 performance (which amount totaled \$165,750); (iii) reimburse Dr. Mendlein for certain benefits continuation through December 31, 2018 (which amount totaled \$19,256); (iv) allow for continued vesting of Dr. Mendlein’s outstanding time-based employee stock options for so long as Dr. Mendlein provided services to our company as a strategic advisor; and (v) provide for an extended option exercise period with respect to certain employee stock options held by Dr. Mendlein (all of which have expired).

Participation in Offerings

In April 2019, we entered into a securities purchase agreement with an institutional investor, The Federated Kaufmann Small Cap Fund (“Federated”) and Paul Schimmel, Ph.D., one of our directors, relating to the issuance and sale of 660,154 shares of our common stock. The shares of common stock were sold in a registered direct offering at a purchase price of \$7.57 per share for gross proceeds of approximately \$5.0 million.

In February 2020, we completed an underwritten public offering of 4,235,294 shares of our common stock at a price to the public of \$4.25 per share. In March 2020, the underwriters fully exercised their over-allotment option resulting in the issuance of an additional 635,294 shares of common stock. The total gross proceeds of the public offering, including the over-allotment, was approximately \$20.7 million, before deducting underwriting discounts, commissions and offering expenses payable by us. Dr. Schimmel, funds affiliated with Federated, a greater than 5% stockholder, and funds affiliated with FMR LLC, another one of our 5% stockholders, participated in this underwritten public offering.

Indemnification Agreements

We have entered into agreements to indemnify our directors and executive officers. These agreements will, among other things, require us to indemnify these individuals for certain expenses (including attorneys' fees), judgments, fines and settlement amounts reasonably incurred by such person in any action or proceeding, including any action by or in our right, on account of any services undertaken by such person on behalf of our company or that person's status as a member of our Board of Directors to the maximum extent allowed under Delaware law.

Procedures for Approval of Related Person Transactions

The Audit Committee conducts an appropriate review of all related person transactions for potential conflict of interest situations on an ongoing basis, and the approval of the Audit Committee is required for all such transactions. The Audit Committee follows the policies and procedures set forth in our written Related Person Transaction Policy in order to facilitate such review.

SECURITY OWNERSHIP OF CERTAIN BENEFICIAL OWNERS AND MANAGEMENT AND RELATED STOCKHOLDER MATTERS

The following table sets forth the beneficial ownership of the Company's common stock as of March 16, 2020 by: (i) each of the executive officers named in the table under the heading "Summary Compensation Table," (ii) each current director, (iii) all current directors and executive officers as a group, and (iv) all persons known to the Company to be the beneficial owners of more than 5% of the Company's common stock. The table is based upon information supplied by our executive officers, directors and principal stockholders and a review of filings by the beneficial owners with the SEC pursuant to Sections 13(d) and 13(g) of the Exchange Act. A total of 9,352,498 shares of the Company's common stock were issued and outstanding as of March 16, 2020.

| Beneficial Owner(1) | Number of Shares of Common Stock Owned(2) | Number of Shares of Common Stock Acquirable Within 60 Days (3) | Total Number of Shares of Common Stock Beneficially Owned(4) | Percentage of Shares Beneficially Owned |
|--|---|--|---|--|
| 5% Stockholders: | | | | |
| Altium Growth Fund(5) 551 Fifth Avenue, Floor 19 New York , New York 10176 | 475,000 | — | 475,000 | 5.08% |
| Federated Hermes Inc.(6) 1001 Liberty Avenue Pittsburgh, PA 15222 | 595,072 | — | 595,072 | 6.36% |
| FMR LLC(7) 245 Summer Street, Boston, Massachusetts 02210 | 491,449 | — | 491,449 | 5.25% |
| Directors and Named Executive Officers: | | | | |
| Sanjay S. Shukla, M.D., M.S.(8) | 1,291 | 53,821 | 55,112 | * |
| Jill M. Broadfoot(9) | 7,125 | 7,366 | 14,491 | * |
| Nancy E. Denyes(10) | 1,987 | 17,762 | 19,749 | * |
| John K. Clarke(11) | 133,075 | 7,405 | 140,480 | 1.50% |
| James C. Blair, Ph.D.(12) | 130,988 | 7,405 | 138,393 | 1.48% |
| Timothy P. Coughlin(13) | — | 6,569 | 6,569 | * |
| Jane A. Gross, Ph.D.(14) | — | 635 | 635 | * |
| Jeffrey S. Hatfield(15) | — | 6,569 | 6,569 | * |
| Svetlana Lucas, Ph.D.(16) | — | 635 | 635 | * |
| Paul Schimmel, Ph.D.(17) | 503,503 | 7,907 | 511,410 | 5.46% |
| All directors and executive officers as a group (10 persons)(18) | 777,969 | 116,074 | 894,043 | 9.44% |

* Represents beneficial ownership of less than 1% of the shares of common stock.

(1) Unless otherwise indicated, the address for each beneficial owner is c/o aTyr Pharma, Inc., 3545 John Hopkins Court, Suite #250, San Diego, CA 92121.

(2) Represents shares of common stock owned, excluding shares of common stock that are listed under the heading "Number of Shares of Common Stock Acquirable Within 60 Days," by the named parties as of March 16, 2020.

(3) Shares of common stock subject to stock options, restricted stock units or warrants acquirable within 60 days of March 16, 2020, regardless of exercise price, are deemed to be outstanding for computing the percentage ownership of the person holding such options and the percentage ownership of any group of which the holder is a member, but are not deemed outstanding for computing the percentage of any other person.

(4) Beneficial ownership is determined in accordance with the rules of the SEC and generally includes voting or investment power with respect to securities. Except as indicated by footnote, and subject to community property laws where applicable, the Company believes that the persons named in the table have sole voting and investment power with respect to all shares of common stock shown as beneficially owned by them, subject to applicable community property laws.

(5) Based on Schedule 13G filed with the SEC on February 18, 2020, which indicates Altium Growth Fund, LP is the record and beneficial owner of the securities. Altium Capital Management LP is the investment adviser of, and may be deemed to beneficially own securities, owned by, Altium Growth Fund, L.P. Altium Growth GP, LLC is the general partner of, and may be deemed to beneficially own securities owned by, Altium Growth Fund, L.P.

(6) Based on Schedule 13G/A filed with the SEC on February 14, 2020; and does not include any shares purchased as part of our underwritten public offering of common stock in February 2020. Shares of common stock owned can vary since the date of such filing. Federated Hermes, Inc. (the Parent) is the parent holding company of Federated Equity Management Company of Pennsylvania and Federated Global Investment Management Corp. (the Investment Advisers), which act as investment advisers to registered investment companies and separate accounts

that own shares of common stock in us (the Reported Securities). The Investment Advisers are wholly owned subsidiaries of FII Holdings, Inc., which is a wholly owned subsidiary of Federated Investors, Inc., the Parent. All of the Parent's outstanding voting stock is held in the Voting Shares Irrevocable Trust (the Trust) for which Thomas R. Donahue, Rhodora J. Donahue and J. Christopher Donahue act as trustees (collectively, the Trustees). The Parent, the Trust, and each of the Trustees expressly disclaim beneficial ownership of the Reported Securities in which they do not have an actual pecuniary interest.

- (7) Based on Schedule 13G/A filed with the SEC on February 6, 2020; and does not include any shares purchased as part of our underwritten public offering of common stock in February 2020. Shares of common stock owned can vary since the date of such filing. FMR LLC had sole voting power with respect to 48,188 shares of common stock and had sole power to dispose or to direct the disposition of 491,449 shares of common stock. Abigail P. Johnson is a Director, the Chairman and the Chief Executive Officer of FMR LLC. Members of the Johnson family including Abigail P. Johnson, are the predominant owners, directly or through trusts, of Series B voting common shares of FMR LLC, representing 49% of the voting power of FMR LLC. The Johnson family group and all other Series B shareholders have entered into a shareholders' voting agreement under which all Series B voting common shares will be voted in accordance with the majority vote of Series B voting common shares. Accordingly, through their ownership of voting common shares and the execution of the shareholders' voting agreement, members of the Johnson family may be deemed, under the Investment Company Act of 1940, to form a controlling group with respect to FMR LLC. Neither FMR LLC nor Abigail P. Johnson have the sole power to vote or direct the voting of the shares owned directly by the various investment companies registered under the Investment Company Act (Fidelity Funds) advised by Fidelity Management & Research Company (FMR Co), a wholly owned subsidiary of FMR LLC, which power resides with the Fidelity Funds' Boards of Trustees. Fidelity Management & Research Company carries out the voting of the shares under written guidelines established by the Fidelity Funds' Boards of Trustees.
- (8) Includes (i) 1,291 shares of common stock held by Dr. Shukla; and (ii) 53,281 shares of common stock that Dr. Shukla has the right to acquire from us within 60 days of March 16, 2020 pursuant to the exercise of stock options.
- (9) Includes (i) 7,125 shares of common stock held by Ms. Broadfoot; and (ii) 7,366 shares of common stock that Ms. Broadfoot has the right to acquire from us within 60 days of March 16, 2020 pursuant to the exercise of stock options.
- (10) Includes (i) 1,987 shares of common stock held by Ms. Denyes; and (ii) 17,762 shares of common stock that Ms. Denyes has the right to acquire from us within 60 days of March 16, 2020 pursuant to the exercise of stock options.
- (11) Includes (i) 7,492 shares of common stock held by our director, Mr. Clarke; and (ii) 7,405 shares of common stock that Mr. Clarke has the right to acquire from us within 60 days of March 16, 2020 pursuant to the exercise of stock options. Based on Schedule 13G filed with the SEC on February 4, 2016, which indicates that 125,583 shares of common stock are held by CHP II, L.P. (CHP). The general partner of CHP is CHP II Management, LLC (CHP Management), which may be deemed to beneficially own certain of the shares held by CHP. CHP Management disclaims beneficial ownership of all shares held by CHP in which it does not have an actual pecuniary interest. John Clarke, Brandon Hull and John Park are managing members of CHP Management and as members of the general partner, they may be deemed to beneficially own certain of the shares held by CHP Management. The managing members disclaim beneficial ownership of all shares held by CHP Management in which they do not have an actual pecuniary interest.
- (12) Includes (i) 449 shares of common stock held by our director, Dr. Blair; and (ii) 7,405 shares of common stock that Dr. Blair has the right to acquire from us within 60 days of March 16, 2020 pursuant to the exercise of stock options. Based on Schedule 13G filed with the SEC on January 19, 2016, consists of (i) 129,130 shares held by Domain Partners VIII, L.P.; (ii) 959 shares held by DP VIII Associates, L.P.; and (iii) 450 shares held by Domain Associates, LLC. Each of the funds has sole voting and dispositive power over such shares. One Palmer Square Associates VIII, LLC (One Palmer) is the general partner of Domain Partners and Domain Associates and may be deemed to have sole voting and investment power over such shares. One Palmer disclaims beneficial ownership of all shares held by Domain Partners and Domain Associates in which it does not have an actual pecuniary interest. Dr. Blair, is a managing member of One Palmer. Dr. Blair disclaims beneficial ownership of all shares held by One Palmer in which he does not have an actual pecuniary interest.
- (13) Represents 6,569 shares of common stock that Mr. Coughlin has the right to acquire from us within 60 days of March 16, 2020 pursuant to the exercise of stock options.
- (14) Represents 635 shares of common stock that Dr. Gross has the right to acquire from us within 60 days of March 16, 2020 pursuant to the exercise of stock options.
- (15) Represents 6,569 shares of common stock that Mr. Hatfield has the right to acquire from us within 60 days of March 16, 2020 pursuant to the exercise of stock options.
- (16) Represents 635 shares of common stock that Dr. Lucas has the right to acquire from us within 60 days of March 16, 2020 pursuant to the exercise of stock options.
- (17) Includes (i) 2,890 shares of common stock held by our director, Dr. Schimmel; (ii) 63,023 shares of common stock held by the Paul Schimmel Prototype PSP, Paul Schimmel, Trustee, FBO Paul Schimmel (Prototype PSP); (iii) 437,590 shares of common stock held by the Schimmel Revocable Trust U/A Dtd 9/6/2000; and (iv) 7,907 shares of common stock that Dr. Schimmel has the right to acquire from us within 60 days of March 16, 2020 pursuant to the exercise of stock options.
- (18) Includes the number of shares beneficially owned by the named executive officers and directors listed in the above table.

The following Audit Committee Report is not considered proxy solicitation material and is not deemed filed with the SEC. Notwithstanding anything to the contrary set forth in any of the Company's filings made under the Securities Act of 1933, as amended, or the Exchange Act that might incorporate filings made by the Company under those statutes, the Audit Committee Report shall not be incorporated by reference into any prior filings or into any future filings made by the Company under those statutes.

AUDIT COMMITTEE REPORT

The Audit Committee of the Board of Directors (the "Audit Committee") has furnished this report concerning the independent audit of the Company's financial statements. Each member of the Audit Committee meets the enhanced independence standards established by the Sarbanes-Oxley Act of 2002 and rulemaking of the Securities and Exchange Commission (the "SEC") and the Nasdaq Stock Market regulations. A copy of the Audit Committee Charter is available on the Company's website at <http://www.atyrpharma.com>.

The Audit Committee's responsibilities include assisting the Board of Directors regarding the oversight of the integrity of the Company's financial statements, the Company's compliance with legal and regulatory requirements, the independent registered public accounting firm's qualifications and independence, and the performance of the Company's internal audit function and the independent registered public accounting firm.

In fulfilling its oversight responsibilities, the Audit Committee reviewed and discussed the Company's audited financial statements for the fiscal year ended December 31, 2019 with the Company's management and Ernst & Young LLP. In addition, the Audit Committee has discussed with Ernst & Young LLP, with and without management present, their evaluation of the Company's internal accounting controls and overall quality of the Company's financial reporting. The Audit Committee also discussed with Ernst & Young LLP the matters required to be discussed by Statement on Auditing Standards No. 114 (formerly SAS 61), as amended (AICPA, *Professional Standards*, Vol. 1 AU section 380), as adopted by the Public Company Accounting Oversight Board in Rule 3200T. The Audit Committee also received the written disclosures and the letter from Ernst & Young LLP required by the Public Company Accounting Oversight Board Rule 3526 and the Audit Committee discussed the independence of Ernst & Young LLP with that firm.

Based on the Audit Committee's review and discussions noted above, the Audit Committee recommended to the Board of Directors, and the Board of Directors approved, that the audited financial statements be included in the Company's Annual Report on Form 10-K for the fiscal year ended December 31, 2019.

The Audit Committee and the Board of Directors have recommended the selection of Ernst & Young LLP as the Company's independent registered public accounting firm for the year ending December 31, 2020.

AUDIT COMMITTEE

TIMOTHY P. COUGHLIN, CHAIRMAN
JOHN C. CLARKE
JEFFREY S. HATFIELD

HOUSEHOLDING OF PROXY MATERIALS

We have made available a procedure approved by the SEC known as "householding." This procedure allows multiple stockholders residing at the same address the convenience of receiving a single copy of our proxy materials. This allows us to save money by reducing the number of documents we must print and mail, and helps protect the environment as well.

Householding is available to both registered stockholders (i.e., those stockholders with certificates registered in their name) and streetname holders (i.e., those stockholders who hold their shares through a brokerage).

Registered Stockholders

If you are a registered stockholder and would like to consent to a mailing of proxy materials and other stockholder information only to one account in your household, as identified by you, we will deliver or mail a single copy of our proxy materials for all registered stockholders residing at the same address. Your consent will be perpetual unless you revoke it, which you may do at any time by contacting the Householding Department of American Stock Transfer & Trust Company, LLC ("AST"), at 6201 15th Avenue, Brooklyn, New York 11219 or by calling AST's toll-free number which is (800) 934-5449.

Registered stockholders who have not consented to householding will continue to receive copies of proxy materials for each registered stockholder residing at the same address. As a registered stockholder, you may elect to participate in householding and receive only a single copy of proxy materials for all registered stockholders residing at the same address by contacting AST as outlined above.

Street Name Holders

Stockholders who hold their shares through a brokerage may elect to participate in householding or revoke their consent to participate in householding by contacting their respective brokers.

OTHER MATTERS

We are not aware of any matters that may come before the meeting other than those referred to in the Notice of Annual Meeting of Stockholders and Proxy Statement. If any other matter shall properly come before the Annual Meeting, however, the persons named in the accompanying proxy intend to vote all proxies in accordance with their best judgment.

Accompanying this Proxy Statement is our Annual Report on Form 10-K. Copies of our Annual Report on Form 10-K are available free of charge on our website at www.atyrpharma.com or you can request a copy free of charge by calling Investor Relations at (858) 223-1163 or sending an e-mail request to investorrelations@atyrpharma.com. Please include your contact information with the request.

By Order of the Board of Directors,



Sanjay S. Shukla, M.D., M.S.
President, Chief Executive Officer and Director

April 2, 2020

ANNEX A

ATYR PHARMA, INC.

2015 STOCK OPTION AND INCENTIVE PLAN

(as amended)

SECTION 1. GENERAL PURPOSE OF THE PLAN; DEFINITIONS

The name of the plan is the aTyr Pharma, Inc. 2015 Stock Option and Incentive Plan (the "Plan"). The purpose of the Plan is to encourage and enable the officers, employees, Non-Employee Directors and Consultants of aTyr Pharma, Inc., a Delaware corporation (the "Company"), and its Subsidiaries upon whose judgment, initiative and efforts the Company largely depends for the successful conduct of its business to acquire a proprietary interest in the Company. It is anticipated that providing such persons with a direct stake in the Company's welfare will assure a closer identification of their interests with those of the Company and its stockholders, thereby stimulating their efforts on the Company's behalf and strengthening their desire to remain with the Company.

The following terms shall be defined as set forth below:

"*Act*" means the Securities Act of 1933, as amended, and the rules and regulations thereunder.

"*Administrator*" means either the Board or the compensation committee of the Board or a similar committee performing the functions of the compensation committee and which is comprised of not less than two Non-Employee Directors who are independent.

"*Award*" or "*Awards*," except where referring to a particular category of grant under the Plan, shall include Incentive Stock Options, Non-Qualified Stock Options, Stock Appreciation Rights, Restricted Stock Units, Restricted Stock Awards, Unrestricted Stock Awards, Cash-Based Awards, Performance Share Awards and Dividend Equivalent Rights.

"*Award Certificate*" means a written or electronic document setting forth the terms and provisions applicable to an Award granted under the Plan. Each Award Certificate is subject to the terms and conditions of the Plan.

"*Board*" means the Board of Directors of the Company.

"*Cash-Based Award*" means an Award entitling the recipient to receive a cash-denominated payment.

"*Code*" means the Internal Revenue Code of 1986, as amended, and any successor Code, and related rules, regulations and interpretations.

"*Consultant*" means any natural person that provides bona fide services to the Company, and such services are not in connection with the offer or sale of securities in a capital-raising transaction and do not directly or indirectly promote or maintain a market for the Company's securities.

"*Covered Employee*" means an employee who is a "Covered Employee" within the meaning of Section 162(m) of the Code.

"*Dividend Equivalent Right*" means an Award entitling the grantee to receive credits based on cash dividends that would have been paid on the shares of Stock specified in the Dividend Equivalent Right (or other award to which it relates) if such shares had been issued to and held by the grantee.

"*Effective Date*" means the date set forth in Section 21.

“Exchange Act” means the Securities Exchange Act of 1934, as amended, and the rules and regulations thereunder.

“Fair Market Value” of the Stock on any given date means the fair market value of the Stock determined in good faith by the Administrator; provided, however, that if the Stock is admitted to quotation on the National Association of Securities Dealers Automated Quotation System (“NASDAQ”), NASDAQ Global Market or another national securities exchange, the determination shall be made by reference to market quotations. If there are no market quotations for such date, the determination shall be made by reference to the last date preceding such date for which there are market quotations; provided further, however, that if the date for which Fair Market Value is determined is the first day when trading prices for the Stock are reported on a national securities exchange, the Fair Market Value shall be the “Price to the Public” (or equivalent) set forth on the cover page for the final prospectus relating to the Company’s Initial Public Offering.

“Incentive Stock Option” means any Stock Option designated and qualified as an “incentive stock option” as defined in Section 422 of the Code.

“Initial Public Offering” means the consummation of the first underwritten, firm commitment public offering pursuant to an effective registration statement under the Act covering the offer and sale by the Company of its equity securities, or such other event as a result of or following which the Stock shall be publicly held.

“Non-Employee Director” means a member of the Board who is not also an employee of the Company or any Subsidiary.

“Non-Qualified Stock Option” means any Stock Option that is not an Incentive Stock Option.

“Option” or “Stock Option” means any option to purchase shares of Stock granted pursuant to Section 5.

“Performance-Based Award” means any Restricted Stock Award, Restricted Stock Units, Performance Share Award or Cash-Based Award granted to a Covered Employee that is intended to qualify as “performance-based compensation” under Section 162(m) of the Code and the regulations promulgated thereunder.

“Performance Criteria” means the criteria that the Administrator selects for purposes of establishing the Performance Goal or Performance Goals for an individual for a Performance Cycle. The Performance Criteria (which shall be applicable to the organizational level specified by the Administrator, including, but not limited to, the Company or a unit, division, group, or Subsidiary of the Company) that will be used to establish Performance Goals are limited to the following: achievement of specified research and development, publication, clinical and/or regulatory milestones, total shareholder return, earnings before interest, taxes, depreciation and amortization, net income (loss) (either before or after interest, taxes, depreciation and/or amortization), changes in the market price of the Stock, economic value-added, funds from operations or similar measure, sales or revenue, acquisitions or strategic transactions, operating income (loss), cash flow (including, but not limited to, operating cash flow and free cash flow), return on capital, assets, equity, or investment, return on sales, gross or net profit levels, productivity, expense, margins, operating efficiency, customer satisfaction, working capital, earnings (loss) per share of Stock, sales or market shares and number of customers, any of which may be measured either in absolute terms or as compared to any incremental increase or as compared to results of a peer group. The Committee may appropriately adjust any evaluation performance under a Performance Criterion to exclude any of the following events that occurs during a Performance Cycle: (i) asset write-downs or impairments, (ii) litigation or claim judgments or settlements, (iii) the effect of changes in tax law, accounting principles or other such laws or provisions affecting reporting results, (iv) accruals for reorganizations and restructuring programs, (v) any extraordinary non-recurring items, including those described in the Financial Accounting Standards Board’s authoritative guidance and/or in management’s discussion and analysis of financial condition of operations appearing the Company’s annual report to stockholders for the applicable year, and (vi) any other extraordinary items adjusted from the Company U.S. GAAP results.

“Performance Cycle” means one or more periods of time, which may be of varying and overlapping durations, as the Administrator may select, over which the attainment of one or more Performance Criteria will be measured for the purpose of determining a grantee’s right to and the payment of a Restricted Stock Award, Restricted

Stock Units, Performance Share Award or Cash-Based Award, the vesting and/or payment of which is subject to the attainment of one or more Performance Goals. Each such period shall not be less than 12 months.

“*Performance Goals*” means, for a Performance Cycle, the specific goals established in writing by the Administrator for a Performance Cycle based upon the Performance Criteria.

“*Performance Share Award*” means an Award entitling the recipient to acquire shares of Stock upon the attainment of specified performance goals.

“*Restricted Shares*” means the shares of Stock underlying a Restricted Stock Award that remain subject to a risk of forfeiture or the Company’s right of repurchase.

“*Restricted Stock Award*” means an Award of Restricted Shares subject to such restrictions and conditions as the Administrator may determine at the time of grant.

“*Restricted Stock Units*” means an Award of stock units subject to such restrictions and conditions as the Administrator may determine at the time of grant.

“*Sale Event*” shall mean (i) the sale of all or substantially all of the assets of the Company on a consolidated basis to an unrelated person or entity, (ii) a merger, reorganization or consolidation pursuant to which the holders of the Company’s outstanding voting power and outstanding stock immediately prior to such transaction do not own a majority of the outstanding voting power and outstanding stock or other equity interests of the resulting or successor entity (or its ultimate parent, if applicable) immediately upon completion of such transaction, (iii) the sale of all of the Stock of the Company to an unrelated person, entity or group thereof acting in concert, or (iv) any other transaction in which the owners of the Company’s outstanding voting power immediately prior to such transaction do not own at least a majority of the outstanding voting power of the Company or any successor entity immediately upon completion of the transaction other than as a result of the acquisition of securities directly from the Company.

“*Sale Price*” means the value as determined by the Administrator of the consideration payable, or otherwise to be received by stockholders, per share of Stock pursuant to a Sale Event.

“*Section 409A*” means Section 409A of the Code and the regulations and other guidance promulgated thereunder.

“*Stock*” means the Common Stock, par value \$0.001 per share, of the Company, subject to adjustments pursuant to Section 3.

“*Stock Appreciation Right*” means an Award entitling the recipient to receive shares of Stock having a value equal to the excess of the Fair Market Value of the Stock on the date of exercise over the exercise price of the Stock Appreciation Right multiplied by the number of shares of Stock with respect to which the Stock Appreciation Right shall have been exercised.

“*Subsidiary*” means any corporation or other entity (other than the Company) in which the Company has at least a 50 percent interest, either directly or indirectly.

“*Ten Percent Owner*” means an employee who owns or is deemed to own (by reason of the attribution rules of Section 424(d) of the Code) more than 10 percent of the combined voting power of all classes of stock of the Company or any parent or subsidiary corporation.

“*Unrestricted Stock Award*” means an Award of shares of Stock free of any restrictions.

SECTION 2. ADMINISTRATION OF PLAN; ADMINISTRATOR AUTHORITY TO SELECT GRANTEEES AND DETERMINE AWARDS

(a) Administration of Plan. The Plan shall be administered by the Administrator.

(b) Powers of Administrator. The Administrator shall have the power and authority to grant Awards consistent with the terms of the Plan, including the power and authority:

(i) to select the individuals to whom Awards may from time to time be granted;

(ii) to determine the time or times of grant, and the extent, if any, of Incentive Stock Options, Non-Qualified Stock Options, Stock Appreciation Rights, Restricted Stock Awards, Restricted Stock Units, Unrestricted Stock Awards, Cash-Based Awards, Performance Share Awards and Dividend Equivalent Rights, or any combination of the foregoing, granted to any one or more grantees;

(iii) to determine the number of shares of Stock to be covered by any Award;

(iv) to determine and modify from time to time the terms and conditions, including restrictions, not inconsistent with the terms of the Plan, of any Award, which terms and conditions may differ among individual Awards and grantees, and to approve the forms of Award Certificates;

(v) to accelerate at any time the exercisability or vesting of all or any portion of any Award in circumstances involving the grantee's death, disability, retirement or termination of employment, or a change in control of the Company (including a Sale Event);

(vi) subject to the provisions of Section 5(c), to extend at any time the period in which Stock Options may be exercised; and

(vii) at any time to adopt, alter and repeal such rules, guidelines and practices for administration of the Plan and for its own acts and proceedings as it shall deem advisable; to interpret the terms and provisions of the Plan and any Award (including related written instruments); to make all determinations it deems advisable for the administration of the Plan; to decide all disputes arising in connection with the Plan; and to otherwise supervise the administration of the Plan.

All decisions and interpretations of the Administrator shall be binding on all persons, including the Company and Plan grantees.

(c) Delegation of Authority to Grant Awards. Subject to applicable law, the Administrator, in its discretion, may delegate to the Chief Executive Officer of the Company all or part of the Administrator's authority and duties with respect to the granting of Awards to individuals who are (i) not subject to the reporting and other provisions of Section 16 of the Exchange Act and (ii) not Covered Employees. Any such delegation by the Administrator shall include a limitation as to the amount of Stock underlying Awards that may be granted during the period of the delegation and shall contain guidelines as to the determination of the exercise price and the vesting criteria. The Administrator may revoke or amend the terms of a delegation at any time but such action shall not invalidate any prior actions of the Administrator's delegate or delegates that were consistent with the terms of the Plan.

(d) Award Certificate. Awards under the Plan shall be evidenced by Award Certificates that set forth the terms, conditions and limitations for each Award which may include, without limitation, the term of an Award and the provisions applicable in the event employment or service terminates.

(e) Indemnification. Neither the Board nor the Administrator, nor any member of either or any delegate thereof, shall be liable for any act, omission, interpretation, construction or determination made in good faith in connection with the Plan, and the members of the Board and the Administrator (and any delegate thereof) shall be entitled in all cases to indemnification and reimbursement by the Company in respect of any claim, loss, damage or expense (including, without limitation, reasonable attorneys' fees) arising or resulting therefrom to the fullest extent permitted by law and/or under the Company's certificate of incorporation or bylaws or any directors' and officers' liability insurance coverage which may be in effect from time to time and/or any indemnification agreement between such individual and the Company.

(f) Foreign Award Recipients. Notwithstanding any provision of the Plan to the contrary, in order to comply with the laws in other countries in which the Company and its Subsidiaries operate or have employees or other individuals eligible for Awards, the Administrator, in its sole discretion, shall have the power and authority to: (i) determine which Subsidiaries shall be covered by the Plan; (ii) determine which individuals outside the United States are eligible to participate in the Plan; (iii) modify the terms and conditions of any Award granted to individuals outside the United States to comply with applicable foreign laws; (iv) establish subplans and modify exercise procedures and other terms and procedures, to the extent the Administrator determines such actions to be necessary or advisable (and such subplans and/or modifications shall be attached to this Plan as appendices); provided, however, that no such

subplans and/or modifications shall increase the share limitations contained in Section 3(a) hereof; and (v) take any action, before or after an Award is made, that the Administrator determines to be necessary or advisable to obtain approval or comply with any local governmental regulatory exemptions or approvals. Notwithstanding the foregoing, the Administrator may not take any actions hereunder, and no Awards shall be granted, that would violate the Exchange Act or any other applicable United States securities law, the Code, or any other applicable United States governing statute or law.

SECTION 3. STOCK ISSUABLE UNDER THE PLAN; MERGERS; SUBSTITUTION

(a) **Stock Issuable.** The maximum number of shares of Stock reserved and available for issuance under the Plan shall be 951,945¹ shares, subject to adjustment as provided in **Section 3(c)** and herein. Subject to such overall limitation, the maximum aggregate number of shares of Stock that may be issued in the form of Incentive Stock Options shall not exceed 488,087, subject in all cases to adjustment as provided in **Section 3(c)**. The shares of Stock underlying any Awards under the Plan and under the Company's 2014 Stock Plan, as amended, that are forfeited, canceled, reacquired by the Company prior to vesting, satisfied without the issuance of Stock or otherwise terminated (other than by exercise) shall be added back to the shares of Stock available for issuance under the Plan. In the event the Company repurchases shares of Stock on the open market, such shares shall not be added to the shares of Stock available for issuance under the Plan. Subject to such overall limitations, shares of Stock may be issued up to such maximum number pursuant to any type or types of Award; provided, however, that Stock Options or Stock Appreciation Rights with respect to no more than 112,469 shares of Stock may be granted to any one individual grantee during any one calendar year period. The shares available for issuance under the Plan may be authorized but unissued shares of Stock or shares of Stock reacquired by the Company.

(b) **[Reserved].**

(c) **Changes in Stock.** Subject to Section 3(d) hereof, if, as a result of any reorganization, recapitalization, reclassification, stock dividend, stock split, reverse stock split or other similar change in the Company's capital stock, the outstanding shares of Stock are increased or decreased or are exchanged for a different number or kind of shares or other securities of the Company, or additional shares or new or different shares or other securities of the Company or other non-cash assets are distributed with respect to such shares of Stock or other securities, or, if, as a result of any merger or consolidation, sale of all or substantially all of the assets of the Company, the outstanding shares of Stock are converted into or exchanged for securities of the Company or any successor entity (or a parent or subsidiary thereof), the Administrator shall make an appropriate or proportionate adjustment in (i) the maximum number of shares reserved for issuance under the Plan, including the maximum number of shares that may be issued in the form of Incentive Stock Options, (ii) the number of Stock Options or Stock Appreciation Rights that can be granted to any one individual grantee and the maximum number of shares that may be granted under a Performance-Based Award, (iii) the number and kind of shares or other securities subject to any then outstanding Awards under the Plan, (iv) the repurchase price, if any, per share subject to each outstanding Restricted Stock Award, and (v) the exercise price for

¹ All numbers herein reflect the 1-for-14 reverse stock split (rounded down to the nearest whole share) of the Company's issued and outstanding common stock that was effectuated as of June 28, 2019. The original maximum number of shares of Stock reserved and available for issuance under the Plan was 112,469 shares, plus on January 1, 2016 until January 1, 2019, the number of shares of Stock reserved and available for issuance under the Plan was increased by the lesser of (i) 131,428 shares of Stock (subject to adjustment as provided in **Section 3(c)**), (ii) four percent (4%) of the number of shares of Stock issued and outstanding on the immediately preceding December 31 and (iii) an amount as determined by the Administrator. As such, immediately prior to the amendment in March 2019, there were 488,087 shares of Stock reserved and available for issuance under the Plan (which includes shares of Stock underlying the Company's 2014 Stock Plan, as amended, that were added back into this Plan because such shares were forfeited, canceled, reacquired by the Company prior to vesting, satisfied without the issuance of Stock or otherwise terminated (other than by exercise)). The Plan was amended by the Board of Directors in March 2019 to increase the maximum number of shares of Stock reserved and available for issuance under the Plan by 71,428 shares, resulting in 559,516 shares as of March 2019, subject to approval by the Company's stockholders. The Company's stockholders approved such amendment to the Plan at the Company's 2019 Annual Meeting of Stockholders held on May 8, 2019. The Plan was amended by the Board of Directors in March 2020 to increase the maximum number of shares of Stock reserved and available for issuance under the Plan by 350,000 shares, resulting in 951,945 shares as of March 2020, subject to approval by the Company's stockholders.

each share subject to any then outstanding Stock Options and Stock Appreciation Rights under the Plan, without changing the aggregate exercise price (i.e., the exercise price multiplied by the number of Stock Options and Stock Appreciation Rights) as to which such Stock Options and Stock Appreciation Rights remain exercisable. The Administrator shall also make equitable or proportionate adjustments in the number of shares subject to outstanding Awards and the exercise price and the terms of outstanding Awards to take into consideration cash dividends paid other than in the ordinary course or any other extraordinary corporate event. The adjustment by the Administrator shall be final, binding and conclusive. No fractional shares of Stock shall be issued under the Plan resulting from any such adjustment, but the Administrator in its discretion may make a cash payment in lieu of fractional shares.

(d) Mergers and Other Transactions. Except as the Administrator may otherwise specify with respect to particular Awards in the relevant Award Certificate, in the case of and subject to the consummation of a Sale Event, the parties thereto may cause the assumption or continuation of Awards theretofore granted by the successor entity, or the substitution of such Awards with new Awards of the successor entity or parent thereof, with appropriate adjustment as to the number and kind of shares and, if appropriate, the per share exercise prices, as such parties shall agree. To the extent the parties to such Sale Event do not provide for the assumption, continuation or substitution of Awards, the Plan and all outstanding Awards hereunder will terminate at the effective time of such Sale Event. Notwithstanding the foregoing, the Administrator may in its discretion, or to the extent specified in the relevant Award Certificate, cause certain Awards to become vested and/or exercisable immediately prior to such Sale Event. In the event of such termination, (i) the Company shall have the right, but not the obligation, to make or provide for a cash payment to the grantees holding Options and Stock Appreciation Rights, in exchange for the cancellation thereof, in an amount equal to the difference between (A) the Sale Price multiplied by the number of shares of Stock subject to outstanding Options and Stock Appreciation Rights (to the extent then exercisable after taking into account any acceleration thereunder at prices not in excess of the Sale Price) and (B) the aggregate exercise price of all such outstanding Options and Stock Appreciation Rights; or (ii) each grantee shall be permitted, within a specified period of time prior to the consummation of the Sale Event as determined by the Administrator, to exercise all outstanding Options and Stock Appreciation Rights (to the extent then exercisable) held by such grantee, including those that will become exercisable upon the consummation of the Sale Event (provided, that such exercise shall be subject to the consummation of the Sale Event). The Company shall also have the right, but not the obligation, to make or provide a cash payment to the grantees holding other Awards, in exchange for cancellation thereof, an amount equal to the Sale Price multiplied by the number of shares subject to such Awards, to be paid at the time of the Sale Event or upon the later vesting of such Awards.

SECTION 4. ELIGIBILITY

Grantees under the Plan will be such full or part-time officers and other employees, Non-Employee Directors and Consultants of the Company and its Subsidiaries as are selected from time to time by the Administrator in its sole discretion.

SECTION 5. STOCK OPTIONS

(a) Award of Stock Options. The Administrator may grant Stock Options under the Plan. Any Stock Option granted under the Plan shall be in such form as the Administrator may from time to time approve.

Stock Options granted under the Plan may be either Incentive Stock Options or Non-Qualified Stock Options. Incentive Stock Options may be granted only to employees of the Company or any Subsidiary that is a "subsidiary corporation" within the meaning of Section 424(f) of the Code. To the extent that any Option does not qualify as an Incentive Stock Option, it shall be deemed a Non-Qualified Stock Option.

Stock Options granted pursuant to this Section 5 shall be subject to the following terms and conditions and shall contain such additional terms and conditions, not inconsistent with the terms of the Plan, as the Administrator shall deem desirable. If the Administrator so determines, Stock Options may be granted in lieu of cash compensation at the optionee's election, subject to such terms and conditions as the Administrator may establish.

(b) Exercise Price. The exercise price per share for the Stock covered by a Stock Option granted pursuant to this Section 5 shall be determined by the Administrator at the time of grant but shall not be less than 100 percent of the Fair Market Value on the date of grant. In the case of an Incentive Stock Option that is granted to a Ten Percent Owner, the option price of such Incentive Stock Option shall be not less than 110 percent of the Fair Market Value on the grant date.

(c) Option Term. The term of each Stock Option shall be fixed by the Administrator, but no Stock Option shall be exercisable more than ten years after the date the Stock Option is granted. In the case of an Incentive Stock Option that is granted to a Ten Percent Owner, the term of such Stock Option shall be no more than five years from the date of grant.

(d) Exercisability; Rights of a Stockholder. Stock Options shall become exercisable at such time or times, whether or not in installments, as shall be determined by the Administrator at or after the grant date. The Administrator may at any time accelerate the exercisability of all or any portion of any Stock Option. An optionee shall have the rights of a stockholder only as to shares acquired upon the exercise of a Stock Option and not as to unexercised Stock Options.

(e) Method of Exercise. Stock Options may be exercised in whole or in part, by giving written or electronic notice of exercise to the Company, specifying the number of shares to be purchased. Payment of the purchase price may be made by one or more of the following methods except to the extent otherwise provided in the Option Award Certificate:

(i) In cash, by certified or bank check or other instrument acceptable to the Administrator;

(ii) Through the delivery (or attestation to the ownership in accordance with such procedures as the Company may prescribe) of shares of Stock that are not then subject to restrictions under any Company plan. Such surrendered shares shall be valued at Fair Market Value on the exercise date;

(iii) By the optionee delivering to the Company a properly executed exercise notice together with irrevocable instructions to a broker to promptly deliver to the Company cash or a check payable and acceptable to the Company for the purchase price; provided that in the event the optionee chooses to pay the purchase price as so provided, the optionee and the broker shall comply with such procedures and enter into such agreements of indemnity and other agreements as the Administrator shall prescribe as a condition of such payment procedure; or

(iv) With respect to Stock Options that are not Incentive Stock Options, by a "net exercise" arrangement pursuant to which the Company will reduce the number of shares of Stock issuable upon exercise by the largest whole number of shares with a Fair Market Value that does not exceed the aggregate exercise price.

Payment instruments will be received subject to collection. The transfer to the optionee on the records of the Company or of the transfer agent of the shares of Stock to be purchased pursuant to the exercise of a Stock Option will be contingent upon receipt from the optionee (or a purchaser acting in his stead in accordance with the provisions of the Stock Option) by the Company of the full purchase price for such shares and the fulfillment of any other requirements contained in the Option Award Certificate or applicable provisions of laws (including the satisfaction of any withholding taxes that the Company is obligated to withhold with respect to the optionee). In the event an optionee chooses to pay the purchase price by previously-owned shares of Stock through the attestation method, the number of shares of Stock transferred to the optionee upon the exercise of the Stock Option shall be net of the number of attested shares. In the event that the Company establishes, for itself or using the services of a third party, an automated system for the exercise of Stock Options, such as a system using an internet website or interactive voice response, then the paperless exercise of Stock Options may be permitted through the use of such an automated system.

(f) Annual Limit on Incentive Stock Options. To the extent required for "incentive stock option" treatment under Section 422 of the Code, the aggregate Fair Market Value (determined as of the time of grant) of the shares of Stock with respect to which Incentive Stock Options granted under this Plan and any other plan of the Company or its parent and subsidiary corporations become exercisable for the first time by an optionee during any calendar year shall not exceed \$100,000. To the extent that any Stock Option exceeds this limit, it shall constitute a Non-Qualified Stock Option.

SECTION 6. STOCK APPRECIATION RIGHTS

(a) Award of Stock Appreciation Rights. The Administrator may grant Stock Appreciation Rights under the Plan. A Stock Appreciation Right is an Award entitling the recipient to receive shares of Stock having a value equal to the excess of the Fair Market Value of a share of Stock on the date of exercise over the exercise price of the Stock Appreciation Right multiplied by the number of shares of Stock with respect to which the Stock Appreciation Right shall have been exercised.

(b) Exercise Price of Stock Appreciation Rights. The exercise price of a Stock Appreciation Right shall not be less than 100 percent of the Fair Market Value of the Stock on the date of grant.

(c) Grant and Exercise of Stock Appreciation Rights. Stock Appreciation Rights may be granted by the Administrator independently of any Stock Option granted pursuant to Section 5 of the Plan.

(d) Terms and Conditions of Stock Appreciation Rights. Stock Appreciation Rights shall be subject to such terms and conditions as shall be determined from time to time by the Administrator. The term of a Stock Appreciation Right may not exceed ten years.

SECTION 7. RESTRICTED STOCK AWARDS

(a) Nature of Restricted Stock Awards. The Administrator may grant Restricted Stock Awards under the Plan. A Restricted Stock Award is any Award of Restricted Shares subject to such restrictions and conditions as the Administrator may determine at the time of grant. Conditions may be based on continuing employment (or other service relationship) and/or achievement of pre-established performance goals and objectives. The terms and conditions of each such Award Certificate shall be determined by the Administrator, and such terms and conditions may differ among individual Awards and grantees.

(b) Rights as a Stockholder. Upon the grant of the Restricted Stock Award and payment of any applicable purchase price, a grantee shall have the rights of a stockholder with respect to the voting of the Restricted Shares and receipt of dividends; provided that if the lapse of restrictions with respect to the Restricted Stock Award is tied to the attainment of performance goals, any dividends paid by the Company during the performance period shall accrue and shall not be paid to the grantee until and to the extent the performance goals are met with respect to the Restricted Stock Award. Unless the Administrator shall otherwise determine, (i) uncertificated Restricted Shares shall be accompanied by a notation on the records of the Company or the transfer agent to the effect that they are subject to forfeiture until such Restricted Shares are vested as provided in Section 7(d) below, and (ii) certificated Restricted Shares shall remain in the possession of the Company until such Restricted Shares are vested as provided in Section 7(d) below, and the grantee shall be required, as a condition of the grant, to deliver to the Company such instruments of transfer as the Administrator may prescribe.

(c) Restrictions. Restricted Shares may not be sold, assigned, transferred, pledged or otherwise encumbered or disposed of except as specifically provided herein or in the Restricted Stock Award Certificate. Except as may otherwise be provided by the Administrator either in the Award Certificate or, subject to Section 18 below, in writing after the Award is issued, if a grantee's employment (or other service relationship) with the Company and its Subsidiaries terminates for any reason, any Restricted Shares that have not vested at the time of termination shall automatically and without any requirement of notice to such grantee from or other action by or on behalf of, the Company be deemed to have been reacquired by the Company at its original purchase price (if any) from such grantee or such grantee's legal representative simultaneously with such termination of employment (or other service relationship), and thereafter shall cease to represent any ownership of the Company by the grantee or rights of the grantee as a stockholder. Following such deemed reacquisition of Restricted Shares that are represented by physical certificates, a grantee shall surrender such certificates to the Company upon request without consideration.

(d) Vesting of Restricted Shares. The Administrator at the time of grant shall specify the date or dates and/or the attainment of pre-established performance goals, objectives and other conditions on which the non-transferability of the Restricted Shares and the Company's right of repurchase or forfeiture shall lapse. Subsequent to such date or dates and/or the attainment of such pre-established performance goals, objectives and other conditions, the shares on which all restrictions have lapsed shall no longer be Restricted Shares and shall be deemed "vested."

SECTION 8. RESTRICTED STOCK UNITS

(a) Nature of Restricted Stock Units. The Administrator may grant Restricted Stock Units under the Plan. A Restricted Stock Unit is an Award of stock units that may be settled in shares of Stock upon the satisfaction of such restrictions and conditions at the time of grant. Conditions may be based on continuing employment (or other service relationship) and/or achievement of pre-established performance goals and objectives. The terms and conditions of each such Award Certificate shall be determined by the Administrator, and such terms and conditions may differ among individual Awards and grantees. Except in the case of Restricted Stock Units with a deferred settlement date that complies with Section 409A, at the end of the vesting period, the Restricted Stock Units, to the extent vested, shall be settled in the form of shares of Stock. Restricted Stock Units with deferred settlement dates are subject to Section 409A and shall contain such additional terms and conditions as the Administrator shall determine in its sole discretion in order to comply with the requirements of Section 409A.

(b) Election to Receive Restricted Stock Units in Lieu of Compensation. The Administrator may, in its sole discretion, permit a grantee to elect to receive a portion of future cash compensation otherwise due to such grantee in the form of an award of Restricted Stock Units. Any such election shall be made in writing and shall be delivered to the Company no later than the date specified by the Administrator and in accordance with Section 409A and such other rules and procedures established by the Administrator. Any such future cash compensation that the grantee elects to defer shall be converted to a fixed number of Restricted Stock Units based on the Fair Market Value of Stock on the date the compensation would otherwise have been paid to the grantee if such payment had not been deferred as provided herein. The Administrator shall have the sole right to determine whether and under what circumstances to permit such elections and to impose such limitations and other terms and conditions thereon as the Administrator deems appropriate. Any Restricted Stock Units that are elected to be received in lieu of cash compensation shall be fully vested, unless otherwise provided in the Award Certificate.

(c) Rights as a Stockholder. A grantee shall have the rights as a stockholder only as to shares of Stock acquired by the grantee upon settlement of Restricted Stock Units; provided, however, that the grantee may be credited with Dividend Equivalent Rights with respect to the stock units underlying his Restricted Stock Units, subject to the provisions of Section 11 and such terms and conditions as the Administrator may determine.

(d) Termination. Except as may otherwise be provided by the Administrator either in the Award Certificate or, subject to Section 18 below, in writing after the Award is issued, a grantee's right in all Restricted Stock Units that have not vested shall automatically terminate upon the grantee's termination of employment (or cessation of service relationship) with the Company and its Subsidiaries for any reason.

SECTION 9. UNRESTRICTED STOCK AWARDS

Grant or Sale of Unrestricted Stock. The Administrator may grant (or sell at par value or such higher purchase price determined by the Administrator) an Unrestricted Stock Award under the Plan. An Unrestricted Stock Award is an Award pursuant to which the grantee may receive shares of Stock free of any restrictions under the Plan. Unrestricted Stock Awards may be granted in respect of past services or other valid consideration, or in lieu of cash compensation due to such grantee.

SECTION 10. CASH-BASED AWARDS

Grant of Cash-Based Awards. The Administrator may grant Cash-Based Awards under the Plan. A Cash-Based Award is an Award that entitles the grantee to a payment in cash upon the attainment of specified Performance Goals. The Administrator shall determine the maximum duration of the Cash-Based Award, the amount of cash to which the Cash-Based Award pertains, the conditions upon which the Cash-Based Award shall become vested or payable, and such other provisions as the Administrator shall determine. Each Cash-Based Award shall specify a cash-denominated payment amount, formula or payment ranges as determined by the Administrator. Payment, if any, with respect to a Cash-Based Award shall be made in accordance with the terms of the Award and may be made in cash.

SECTION 11. PERFORMANCE SHARE AWARDS

(a) Nature of Performance Share Awards. The Administrator may grant Performance Share Awards under the Plan. A Performance Share Award is an Award entitling the grantee to receive shares of Stock upon the attainment

of performance goals. The Administrator shall determine whether and to whom Performance Share Awards shall be granted, the performance goals, the periods during which performance is to be measured, which may not be less than one year except in the case of a Sale Event, and such other limitations and conditions as the Administrator shall determine.

(b) Rights as a Stockholder. A grantee receiving a Performance Share Award shall have the rights of a stockholder only as to shares of Stock actually received by the grantee under the Plan and not with respect to shares subject to the Award but not actually received by the grantee. A grantee shall be entitled to receive shares of Stock under a Performance Share Award only upon satisfaction of all conditions specified in the Performance Share Award Certificate (or in a performance plan adopted by the Administrator).

(c) Termination. Except as may otherwise be provided by the Administrator either in the Award agreement or, subject to Section 18 below, in writing after the Award is issued, a grantee's rights in all Performance Share Awards shall automatically terminate upon the grantee's termination of employment (or cessation of service relationship) with the Company and its Subsidiaries for any reason.

SECTION 12. PERFORMANCE-BASED AWARDS TO COVERED EMPLOYEES

(a) Performance-Based Awards. The Administrator may grant one or more Performance-Based Awards in the form of a Restricted Stock Award, Restricted Stock Units, Performance Share Awards or Cash-Based Award payable upon the attainment of Performance Goals that are established by the Administrator and relate to one or more of the Performance Criteria, in each case on a specified date or dates or over any period or periods determined by the Administrator. The Administrator shall define in an objective fashion the manner of calculating the Performance Criteria it selects to use for any Performance Cycle. Depending on the Performance Criteria used to establish such Performance Goals, the Performance Goals may be expressed in terms of overall Company performance or the performance of a division, business unit, or an individual. Each Performance-Based Award shall comply with the provisions set forth below.

(b) Grant of Performance-Based Awards. With respect to each Performance-Based Award granted to a Covered Employee, the Administrator shall select, within the first 90 days of a Performance Cycle (or, if shorter, within the maximum period allowed under Section 162(m) of the Code) the Performance Criteria for such grant, and the Performance Goals with respect to each Performance Criterion (including a threshold level of performance below which no amount will become payable with respect to such Award). Each Performance-Based Award will specify the amount payable, or the formula for determining the amount payable, upon achievement of the various applicable performance targets. The Performance Criteria established by the Administrator may be (but need not be) different for each Performance Cycle and different Performance Goals may be applicable to Performance-Based Awards to different Covered Employees.

(c) Payment of Performance-Based Awards. Following the completion of a Performance Cycle, the Administrator shall meet to review and certify in writing whether, and to what extent, the Performance Goals for the Performance Cycle have been achieved and, if so, to also calculate and certify in writing the amount of the Performance-Based Awards earned for the Performance Cycle. The Administrator shall then determine the actual size of each Covered Employee's Performance-Based Award.

(d) Maximum Award Payable. The maximum Performance-Based Award payable to any one Covered Employee under the Plan for a Performance Cycle is 112,469 shares of Stock (subject to adjustment as provided in Section 3(c) hereof) or \$2,000,000 in the case of a Performance-Based Award that is a Cash-Based Award.

SECTION 13. DIVIDEND EQUIVALENT RIGHTS

(a) Dividend Equivalent Rights. The Administrator may grant Dividend Equivalent Rights under the Plan. A Dividend Equivalent Right is an Award entitling the grantee to receive credits based on cash dividends that would have been paid on the shares of Stock specified in the Dividend Equivalent Right (or other Award to which it relates) if such shares had been issued to the grantee. A Dividend Equivalent Right may be granted hereunder to any grantee as a component of an award of Restricted Stock Units, Restricted Stock Award or Performance Share Award or as a freestanding award. The terms and conditions of Dividend Equivalent Rights shall be specified in the Award Certificate. Dividend equivalents credited to the holder of a Dividend Equivalent Right may be paid currently or may be deemed to be reinvested in additional shares of Stock, which may thereafter accrue additional equivalents. Any

such reinvestment shall be at Fair Market Value on the date of reinvestment or such other price as may then apply under a dividend reinvestment plan sponsored by the Company, if any. Dividend Equivalent Rights may be settled in cash or shares of Stock or a combination thereof, in a single installment or installments. A Dividend Equivalent Right granted as a component of an Award of Restricted Stock Units or Performance Share Award shall provide that such Dividend Equivalent Right shall be settled only upon settlement or payment of, or lapse of restrictions on, such other Award, and that such Dividend Equivalent Right shall expire or be forfeited or annulled under the same conditions as such other Award.

(b) **Termination.** Except as may otherwise be provided by the Administrator either in the Award Certificate or, subject to Section 18 below, in writing after the Award is issued, a grantee's rights in all Dividend Equivalent Rights shall automatically terminate upon the grantee's termination of employment (or cessation of service relationship) with the Company and its Subsidiaries for any reason.

SECTION 14. TRANSFERABILITY OF AWARDS

(a) **Transferability.** Except as provided in Section 14(b) below, during a grantee's lifetime, his or her Awards shall be exercisable only by the grantee, or by the grantee's legal representative or guardian in the event of the grantee's incapacity. No Awards shall be sold, assigned, transferred or otherwise encumbered or disposed of by a grantee other than by will or by the laws of descent and distribution or pursuant to a domestic relations order. No Awards shall be subject, in whole or in part, to attachment, execution, or levy of any kind, and any purported transfer in violation hereof shall be null and void.

(b) **Administrator Action.** Notwithstanding Section 14(a), the Administrator, in its discretion, may provide either in the Award Certificate regarding a given Award or by subsequent written approval that the grantee (who is an employee or director) may transfer his or her Non-Qualified Options to his or her immediate family members, to trusts for the benefit of such family members, or to partnerships in which such family members are the only partners, provided that the transferee agrees in writing with the Company to be bound by all of the terms and conditions of this Plan and the applicable Award. In no event may an Award be transferred by a grantee for value.

(c) **Family Member.** For purposes of Section 14(b), "family member" shall mean a grantee's child, stepchild, grandchild, parent, stepparent, grandparent, spouse, former spouse, sibling, niece, nephew, mother-in-law, father-in-law, son-in-law, daughter-in-law, brother-in-law, or sister-in-law, including adoptive relationships, any person sharing the grantee's household (other than a tenant of the grantee), a trust in which these persons (or the grantee) have more than 50 percent of the beneficial interest, a foundation in which these persons (or the grantee) control the management of assets, and any other entity in which these persons (or the grantee) own more than 50 percent of the voting interests.

(d) **Designation of Beneficiary.** To the extent permitted by the Company, each grantee to whom an Award has been made under the Plan may designate a beneficiary or beneficiaries to exercise any Award or receive any payment under any Award payable on or after the grantee's death. Any such designation shall be on a form provided for that purpose by the Administrator and shall not be effective until received by the Administrator. If no beneficiary has been designated by a deceased grantee, or if the designated beneficiaries have predeceased the grantee, the beneficiary shall be the grantee's estate.

SECTION 15. TAX WITHHOLDING

(a) **Payment by Grantee.** Each grantee shall, no later than the date as of which the value of an Award or of any Stock or other amounts received thereunder first becomes includable in the gross income of the grantee for Federal income tax purposes, pay to the Company, or make arrangements satisfactory to the Administrator regarding payment of, any Federal, state, or local taxes of any kind required by law to be withheld by the Company with respect to such income. The Company and its Subsidiaries shall, to the extent permitted by law, have the right to deduct any such taxes from any payment of any kind otherwise due to the grantee. The Company's obligation to deliver evidence of book entry (or stock certificates) to any grantee is subject to and conditioned on tax withholding obligations being satisfied by the grantee.

(b) **Payment in Stock.** Subject to approval by the Administrator, a grantee may elect to have the Company's minimum required tax withholding obligation satisfied, in whole or in part, by authorizing the Company to withhold from shares of Stock to be issued pursuant to any Award a number of shares with an aggregate Fair Market Value (as of the date the withholding is effected) that would satisfy the withholding amount due. The Administrator may also require Awards to be subject to mandatory share withholding up to the required withholding amount. For purposes

of share withholding, the Fair Market Value of withheld shares shall be determined in the same manner as the value of Stock includible in income of the Participants.

SECTION 16. SECTION 409A AWARDS

To the extent that any Award is determined to constitute "nonqualified deferred compensation" within the meaning of Section 409A (a "409A Award"), the Award shall be subject to such additional rules and requirements as specified by the Administrator from time to time in order to comply with Section 409A. In this regard, if any amount under a 409A Award is payable upon a "separation from service" (within the meaning of Section 409A) to a grantee who is then considered a "specified employee" (within the meaning of Section 409A), then no such payment shall be made prior to the date that is the earlier of (i) six months and one day after the grantee's separation from service, or (ii) the grantee's death, but only to the extent such delay is necessary to prevent such payment from being subject to interest, penalties and/or additional tax imposed pursuant to Section 409A. Further, the settlement of any such Award may not be accelerated except to the extent permitted by Section 409A.

SECTION 17. TERMINATION OF EMPLOYMENT, TRANSFER, LEAVE OF ABSENCE, ETC.

(a) Termination of Employment. If the grantee's employer ceases to be a Subsidiary, the grantee shall be deemed to have terminated employment for purposes of the Plan.

(b) For purposes of the Plan, the following events shall not be deemed a termination of employment:

(i) a transfer to the employment of the Company from a Subsidiary or from the Company to a Subsidiary, or from one Subsidiary to another; or

(ii) an approved leave of absence for military service or sickness, or for any other purpose approved by the Company, if the employee's right to re-employment is guaranteed either by a statute or by contract or under the policy pursuant to which the leave of absence was granted or if the Administrator otherwise so provides in writing.

SECTION 18. AMENDMENTS AND TERMINATION

The Board may, at any time, amend or discontinue the Plan and the Administrator may, at any time, amend or cancel any outstanding Award for the purpose of satisfying changes in law or for any other lawful purpose, but no such action shall adversely affect rights under any outstanding Award without the holder's consent. Except as provided in Section 3(c) or 3(d), without prior stockholder approval, in no event may the Administrator exercise its discretion to reduce the exercise price of outstanding Stock Options or Stock Appreciation Rights or effect repricing through cancellation and re-grants or cancellation of Stock Options or Stock Appreciation Rights in exchange for cash. To the extent required under the rules of any securities exchange or market system on which the Stock is listed, to the extent determined by the Administrator to be required by the Code to ensure that Incentive Stock Options granted under the Plan are qualified under Section 422 of the Code, or to ensure that compensation earned under Awards qualifies as performance-based compensation under Section 162(m) of the Code, Plan amendments shall be subject to approval by the Company stockholders entitled to vote at a meeting of stockholders. Nothing in this Section 18 shall limit the Administrator's authority to take any action permitted pursuant to Section 3(c) or 3(d).

SECTION 19. STATUS OF PLAN

With respect to the portion of any Award that has not been exercised and any payments in cash, Stock or other consideration not received by a grantee, a grantee shall have no rights greater than those of a general creditor of the Company unless the Administrator shall otherwise expressly determine in connection with any Award or Awards. In its sole discretion, the Administrator may authorize the creation of trusts or other arrangements to meet the Company's obligations to deliver Stock or make payments with respect to Awards hereunder, provided that the existence of such trusts or other arrangements is consistent with the foregoing sentence.

SECTION 20. GENERAL PROVISIONS

(a) No Distribution. The Administrator may require each person acquiring Stock pursuant to an Award to represent to and agree with the Company in writing that such person is acquiring the shares without a view to distribution thereof.

(b) Delivery of Stock Certificates. Stock certificates to grantees under this Plan shall be deemed delivered for all purposes when the Company or a stock transfer agent of the Company shall have mailed such certificates in the United States mail, addressed to the grantee, at the grantee's last known address on file with the Company. Uncertificated Stock shall be deemed delivered for all purposes when the Company or a Stock transfer agent of the Company shall have given to the grantee by electronic mail (with proof of receipt) or by United States mail, addressed to the grantee, at the grantee's last known address on file with the Company, notice of issuance and recorded the issuance in its records (which may include electronic "book entry" records). Notwithstanding anything herein to the contrary, the Company shall not be required to issue or deliver any certificates evidencing shares of Stock pursuant to the exercise of any Award, unless and until the Administrator has determined, with advice of counsel (to the extent the Administrator deems such advice necessary or advisable), that the issuance and delivery of such certificates is in compliance with all applicable laws, regulations of governmental authorities and, if applicable, the requirements of any exchange on which the shares of Stock are listed, quoted or traded. All Stock certificates delivered pursuant to the Plan shall be subject to any stop-transfer orders and other restrictions as the Administrator deems necessary or advisable to comply with federal, state or foreign jurisdiction, securities or other laws, rules and quotation system on which the Stock is listed, quoted or traded. The Administrator may place legends on any Stock certificate to reference restrictions applicable to the Stock. In addition to the terms and conditions provided herein, the Administrator may require that an individual make such reasonable covenants, agreements, and representations as the Administrator, in its discretion, deems necessary or advisable in order to comply with any such laws, regulations, or requirements. The Administrator shall have the right to require any individual to comply with any timing or other restrictions with respect to the settlement or exercise of any Award, including a window-period limitation, as may be imposed in the discretion of the Administrator.

(c) Stockholder Rights. Until Stock is deemed delivered in accordance with Section 20(b), no right to vote or receive dividends or any other rights of a stockholder will exist with respect to shares of Stock to be issued in connection with an Award, notwithstanding the exercise of a Stock Option or any other action by the grantee with respect to an Award.

(d) Other Compensation Arrangements; No Employment Rights. Nothing contained in this Plan shall prevent the Board from adopting other or additional compensation arrangements, including trusts, and such arrangements may be either generally applicable or applicable only in specific cases. The adoption of this Plan and the grant of Awards do not confer upon any employee any right to continued employment with the Company or any Subsidiary.

(e) Trading Policy Restrictions. Option exercises and other Awards under the Plan shall be subject to the Company's insider trading policies and procedures, as in effect from time to time.

(f) Clawback Policy. Awards under the Plan shall be subject to the Company's clawback policy, as in effect from time to time.

SECTION 21. EFFECTIVE DATE OF PLAN

This Plan shall become effective upon the effectiveness of the Company's registration statement on Form S-1 in connection with its Initial Public Offering, following stockholder approval of the Plan in accordance with applicable state law, the Company's bylaws and certificate of incorporation, and applicable stock exchange rules or pursuant to written consent. No grants of Stock Options and other Awards may be made hereunder after the tenth anniversary of the Effective Date and no grants of Incentive Stock Options may be made hereunder after the tenth anniversary of the date the Plan is approved by the Board.

SECTION 22. GOVERNING LAW

This Plan and all Awards and actions taken thereunder shall be governed by, and construed in accordance with, the laws of the State of Delaware, applied without regard to conflict of law principles.

DATE APPROVED BY THE BOARD OF DIRECTORS: April 25, 2015

DATE APPROVED BY THE STOCKHOLDERS: April 25, 2015

AMENDMENT APPROVED BY THE BOARD OF DIRECTORS: March 4, 2019

AMENDMENT APPROVED BY THE STOCKHOLDERS: May 8, 2019

AMENDMENT APPROVED BY THE BOARD OF DIRECTORS: March 16, 2020

AMENDMENT APPROVED BY THE STOCKHOLDERS: [_____, 2020]

ANNEX B

**CERTIFICATE OF AMENDMENT
TO THE
RESTATED CERTIFICATE OF INCORPORATION
OF
ATYR PHARMA, INC.**

aTyr Pharma, Inc. (the "**Corporation**"), a corporation organized and existing under the laws of the State of Delaware, hereby certifies as follows:

FIRST: That the name of the Corporation is aTyr Pharma, Inc. The date of the filing of its original Certificate of Incorporation with the Secretary of State of Delaware was September 8, 2005.

SECOND: That the Board of Directors of the Corporation duly adopted resolutions approving the following amendment of the Restated Certificate of Incorporation, declaring said amendment to be advisable and providing for such consideration of such amendment at the Corporation's annual meeting of the stockholders.

THIRD: On May 6, 2020, the Corporation's annual meeting of the stockholders was duly called and held, upon notice in accordance with Section 222 of the Delaware General Corporation Law, at which meeting the necessary number of shares as required by statute were voted in favor of the amendment.

FOURTH: The first sentence of Article IV of the Restated Certificate of Incorporation of the Corporation is hereby amended and restated to read in its entirety as follows:

The total number of shares of capital stock which the Corporation shall have authority to issue is Twenty Eight Million Seven Hundred Ten Thousand Four Hundred Fifty-Six (28,710,456), of which (i) Twenty One Million Four Hundred Twenty-Five Thousand (21,425,000) shares shall be a class designated as common stock, par value \$0.001 per share (the "**Common Stock**"), and (ii) Seven Million Two Hundred Eighty-Five Thousand Four Hundred Fifty Six (7,285,456) shares shall be a class designated as preferred stock, par value \$0.001 per share (the "**Preferred Stock**"), of which 72,000 shares are designated Series B Convertible Preferred Stock ("**Series B Preferred Stock**"), 15,957 shares are designated Series C Convertible Preferred Stock ("**Series C Preferred Stock**"), 2,197,499 shares are designated Series D Convertible Preferred Stock ("**Series D Preferred Stock**"), and together with the Series B Preferred Stock and Series C Preferred Stock, the "**Designated Preferred Stock**"), and Five Million (5,000,000) shares shall be undesignated preferred stock (the "Undesignated Preferred Stock").

FIFTH: That this Certificate of Amendment to the Restated Certificate of Incorporation shall be effective on and as of the date of filing with the Secretary of State of the State of Delaware.

IN WITNESS WHEREOF, this Certificate of Amendment to the Restated Certificate of Incorporation has been executed by a duly authorized officer of this Corporation on this [__] day of [__], 2020.

By:

Sanjay S. Shukla, M.D., M.S.
President and Chief Executive Officer



ANNUAL MEETING OF ATYR PHARMA, INC.

Date: May 6, 2020
Time: 8:30 A.M. (Pacific Daylight Time)
Place: Annual Meeting to be held virtually via live webcast – please visit www.proxydocs/LIFE for more details.

Please make your marks like this: Use dark black pencil or pen only

Board of Directors Recommends a Vote **FOR** proposals 1, 2, 3, 4 and 5.

1: To elect two Class II directors, as nominated by the Board of Directors, to hold office until the 2023 Annual Meeting of Stockholders or until their successors are duly elected and qualified.

For Withhold
For Withhold

2: To ratify the appointment of Ernst & Young LLP as the independent registered public accounting firm of the Company for its fiscal year ending December 31, 2020.

For Against Abstain

3: To approve an amendment to the aTyr Pharma, Inc. 2015 Stock Option and Incentive Plan to increase the number of shares of common stock reserved for issuance thereunder by 350,000 shares.

For Against Abstain

4: To approve an amendment to the Company's Restated Certificate of Incorporation to increase the authorized number of shares from 10,714,286 to 21,425,000.

For Against Abstain

5: To approve the authorization to adjourn the Annual Meeting, if necessary, to solicit additional proxies if there are not sufficient votes in favor of Proposal 3 or Proposal 4.

For Against Abstain

6: To transact such other business as may properly come before the meeting or any adjournment or postponement thereof.

Authorized Signatures - This section must be completed for your instructions to be executed.

TO VIRTUALLY ATTEND the Annual Meeting of aTyr Pharma, Inc., you must register in advance at www.proxydocs.com/LIFE prior to the deadline of Monday, May 4, 2020 at 2:00 p.m. (Pacific Daylight Time). The control number in the shaded gray box will be required to register.

Please Sign Here Please Date Above

Please Sign Here Please Date Above

Please sign exactly as your name(s) appears on your stock certificate. If held in joint tenancy, all persons should sign. Trustees, administrators, etc., should include title and authority. Corporations should provide full name of corporation and title of authorized officer signing the proxy.



**Annual Meeting of aTyr Pharma, Inc.
to be held on Wednesday, May 6, 2020
for Holders as of March 16, 2020**

This proxy is being solicited on behalf of the Board of Directors

VOTE BY:
INTERNET **TELEPHONE**

Go To www.proxypush.com/LIFE
• Cast your vote online.
• View Meeting Documents
• Vote up until 8:30 a.m. (PDT) on May 6, 2020.

OR

MAIL

866-284-6674
• Use any touch-tone telephone.
• Have your Proxy Card/Voting Instruction Form ready.
• Follow the simple recorded instructions.
• Vote up until 8:30 a.m. (PDT) on May 6, 2020.

OR

• Mark, sign and date your Proxy Card/Voting Instruction Form.
• Detach your Proxy Card/Voting Instruction Form.
• Return your Proxy Card/Voting Instruction Form in the postage-paid envelope provided and ensure that it is received prior to the start of the Annual Meeting.

TO VIRTUALLY ATTEND the Annual Meeting of aTyr Pharma, Inc., please visit www.proxydocs/LIFE for virtual meeting registration details. The control number in the shaded gray box will be required to register.

The undersigned hereby appoints Sanjay S. Shukla, M.D., M.S. and Nancy E. Danyes, and each or either of them, as the true and lawful attorneys of the undersigned, with full power of substitution and revocation, and authorizes them, and each of them, to vote all the shares of common stock of aTyr Pharma, Inc. which the undersigned is entitled to vote at said meeting and any adjournment thereof upon the matters specified and upon such other matters as may be properly brought before the meeting or any adjournment thereof, conferring authority upon such true and lawful attorneys to vote in their discretion on such other matters as may properly come before the meeting and revoking any proxy heretofore given.

THE SHARES REPRESENTED BY THIS PROXY WILL BE VOTED AS DIRECTED OR, IF NO DIRECTION IS GIVEN, SHARES WILL BE VOTED FOR THE ELECTION OF THE DIRECTORS IN ITEM 1 AND FOR THE PROPOSALS IN ITEMS 2, 3, 4 AND 5.

**PROXY TABULATOR FOR
ATYR PHARMA, INC.
P.O. BOX 6016
CARY, NC 27512-9903**



Please separate carefully at the perforation and return just this portion in the envelope provided.

Directors
Recommendation
↓
For
For

For

For

For

For



Proxy — aTyr Pharma, Inc.
Annual Meeting of Stockholders
May 6, 2020, 8:30 a.m. (Pacific Daylight Time)
This Proxy is Solicited on Behalf of the Board of Directors

The undersigned appoints Sanjay S. Shukla, M.D., M.S. and Nancy E. Denyes (the "Named Proxies") and each of them as proxies for the undersigned, with full power of substitution, to vote the shares of common stock of aTyr Pharma, Inc., a Delaware corporation ("the Company"), the undersigned is entitled to vote at the Annual Meeting of Stockholders of the Company to be held virtually via live webcast, on Wednesday, May 6, 2020 at 8:30 a.m. (PDT) and all adjournments thereof.

↓ TO VIRTUALLY ATTEND the Annual Meeting of aTyr Pharma, Inc., you must register in advance at www.proxydocs.com/LIFE prior to the deadline of Monday, May 4, 2020 at 2:00 p.m. (Pacific Daylight Time). The control number in the shaded gray box will be required to register.

The purpose of the Annual Meeting is to take action on the following:

1. Proposal 1: To elect two Class II directors, as nominated by the Board of Directors, to hold office until the 2023 Annual Meeting of Stockholders or until their successors are duly elected and qualified.
2. Proposal 2: To ratify the appointment of Ernst & Young LLP as the independent registered public accounting firm of the Company for its fiscal year ending December 31, 2020.
3. Proposal 3: To approve an amendment to the aTyr Pharma, Inc. 2015 Stock Option and Incentive Plan to increase the number of shares of common stock reserved for issuance thereunder by 350,000 shares.
4. Proposal 4: To approve an amendment to the Company's Restated Certificate of Incorporation to increase the authorized number of shares from 10,714,286 to 21,428,572.
5. Proposal 5: To approve the authorization to adjourn the Annual Meeting, if necessary, to solicit additional proxies if there are not sufficient votes in favor of Proposal 3 or Proposal 4.
6. To transact such other business as may properly come before the Annual Meeting or any adjournment or postponement of the Annual Meeting.

The two Class II directors that are up for election are: Timothy P. Coughlin and Jane A. Gross, Ph. D.

The Board of Directors of the Company recommends a vote "FOR" all nominees for director and "FOR" each proposal.

↓ This proxy, when properly executed, will be voted in the manner directed herein. If no direction is made, this proxy will be voted "FOR" all nominees for director and "FOR" each proposal. In their discretion, the Named Proxies are authorized to vote upon such other matters that may properly come before the Annual Meeting or any adjournment or postponement thereof.

You are encouraged to specify your choice by marking the appropriate box (SEE REVERSE SIDE) but you need not mark any box if you wish to vote in accordance with the Board of Directors' recommendation. The Named Proxies cannot vote your shares unless you sign and return this card.

To virtually attend the meeting via live webcast and vote your shares online, please mark this box.