Filed pursuant to Rule 424(b)(5)
Registration No. 333-282530

PROSPECTUS SUPPLEMENT
(to Prospectus dated October 7, 2024)

Scholar Rock Holding Corporation



Up to $200,000,000
Common Stock

We previously entered into a certain Open Market Sale Agreement[SM] dated November 14, 2022, or sales agreement, with Jefferies LLC, or Jefferies, relating to shares of our common stock offered by this prospectus. In accordance with the terms of the sales agreement, we may offer and sell shares of our common stock having an aggregate offering price of up to $200,000,000 from time to time through Jefferies, acting as agent.

Our common stock is listed on The Nasdaq Global Select Market under the symbol "SRRK." On November 12, 2025, the closing price of our common stock, as reported on The Nasdaq Global Select Market, was $30.82 per share.

Sales of our common stock, if any, under this prospectus may be made in sales deemed to be "at the market offerings" as defined in Rule 415(a)(4) promulgated under the Securities Act of 1933, as amended, or the Securities Act. Jefferies is not required to sell any specific number or dollar amount of securities, but will act as a sales agent using commercially reasonable efforts consistent with its normal trading and sales practices, on mutually agreed terms between Jefferies and us. There is no arrangement for funds to be received in any escrow, trust or similar arrangement.

The compensation to Jefferies for sales of common stock sold pursuant to the sales agreement will be up to 3.0% of the gross proceeds of any shares of common stock sold under the sales agreement. In connection with the sale of the common stock on our behalf, Jefferies will be deemed to be an "underwriter" within the meaning of the Securities Act and the compensation of Jefferies will be deemed to be underwriting commissions or discounts. We have also agreed to provide indemnification and contribution to Jefferies with respect to certain liabilities, including liabilities under the Securities Act. See the section titled "Plan of Distribution" on page S-14 of this prospectus.

Investing in our common stock involves a high degree of risk. You should review carefully the risks and uncertainties referenced under the heading "*Risk Factors*" on page S-7 of this prospectus and in the documents that are incorporated by reference into this prospectus.

Neither the Securities and Exchange Commission nor any state securities commission has approved or disapproved of these securities or determined if this prospectus is truthful or complete. Any representation to the contrary is a criminal offense.

Jefferies

The date of this prospectus is November 14, 2025

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We are responsible for the information contained and incorporated by reference in this prospectus, in any accompanying prospectus, and in any related free writing prospectus we prepare or authorize. We have not authorized anyone to give you any other information, and we take no responsibility for any other information that others may give you. If you are in a jurisdiction where offers to sell, or solicitations of offers to purchase, the securities offered by this documentation are unlawful, or if you are a person to whom it is unlawful to direct these types of activities, then the offer presented in this document does not extend to you. The information contained in this document speaks only as of the date of this document, unless the information specifically indicates that another date applies. Our business, financial condition, results of operations and prospects may have changed since those dates.

ABOUT THIS PROSPECTUS

This prospectus is part of an automatic shelf registration statement on Form S-3 that we filed with the Securities and Exchange Commission, or the SEC, as a "well-known seasoned issuer" as defined in Rule 405 under the Securities Act of 1933, as amended, or the Securities Act. Under the shelf registration, we and/or selling stockholders may offer shares of our common stock, from time to time in one or more offerings.

This prospectus relates to the offering of our common stock. Before buying any of the common stock that we are offering, we urge you to carefully read this prospectus together with the information incorporated by reference as described under the headings "Where You Can Find More Information" and "Incorporation of Certain Information by Reference" in this prospectus, and any free writing prospectus or prospectus supplement that we have authorized for use in connection with this offering. These documents contain important information that you should consider when making your investment decision.

This prospectus describes the terms of this offering of common stock and also adds to and updates information contained in the documents incorporated by reference into this prospectus. To the extent there is a conflict between the information contained in this prospectus, on the one hand, and the information contained in any document incorporated by reference into this prospectus that was filed with the SEC before the date of this prospectus, on the other hand, you should rely on the information in this prospectus. If any statement in one of these documents is inconsistent with a statement in another document having a later date — for example, a document incorporated by reference into this prospectus — the statement in the document having the later date modifies or supersedes the earlier statement.

We have not authorized anyone to provide you with information in addition to or different from that contained in this prospectus, any applicable prospectus supplement and any related free writing prospectus. We take no responsibility for, and can provide no assurances as to the reliability of, any information not contained in this prospectus, any applicable prospectus supplement or any related free writing prospectus that we may authorize to be provided to you. This prospectus is an offer to sell only the securities offered hereby, but only under circumstances and in jurisdictions where it is lawful to do so. You should assume that the information in this prospectus, the accompanying prospectus or any related free writing prospectus is accurate only as of the date on the front of the document and that any information incorporated by reference is accurate only as of the date of the document incorporated by reference, regardless of the time of delivery of this prospectus, the accompanying prospectus or any related free writing prospectus, or any sale of a security.

This prospectus contains summaries of certain provisions contained in some of the documents described herein, but reference is made to the actual documents for complete information. All of the summaries are qualified in their entirety by the actual documents. Copies of some of the documents referred to herein have been filed, will be filed or will be incorporated by reference as exhibits to the registration statement of which this prospectus and the accompanying prospectus is a part, and you may obtain copies of those documents as described below under the heading "Where You Can Find More Information".

Unless the context otherwise indicates, references in this prospectus to "Scholar Rock", "we", "our", "us" and "the Company" refer, collectively, to Scholar Rock Holding Corporation and its subsidiaries.

We own various U.S. federal trademark applications and unregistered trademarks, including "Scholar Rock" and our corporate logo. All other trademarks or trade names referred to in this prospectus are the property of their respective owners. Solely for convenience, the trademarks and trade names in this prospectus are referred to without the symbols® and ™, but such references should not be construed as any indicator that their respective owners will not assert, to the fullest extent under applicable law, their rights thereto. We do not intend our use or display of other companies' trademarks and trade names to imply a relationship with, or endorsement or sponsorship of us by, any other companies.

PROSPECTUS SUMMARY

The following summary of our business highlights some of the information contained elsewhere in, or incorporated by reference into, this prospectus. Because this is only a summary, however, it does not contain all of the information that may be important to you. You should carefully read this prospectus and the accompanying prospectus, including the documents incorporated by reference, which are described under "Incorporation of certain information by reference" in this prospectus. You should also carefully consider the matters discussed in the section of this prospectus entitled "Risk factors" and under similar sections of the accompanying prospectus and other periodic reports incorporated herein and therein by reference.

Company overview

We are a global biopharmaceutical company dedicated to dramatically improving the lives of children and adults with SMA and additional rare, severe and debilitating neuromuscular diseases. As a global leader in the biology of TGFβ superfamily, our novel understanding of the molecular mechanisms of growth factor activation enabled us to develop a proprietary platform for the discovery and development of monoclonal antibodies that locally and selectively target the precursor, or latent, forms of growth factors. By targeting the signaling proteins at the cellular level and acting in the disease microenvironment, we believe we may avoid the historical dose-limiting safety challenges associated with inhibiting growth factors for therapeutic effect. We believe our focus on biologically validated growth factors may facilitate a more efficient development path.

Based on this proprietary and scalable technology platform, we are building a growing portfolio of novel product candidates to deliver life-changing therapies for people with serious diseases that have high unmet need, including neuromuscular disorders, cardiometabolic disorders, cancer, and other conditions where growth factor-targeted therapies can play a transformational role. We have discovered and progressed the development of:

- Apitegromab, an investigational, highly selective, fully human monoclonal antibody that inhibits myostatin activation by selectively binding the pro- and latent forms of myostatin in skeletal muscle and is being developed as a potential first muscle-targeted treatment for SMA. We also believe apitegromab could have potential in the treatment of other neuromuscular disorders where the inhibition of myostatin may be beneficial.
- SRK-439, a novel, investigational myostatin inhibitor that has high in vitro affinity for pro- and latent myostatin and maintains myostatin specificity and is being developed for the treatment of neuromuscular diseases.
- SRK-181, an investigational inhibitor of the activation of latent TGFβ1, that is being developed for the treatment of cancers that are resistant to anti-PD-(L)1 antibody therapies.
- SRK-373, a novel, preclinical, investigational TGFβ inhibitor that selectively inhibits the activation of latent TGFβ1 isoform in the context of fibrotic extracellular matrix and that avoids perturbing TGFβ1 presented by cells of the immune system and is being developed for the treatment of fibrotic diseases.
- SRK-256, a novel, preclinical, investigational inhibitor that selectively inhibits RGMc or hemojuvelin, the co-receptor of bone morphogenic protein 6 ("BMP6"), and hence inhibits BMP6 signaling. BMP6 signaling is critical for iron homeostasis and SRK-256 has wide potential applicability in states of iron-restricted anemias.
- Additional discovery and early preclinical programs related to the selective modulation of growth factor signaling.

Our first product candidate, apitegromab, is a highly selective, fully human, monoclonal antibody, with a unique mechanism of action that results in inhibition of the activation of the growth factor, myostatin, in skeletal muscle. Apitegromab is being developed as a potential first muscle-targeted treatment for SMA. In October 2024, we announced positive top-line results in SAPPHIRE, a pivotal Phase 3 clinical trial to evaluate the efficacy and safety of apitegromab in patients with non-ambulatory Type 2 and Type 3 SMA (which is estimated to represent the majority of the current prevalent SMA patient population in the U.S. and Europe). The study achieved its primary endpoint. At the March 2025 Muscular Dystrophy Association Clinical & Scientific Conference, we presented additional data related to secondary endpoint analyses in which apitegromab demonstrated a clinically meaningful and consistent benefit in motor function across pre-specified patient subgroups. We submitted a U.S. Biologics License Application to the FDA in January 2025 and the BLA was

granted priority review designation. Priority review designation conveys that the FDA has determined that if apitegromab is approved, it could offer significant improvement in the safety or effectiveness of treatment of the serious condition of SMA. In September 2025, we received a Complete Response Letter ("CRL") from the FDA related to observations identified during a routine general site inspection of a third-party fill-finish facility. The facility was issued a Form 483 by the FDA in July 2025 and the inspection classification of this facility is "official action indicated" (OAI). The observations were not specific to apitegromab. The CRL did not cite any other approvability concerns, including apitegromab's efficacy and safety data or the third-party drug substance manufacturer. In November 2025, we completed a constructive in-person Type A meeting with the FDA that included participation of representatives from the third-party fill-finish facility. We plan to resubmit the apitegromab BLA at such time as the facility has been reclassified by the FDA. In March 2025, we submitted to the European Medicines Agency ("EMA") and received validation of our marketing authorisation application ("MAA") for apitegromab for the treatment of SMA. Validation confirms that the application includes the essential regulatory elements required for scientific assessment of the MAA and the scientific evaluation process by the EMA's Committee for Medicinal Products for Human Use can begin. If apitegromab is approved by the FDA or EMA, we expect to initiate a commercial product launch in the applicable jurisdictions upon approval.

Apitegromab was evaluated in our Phase 2 TOPAZ proof-of-concept clinical trial for the treatment of patients with Type 2 and Type 3 SMA. Positive 12-month top-line results were initially announced in April 2021. We have subsequently presented data from the TOPAZ trial over 24-months (2022), 36-months (2023) and 48-months (2024). At 48-months over 90% of TOPAZ patients with non-ambulatory Type 2 and 3 SMA receiving a survival motor neuron ("SMN") targeted treatment remained on apitegromab and showed sustained clinical benefit, with a continued generally favorable safety profile and no new safety findings. Additionally, we are conducting a long-term extension study, ONYX, for patients from both the TOPAZ and SAPPHIRE studies, who are receiving apitegromab in conjunction with an approved SMN-targeted treatment. The FDA granted Fast Track designation, Rare Pediatric Disease designation and Orphan Drug designation to apitegromab for the treatment of SMA in May 2021, August 2020 and March 2018, respectively. The EMA granted Priority Medicines ("PRIME") designation in March 2021 and the EC granted orphan medicinal product designation in December 2018 to apitegromab for the treatment of SMA.

We believe that apitegromab has the potential to be the first muscle-targeted treatment that is aimed at improving motor function in children and adults with SMA who are receiving an SMN-targeted therapy. We also have identified opportunities to potentially expand the therapeutic benefit of apitegromab, including additional patient populations in SMA (such as patients with SMA under two years of age) and multiple other diseases beyond SMA where selective inhibition of myostatin activation may offer therapeutic benefit. We initiated the Phase 2 OPAL trial in SMA patients under two years of age in the third quarter of 2025.

In addition to advancing development of apitegromab in neuromuscular diseases, we continue to advance our efforts for a second anti-myostatin product candidate and explore therapeutic benefit beyond neuromuscular disorders. In October 2023, we announced an expansion of our anti-myostatin program with SRK-439, a novel, fully human anti-myostatin monoclonal antibody and in September 2025, an investigational new drug application was cleared by the FDA. The Company plans to initiate dosing of SRK-439 in healthy volunteers in the fourth quarter of 2025.

In 2024, we presented preclinical data at scientific conferences which support the potential of SRK-439 to increase lean mass and contribute to a favorable body composition in conjunction with GLP-1 receptor agonist ("GLP-1 RA") treatment. In June 2025, the Company announced positive top-line results from the Phase 2 EMBRAZE proof-of-concept trial, designed to assess the safety and efficacy of apitegromab to preserve lean mass in individuals living with obesity and on background therapy of a GLP-1 RA (tirzepatide). The trial demonstrated that patients receiving apitegromab with tirzepatide over 24 weeks showed a 54.9% preservation of lean mass (+4.2 lbs of lean mass) versus tirzepatide alone (p=0.001).

Our product candidate, SRK-181, a highly selective inhibitor of the activation of latent TGFβ1, is being developed for the treatment of cancers that are resistant to checkpoint inhibitor therapies, such as anti-PD-1 or anti-PD-L1 antibody therapies (referred to together as anti-PD-(L)1 antibody therapies). SRK-181 has been evaluated in our Phase 1 DRAGON proof-of-concept clinical trial in patients with locally advanced or metastatic solid tumors that exhibit resistance to anti-PD-(L)1 antibody therapies. We completed the DRAGON trial in June 2025. This two-part clinical trial consisted of a dose escalation portion (Part A) and a dose

expansion portion evaluating SRK-181 in combination with an approved anti-PD-(L)1 antibody therapy (Part B). Part B included the following cohorts: urothelial carcinoma, cutaneous melanoma, non-small cell lung cancer, clear cell renal cell carcinoma ("ccRCC"), and head and neck squamous cell carcinoma. The data showed encouraging responses in heavily pretreated and anti-PD-(L)1 resistant patients across multiple tumor types. We believe that the DRAGON trial achieved its study objectives by showing objective, durable clinical responses in patients with ccRCC resistant to PD-1 therapy above what is expected from continuing PD-1 alone.

Using our innovative approach and proprietary platform, we are creating a pipeline of novel product candidates that selectively modulate the activation of growth factors implicated in a variety of serious diseases with high unmet need, including neuromuscular disorders, cardiometabolic disorders, cancer, and other serious diseases where growth factor-targeted therapies can play a transformational role. Our proprietary platform is designed to generate highly selective antibodies that target the growth factor's latent precursor form prior to its activation within the disease microenvironment, or tissue where it is localized. Our structural insights and unique antibody discovery capabilities can also be applied to other protein classes beyond growth factors, with an aim of generating differentiated candidates targeting cell surface receptors such as immune cell receptors or G-protein coupled receptors, where selectivity remains challenging.

Company information

We were incorporated in 2017 under the laws of the State of Delaware as the holding company for Scholar Rock, Inc. Scholar Rock, Inc. is a wholly owned subsidiary of Scholar Rock Holding Corporation. On December 22, 2017, we completed a series of transactions pursuant to which Scholar Rock Merger Sub, LLC, a wholly owned subsidiary of Scholar Rock Holding Corporation, was merged with and into Scholar Rock, LLC (the "Reorganization"). The purpose of the Reorganization was to reorganize our corporate structure so that we would continue as a corporation and so that our investors prior to the Reorganization would own our capital stock after the Reorganization rather than equity interests in a limited liability company. All of our convertible preferred stock converted into shares of common stock upon the completion of our initial public offering at the then effective conversion ratio.

Our principal executive offices are located at 301 Binney Street, Cambridge, MA 02142, and our phone number is (857) 259-3860. Our website address is www.scholarrock.com. The information contained on our website or social media accounts, or that can be accessed through our website or social media accounts, is not a part of this prospectus and is not incorporated by reference into this prospectus. You should not rely on any such information in deciding whether to purchase our common stock.

Implications of being a smaller reporting company

We are a "smaller reporting company" as defined under Rule 405 of the Securities Act. We may continue to be a smaller reporting company if either (i) the market value of our stock held by non-affiliates was less than $250 million on the last business day of our most recently completed second fiscal quarter or (ii) our annual revenue was less than $100 million during the most recently completed fiscal year and the market value of our stock held by non-affiliates was less than $700 million on the last business day of our most recently completed second fiscal quarter. For so long as we remain a smaller reporting company, we are permitted and plan to rely on exemptions from certain disclosure and other requirements that are applicable to other public companies that are not smaller reporting companies. Decreased disclosures in our SEC filings due to our status as a "smaller reporting company" may make it harder for investors to analyze our results of operations and financial prospects.

THE OFFERING

Common stock offered by us	Shares of our common stock having an aggregate offering price of up to $200,000,000.
Common stock to be outstanding immediately after this offering	Up to 105,660,778 shares (as more fully described in the notes following this table), assuming sales of 6,489,292 shares of our common stock in this offering at an offering price of $30.82 per share, which was the last reported sale price of our common stock on The Nasdaq Global Select Market on November 12, 2025. The actual number of shares issued will vary depending on the sales price under this offering.
Plan of Distribution	"At the market offering" that may be made from time to time through our sales agent, Jefferies LLC, or Jefferies. See "Plan of Distribution" on page S-14 of this prospectus.
Use of Proceeds	We intend to use the net proceeds we receive, together with our existing cash, cash equivalents and investments, to support commercialization of apitegromab, including further buildout of our commercial infrastructure and supply chain, advance our ongoing and future clinical programs, to further develop our technology platform to continue to advance our clinical and preclinical pipeline, and for working capital and other general corporate purposes. We may temporarily invest the net proceeds in a variety of capital preservation instruments, including investment grade, interest bearing instruments and U.S. government securities, until they are used for their stated purpose. We have not determined the amount of net proceeds to be used specifically for such purposes. As a result, management will retain broad discretion over the allocation of net proceeds. See "Use of Proceeds" on page S-11 of this prospectus.
Risk Factors	Investing in our common stock involves significant risks. See "Risk Factors" on page S-7 of this prospectus and under similar headings in other documents incorporated by reference into this prospectus.
The Nasdaq Global Select Market symbol	"SRRK"

The number of shares of our common stock that will be outstanding immediately after this offering as shown above is based on 99,171,486 shares outstanding as of September 30, 2025. The number of shares outstanding as of September 30, 2025 as used throughout this prospectus, unless otherwise indicated, excludes:

- 17,362,147 pre-funded warrants to purchase shares of common stock with an exercise price of $0.0001 per share;
- 8,220,620 common warrants to purchase shares of common stock with a weighted-average exercise price of $7.35 per share;
- 167,626 shares of common stock issuable upon the exercise of stock options outstanding under our 2017 Stock Option and Incentive Plan at a weighted-average exercise price of $6.17 per share;

- 5,466,285 shares of common stock issuable upon the exercise of stock options outstanding under our 2018 Stock Option and Incentive Plan at a weighted-average exercise price of $21.19 per share;
- 2,042,249 shares of common stock issuable upon the vesting and settlement of restricted stock units issued under our 2018 Stock Option and Incentive Plan;
- 700,000 shares of common stock issuable upon the vesting and settlement of performance stock units issued under our 2018 Stock Option and Incentive Plan;
- 3,816,104 shares of our common stock reserved for future issuance under our 2018 Stock Option and Incentive Plan;
- 2,550,305 shares of our common stock available for future issuance under our 2018 Employee Stock Purchase Equity Plan;
- 3,277,071 shares of common stock issuable upon the exercise of stock options outstanding under our 2022 Inducement Equity Plan at a weighted-average exercise price of $20.06 per share;
- 1,493,671 shares of our common stock issuable upon the vesting and settlement of restricted stock units issued under our 2022 Inducement Equity Plan;
- 400,000 shares of our common stock issuable upon the vesting and settlement of performance stock units issued under our 2022 Inducement Equity Plan; and
- 1,155,782 shares of our common stock available for future issuance under our 2022 Inducement Equity Plan.

RISK FACTORS

Investing in our securities involves a high degree of risk. You should carefully consider the risks and uncertainties described below and in the documents incorporated by reference in this prospectus, as well as other information we include or incorporate by reference into this prospectus, before making an investment decision. Our business, financial condition and results of operations could be materially adversely affected by the materialization of any of these risks. The trading price of our securities could decline due to the materialization of any of these risks, and you may lose all or part of your investment. This prospectus and the documents incorporated herein by reference also contain forward-looking statements that involve risks and uncertainties. Actual results could differ materially from those anticipated in these forward-looking statements as a result of certain factors, including the risks described in the documents incorporated herein by reference, including our Annual Report on Form 10-K for the fiscal year ended December 31, 2024, which is on file with the SEC and is incorporated herein by reference, and our subsequent Quarterly Reports on Form 10-Q or Current Reports on Form 8-K and other reports and documents that are incorporated by reference into this prospectus and other documents we file with the SEC that are deemed incorporated by reference into this prospectus.

Risks related to this offering

You will experience immediate and substantial dilution.

The offering price per share in this offering will be substantially higher than the net tangible book value per share of our common stock outstanding prior to this offering. Based on an estimated public offering price of $30.82 per share, and a net tangible book value of $245 million, or $2.47 per share of common stock, as of September 30, 2025, if you purchase securities in this offering, you will suffer immediate and substantial dilution of $26.67 per share in the net tangible book value of the securities you purchase representing the difference between our as adjusted net tangible book value per share after giving effect to this offering and the public offering price per share of common stock. The exercise of outstanding stock options and warrants will result in further dilution of your investment. See the section titled “Dilution” below for a more detailed illustration of the dilution you would incur if you participate in this offering.

We have broad discretion in the use of our existing cash, cash equivalents and marketable securities and the net proceeds from this offering and may not use them effectively.

Our management will have broad discretion in the application of our existing cash, cash equivalents and marketable securities and the net proceeds from this offering, including for any of the purposes described in the section titled “Use of proceeds,” and you will not have the opportunity as part of your investment decision to assess whether such proceeds are being used appropriately. Because of the number and variability of factors that will determine our use of our existing cash and cash equivalents and the net proceeds from this offering, their ultimate use may vary substantially from their currently intended use. Our management might not apply our existing cash and cash equivalents and the net proceeds from this offering in ways that ultimately increase the value of your investment. The failure by our management to apply these funds effectively could harm our business. Pending their use, we may invest the net proceeds from this offering in short-term, investment-grade, interest-bearing securities. These investments may not yield a favorable return to our stockholders. If we do not invest or apply the net proceeds from this offering in ways that enhance stockholder value, we may fail to achieve expected financial results, which could cause our stock price to decline.

You may experience future dilution as a result of future equity offerings.

In order to raise additional capital, we may in the future offer additional shares of our common stock or other securities convertible into or exchangeable for our common stock at prices that may not be the same as the price per share in this offering. We may sell shares or other securities in any other offering at a price per share that is less than the price per share paid by investors in this offering, and investors purchasing shares or other securities in the future could have rights superior to those of existing stockholders. The price per share at which we sell additional shares of our common stock, or securities convertible or exchangeable into common stock, in future transactions may be higher or lower than the price per share paid by investors in this offering.

Sales of a substantial number of shares of our common stock in the public market after this offering could cause our stock price to fall.

Sales of a substantial number of shares of our common stock in the public market or the perception that these sales might occur could depress the market price of our common stock and could impair our ability to raise capital through the sale of additional equity securities. We are unable to predict the effect that sales may

have on the prevailing market price of our common stock. In addition, the sale of substantial amounts of our common stock could adversely impact the price of our common stock. As of September 30, 2025, 99,171,486 shares of our common stock were outstanding. The sale, or the availability for sale, of a large number of shares of our common stock in the public market could cause the price of our common stock to decline.

The common stock offered hereby will be sold in "at the market" offerings, and investors who buy shares at different times will likely pay different prices.

Investors who purchase shares in this offering at different times will likely pay different prices, and so may experience different outcomes in their investment results. We will have discretion, subject to market demand, to vary the timing, prices, and numbers of shares sold, and there is no minimum or maximum sales price. Investors may experience a decline in the value of their shares as a result of share sales made at prices lower than the prices they paid.

The actual number of shares we will issue under the sales agreement, at any one time or in total, is uncertain.

Subject to certain limitations in the sales agreement and compliance with applicable law, we have the discretion to deliver placement notices to Jefferies LLC, or Jefferies, at any time throughout the term of the sales agreement. The number of shares that are sold by Jefferies after delivering a placement notice will fluctuate based on the market price of the common stock during the sales period and limits we set with Jefferies. Because the price per share of each share sold will fluctuate based on the market price of our common stock during the sales period, it is not possible at this stage to predict the number of shares that will be ultimately issued.

The price of our stock is volatile, and you could lose all or part of your investment.

Similar to the trading prices of the common stock of other biopharmaceutical companies, the trading price of our common stock is subject to wide fluctuations in response to various factors, some of which are beyond our control, including limited trading volume. In addition to the factors discussed in this "Risk Factors" section and elsewhere in this prospectus, these factors include:

- announcements of significant acquisitions, strategic collaborations or partnerships, joint ventures or capital commitments by us, our collaborators or our competitors;
- actual or anticipated variations in quarterly operating results or our cash position;
- our failure to meet the estimates and projections of the investment community or that we may otherwise provide to the public;
- changes in accounting practices; and
- significant lawsuits, including patent or stockholder litigation.

In addition, the stock market in general, and the market for biopharmaceutical companies in particular, have experienced extreme price and volume fluctuations that have often been unrelated or disproportionate to the operating performance of these companies. Broad market and industry factors may negatively affect the market price of our common stock, regardless of our actual operating performance. In the past, securities class action litigation has often been instituted against companies following periods of volatility in the market price of a company's securities. This type of litigation, if instituted, could result in substantial costs and a diversion of management's attention and resources, which would harm our business, operating results or financial condition.

We do not intend to pay dividends on our common stock so any returns will be limited to the value of our stock.

We currently anticipate that we will retain future earnings for the development, operation and expansion of our business and do not anticipate declaring or paying any cash dividends for the foreseeable future. Any return to stockholders will therefore be limited to the appreciation of their stock.

CAUTIONARY STATEMENT REGARDING FORWARD-LOOKING STATEMENTS

This prospectus, including the documents that we incorporate by reference herein and therein, contain forward-looking statements within the meaning of Section 27A of the Securities Act of 1933, as amended, or the Securities Act, and Section 21E of the Securities Exchange Act of 1934, as amended, or the Exchange Act. Any statements about our expectations, beliefs, plans, objectives, assumptions or future events or performance are not historical facts and may be forward- looking. These statements are often, but are not always, made through the use of words or phrases such as “anticipate,” “believe,” “contemplate,” “continue,” “could,” “estimate,” “expect,” “intend,” “may,” “plan,” “potential,” “predict,” “project,” “seek,” “should,” “target,” “will,” “would,” and similar expressions, or the negative of these terms, or similar expressions. Accordingly, these statements involve estimates, assumptions and uncertainties which could cause actual results to differ materially from those expressed in them. Any forward-looking statements are qualified in their entirety by reference to the factors discussed throughout this prospectus and the accompanying prospectus, and in particular those factors referenced in the section “Risk factors.”

This prospectus contain forward-looking statements that are based on our management’s belief and assumptions and on information currently available to our management. These statements relate to future events or our future financial performance, and involve known and unknown risks, uncertainties and other factors that may cause our actual results, levels of activity, performance or achievements to be materially different from any future results, levels of activity, performance or achievements expressed or implied by these forward-looking statements. Forward-looking statements include, but are not limited to, statements about:

- the timing, scope, or likelihood of our ability to obtain and maintain regulatory approval from the U.S. Food and Drug Administration (“FDA”), the European Commission (“EC”) and other regulatory authorities for apitegromab, and any related restrictions, limitations or warnings in the label of any approval for apitegromab;
- our ability to obtain regulatory approval for apitegromab is dependent on the timely and satisfactory response to the Complete Response Letter (“CRL”) received from the FDA in September 2025 and resolution of the observations identified during the FDA’s routine general site inspection of our third-party fill-finish facility. This facility was issued a Form 483 by the FDA in July 2025 and the inspection classification of this facility is “official action indicated” (OAI);
- our plans to address the CRL;
- our ability to successfully build a commercial infrastructure to launch and market apitegromab, or otherwise provide access to apitegromab, if and when it is approved or receives pricing or reimbursement approval;
- our ability, through third party manufacturers, to successfully manufacture commercial supply of apitegromab;
- the rate and degree of market acceptance of apitegromab, if approved;
- the size and growth potential of the markets for apitegromab, and our ability to serve those markets, either alone or in combination with others;
- the clinical utility of apitegromab and its potential advantages over other therapeutic options;
- the potential benefit of orphan drug exclusivity, Orphan Drug designation, Fast Track designation and Rare Pediatric Disease designation for apitegromab;
- our success in identifying and executing development programs for additional indications for apitegromab;
- the success, cost and timing of clinical trials, including the progress, completion, timing of results, and actual results of our clinical trials;
- our ability, through third party manufacturers, to successfully manufacture our product candidates for clinical trials;
- the fact that top-line or interim data from our clinical studies may not be predictive of the final or more detailed results of such study or the results of other ongoing or future studies;

- our success in identifying and executing a development program for our preclinical product candidates, including SRK-439, SRK-373, SRK-256 and identifying additional product candidates from our preclinical programs and research pipeline;
- our ability to retain our executives and highly skilled technical and managerial personnel, which could be affected due to any transition in management, or if we fail to recruit additional highly skilled personnel;
- our expectations regarding our ability to obtain and maintain intellectual property protection for our product candidates and the duration of such protection and our ability to operate our business without infringing on the intellectual property rights of others;
- our ability to obtain, generally or on terms acceptable to us, funding for our operations, including funding necessary to complete further development and, upon successful development, if approved, commercialization of apitegromab, SRK-181, SRK-439, SRK-373, SRK-256 or any of our future product candidates;
- our ability to establish or maintain collaborations or strategic relationships;
- our expectations relating to the potential of our proprietary platform technology;
- the impact of new laws and regulations or amendments to existing laws and regulations in the United States and foreign countries;
- risks associated with the impact of global economic and political developments on our business, including rising inflation and capital market disruptions, tariff policies, economic sanctions and economic slowdowns or recessions or public health pandemics;
- developments and projections relating to our competitors and our industry;
- our expected use of proceeds from this offering;
- our estimates and expectations regarding cash and expense levels, future revenues, capital requirements and needs for additional financing, including our expected use of proceeds from our public offerings, and liquidity sources; and
- our expectations regarding the period during which we qualify as a “smaller reporting company” as defined by Rule 12b-2 of the Securities Exchange Act of 1934.

We have included important factors in the cautionary statements included in this prospectus and the documents we incorporate by reference herein and therein, particularly in the “Risk factors” sections of these documents, that we believe could cause actual results or events to differ materially from the forward-looking statements that we make. Our forward-looking statements do not reflect the potential impact of any future acquisitions, mergers, dispositions, joint ventures or investments we may make. No forward-looking statement is a guarantee of future performance.

You should read this prospectus, the accompanying prospectus and the documents that we incorporate by reference herein and therein completely and with the understanding that our actual future results may be materially different from what we expect. The forward-looking statements in this prospectus and the accompanying prospectus and the documents we incorporate by reference herein and therein represent our views as of the date of this prospectus. We anticipate that subsequent events and developments will cause our views to change. However, while we may elect to update these forward- looking statements at some point in the future, we have no current intention of doing so except to the extent required by applicable law. You should, therefore, not rely on these forward-looking statements as representing our views as of any date subsequent to the date of this prospectus.

In addition, statements that “we believe” and similar statements reflect our beliefs and opinions on the relevant subject. These statements are based upon information available to us as of the date of this prospectus, and while we believe such information forms a reasonable basis for such statements, such information may be limited or incomplete, and our statements should not be read to indicate that we have conducted an exhaustive inquiry into, or review of, all potentially available relevant information.

USE OF PROCEEDS

We may issue and sell shares of our common stock having aggregate sales proceeds of up to $200,000,000 from time to time. Because there is no minimum offering amount required as a condition to close this offering, the actual total public offering amount, commissions and proceeds to us, if any, are not determinable at this time.

We intend to use the net proceeds we receive, together with our existing cash, cash equivalents and investments, to support commercialization of apitegromab, including further buildout of our commercial infrastructure and supply chain, advance our ongoing and future clinical programs, to further develop our technology platform to continue to advance our clinical and preclinical pipeline, and for working capital and other general corporate purposes. Any remaining proceeds will be used for other ongoing research and development activities and general corporate purposes, such as working capital, operating expenses and capital expenditures. We may temporarily invest the net proceeds in a variety of capital preservation instruments, including investment grade, interest bearing instruments and U.S. government securities, until they are used for their stated purpose. We have not determined the amount of net proceeds to be used specifically for such purposes. As a result, management will retain broad discretion over the allocation of net proceeds.

DILUTION

Purchasers of common stock offered by this prospectus will suffer immediate and substantial dilution in the net tangible book value per share of common stock. Our net tangible book value as of September 30, 2025 was approximately $245.0 million, or approximately $2.47 per share of common stock. Net tangible book value per share represents the amount of total tangible assets (total assets less intangible assets) less total liabilities, divided by the number of shares of our common stock outstanding as of September 30, 2025.

Dilution in net tangible book value per share represents the difference between the amount per share paid by purchasers in this offering and the net tangible book value (deficit) per share of our common stock immediately after this offering. After giving effect to the assumed sale of shares of our common stock in the aggregate amount of approximately $200.0 million at an assumed offering price of $30.82 per share, the last reported sale price of our common stock on November 12, 2025, and after deduction of commissions and offering expenses payable by us, our as adjusted net tangible book value as of September 30, 2025 would have been approximately $438.8 million, or $4.15 per share of common stock. This represents an immediate increase in net tangible book value of $1.68 per share of common stock to our existing stockholders and an immediate dilution in net tangible book value of $26.67 per share of common stock to investors participating in this offering at an assumed offering price of $30.82 per share.

The following table illustrates this per share dilution:

Assumed offering price per share		$ 30.82
Net tangible book value per share as of September 30, 2025	$ 2.47	
Increase in per share attributable to new investors attributable to this offering	$ 1.68	
As adjusted net tangible book value per share as of September 30, 2025, after giving effect to this offering		$ 4.15
Dilution per share to new investors participating in this offering		$ 26.67

The table above assumes for illustrative purposes that an aggregate of 6,489,292 shares of our common stock are sold at a price of $30.82 per share, the last reported sale price of our common stock on the Nasdaq Global Select Market on November 12, 2025, for aggregate gross proceeds of approximately $200.0 million. The shares sold in this offering, if any, will be sold from time to time at various prices. An increase of $1.00 per share in the price at which the shares are sold from the assumed offering price of $30.82 per share shown in the table above, assuming all of our common stock in the aggregate amount of approximately $200.0 million is sold at that price, would result in an increase to our adjusted net tangible book value per share after the offering to $4.16 and an increase in the dilution in net tangible book value per share to new investors in this offering to $27.66, after deducting commissions and estimated offering expenses payable by us. A decrease of $1.00 per share in the price at which the shares are sold from the assumed offering price of $30.82 per share shown in the table above, assuming all of our common stock in the aggregate amount of approximately $200.0 million is sold at that price, would result in a decrease to our adjusted net tangible book value per share after the offering to $4.14 and a decrease in the dilution in net tangible book value per share to new investors in this offering to $25.68, after deducting commissions and estimated offering expenses payable by us. This information is supplied for illustrative purposes only, and will adjust based on the actual offering prices, the actual number of shares that we offer and sell in this offering and other terms of each sale of shares in this offering.

The information above and in the foregoing table is based upon 99,171,486 shares of our common stock outstanding as of September 30, 2025. The information above and in the foregoing table excludes as of September 30, 2025:

- 17,362,147 pre-funded warrants to purchase shares of common stock with an exercise price of $0.0001 per share;
- 8,220,620 common warrants to purchase shares of common stock with a weighted-average exercise price of $7.35 per share;

- 167,626 shares of common stock issuable upon the exercise of stock options outstanding as of September 30, 2025 under our 2017 Stock Option and Incentive Plan at a weighted-average exercise price of $6.17 per share;
- 5,466,285 shares of common stock issuable upon the exercise of stock options outstanding as of September 30, 2025 under our 2018 Stock Option and Incentive Plan at a weighted-average exercise price of $21.19 per share;
- 2,042,249 shares of common stock issuable upon the vesting and settlement of restricted stock units issued under our 2018 Stock Option and Incentive Plan;
- 700,000 shares of our common stock issuable upon the vesting and settlement of performance stock units issued under our 2018 Stock Option and Incentive Plan;
- 3,816,104 shares of common stock reserved for future issuance under our 2018 Stock Option and Incentive Plan as of September 30, 2025;
- 2,550,305 shares of our common stock available for future issuance under our 2018 Employee Stock Purchase Plan as of September 30, 2025;
- 3,277,071 shares of common stock issuable upon the exercise of stock options outstanding as of September 30, 2025 under our 2022 Inducement Equity Plan at a weighted-average exercise price of $20.06 per share;
- 1,493,671 shares of common stock issuable upon the vesting and settlement of restricted stock units issued under our 2022 Inducement Equity Plan;
- 400,000 shares of our common stock issuable upon the vesting and settlement of performance stock units issued under our 2022 Inducement Equity Plan; and
- 1,155,782 shares of our common stock available for future issuance under our 2022 Inducement Equity Plan as of September 30, 2025.

In addition, we may choose to raise additional capital in the future through the sale of equity or convertible debt securities due to market conditions or strategic considerations, even if we believe we have sufficient funds for our current or future operating plans. To the extent that any of our outstanding options are exercised, new options are issued under our equity incentive plans or we issue additional shares of common stock or other equity or convertible debt securities in the future, there will be further dilution to investors participating in this offering.

PLAN OF DISTRIBUTION

We have previously entered into a certain Open Market Sale Agreement[SM], or sales agreement, with Jefferies LLC, or Jefferies, under which we may offer and sell shares of our common stock from time to time through Jefferies, acting as agent. Pursuant to this prospectus, we may offer and sell up to $200,000,000 of our shares of common stock. Sales of our shares of common stock, if any, under this prospectus will be made by any method that is deemed to be an "at the market offering" as defined in Rule 415(a)(4) under the Securities Act.

Each time we wish to issue and sell shares of common stock under the sales agreement, we will notify Jefferies of the number of shares to be issued, the dates on which such sales are anticipated to be made, any limitation on the number of shares to be sold in any one day and any minimum price below which sales may not be made. Once we have so instructed Jefferies, unless Jefferies declines to accept the terms of such notice, Jefferies has agreed to use its commercially reasonable efforts consistent with its normal trading and sales practices to sell such shares up to the amount specified on such terms. The obligations of Jefferies under the sales agreement to sell our shares of common stock are subject to a number of conditions that we must meet.

The settlement of sales of shares between us and Jefferies is generally anticipated to occur on the first trading day following the date on which the sale was made. Sales of our shares of common stock as contemplated in this prospectus will be settled through the facilities of The Depository Trust Company or by such other means as we and Jefferies may agree upon. There is no arrangement for funds to be received in an escrow, trust or similar arrangement.

We will pay Jefferies a commission of up to 3.0% of the aggregate gross proceeds we receive from each sale of our shares of common stock. Because there is no minimum offering amount required as a condition to close this offering, the actual total public offering amount, commissions and proceeds to us, if any, are not determinable at this time. In addition, we have agreed to reimburse Jefferies for certain ongoing disbursements of its legal counsel unless we and Jefferies otherwise agree. We estimate that the total expenses for the offering, excluding any commissions or expense reimbursement payable to Jefferies under the terms of the sales agreement, will be approximately $0.2 million. The remaining sale proceeds, after deducting any other transaction fees, will equal our net proceeds from the sale of such shares.

Jefferies will provide written confirmation to us before the open on The Nasdaq Global Select Market on the day following each day on which shares of common stock are sold under the sales agreement. Each confirmation will include the number of shares sold on that day, the aggregate gross proceeds of such sales and the proceeds to us.

In connection with the sale of the shares of common stock on our behalf, Jefferies will be deemed to be an "underwriter" within the meaning of the Securities Act, and the compensation of Jefferies will be deemed to be underwriting commissions or discounts. We have agreed to indemnify Jefferies against certain civil liabilities, including liabilities under the Securities Act. We have also agreed to contribute to payments Jefferies may be required to make in respect of such liabilities.

The offering of our shares of common stock pursuant to the sales agreement will terminate upon the termination of the sales agreement permitted therein.

This summary of the material provisions of the sales agreement does not purport to be a complete statement of its terms and conditions. A copy of the sales agreement was filed as an exhibit to the registration statement filed on November 14, 2022, and is incorporated by reference in this prospectus supplement.

Jefferies and its affiliates may in the future provide various investment banking, commercial banking, financial advisory and other financial services for us and our affiliates, for which services they may in the future receive customary fees. In the course of its business, Jefferies may actively trade our securities for its own account or for the accounts of customers, and, accordingly, Jefferies may at any time hold long or short positions in such securities.

A prospectus and the accompanying prospectus in electronic format may be made available on a website maintained by Jefferies, and Jefferies may distribute the prospectus and the accompanying prospectus electronically.

LEGAL MATTERS

Certain legal matters, including the legality of the securities offered, will be passed upon for us by Goodwin Procter LLP, Boston, Massachusetts. Jefferies LLC is being represented in this offering by Cooley LLP, New York, New York.

EXPERTS

Ernst & Young LLP, independent registered public accounting firm, has audited our consolidated financial statements included in our Annual Report on Form 10-K for the year ended December 31, 2024, as set forth in their report, which is incorporated by reference in this prospectus and elsewhere in the registration statement. Our financial statements are incorporated by reference in reliance on Ernst & Young LLP's report, given on their authority as experts in accounting and auditing.

WHERE YOU CAN FIND MORE INFORMATION

This prospectus is part of a registration statement that we have filed with the SEC. Certain information in the registration statement has been omitted from this prospectus in accordance with the rules of the SEC. We are subject to the information requirements of the Exchange Act and, in accordance therewith, file annual, quarterly and special reports, proxy statements and other information with the SEC. These documents also may be accessed through the SEC's electronic data gathering, analysis and retrieval system, or EDGAR, via electronic means, including the SEC's home page on the Internet (www.sec.gov). You may also inspect the registration statement and this prospectus on this website.

We have the authority to designate and issue more than one class or series of stock having various preferences, conversion and other rights, voting powers, restrictions, limitations as to dividends, qualifications, and terms and conditions of redemption. We will furnish a full statement of the relative rights and preferences of each class or series of our stock which has been so designated and any restrictions on the ownership or transfer of our stock to any shareholder upon request and without charge. Written requests for such copies should be directed Investor Relations, Scholar Rock Holding Corporation, 301 Binney Street, Cambridge, MA 02142. Our website is located at www.scholarrock.com. Information contained on our website is not incorporated by reference into this prospectus, and, except for the documents incorporated by reference as noted below, you should not consider any information on, or that can be accessed from, our website as part of this prospectus or any accompanying prospectus supplement.

INCORPORATION OF CERTAIN INFORMATION BY REFERENCE

The SEC allows us to incorporate by reference the information and reports we file with it, which means that we can disclose important information to you by referring you to these documents. The information incorporated by reference is an important part of this prospectus, and information that we file after the date hereof with the SEC will automatically update and supersede the information already incorporated by reference. We are incorporating by reference the documents listed below, which we have already filed with the SEC, and any future filings we make with the SEC under Sections 13(a), 13(c), 14 or 15(d) of the Exchange Act, except as to any portion of any future report or document that is not deemed filed under such provisions, after the date of this prospectus and prior to the termination of this offering:

- our Annual Report on Form 10-K for the year ended December 31, 2024, filed with the SEC on February 27, 2025;
- our Quarterly Reports on Form 10-Q for the quarters ended March 31, 2025, June 30, 2025 and September 30, 2025 filed with the SEC on May 14, 2025, August 6, 2025 and November 14, 2025, respectively;
- our Current Reports on Form 8-K (other than information furnished rather than filed) filed with the SEC on January 13, 2025, January 29, 2025, March 21, 2025, April 28, 2025, May 12, 2025, May 23, 2025, June 3, 2025, June 18, 2025, August 6, 2025, September 23, 2025 and October 14, 2025;
- our Definitive Proxy Statement on Schedule 14A (other than information furnished rather than filed), filed with the SEC on April 11, 2025 and as amended on April 28, 2025 and May 12, 2025; and
- the description of our common stock contained in our registration statement on Form 8-A filed with the SEC on May 21, 2018, including any amendments or reports filed for the purposes of updating this description.

Pursuant to Rule 412 under the Securities Act, any statement contained in a document incorporated or deemed to be incorporated by reference into this prospectus will be deemed to be modified or superseded for purposes of this prospectus to the extent that a statement contained in this prospectus or any other subsequently filed document that is deemed to be incorporated by reference into this prospectus modifies or supersedes the statement. Any statement so modified or superseded will not be deemed, except as so modified or superseded, to constitute a part of this prospectus.

Upon request, we will provide, without charge, to each person, including any beneficial owner, to whom a copy of this prospectus is delivered, a copy of the documents incorporated by reference into this prospectus but not delivered with the prospectus. You may request a copy of these filings, and any exhibits.

we have specifically incorporated by reference as an exhibit in this prospectus, at no cost by writing us at the following address: Investor Relations, Scholar Rock Holding Corporation, 301 Binney Street, Cambridge, MA 02142. Our website is located at *www.scholarrock.com*. The reference to our website is intended to be an inactive textual reference and, except for the documents incorporated by reference as noted above, the information on, or accessible through, our website is not intended to be part of this prospectus.

You should rely only on the information incorporated by reference or provided in this prospectus and the accompanying prospectus. We have not authorized anyone else to provide you with different information. You should not assume that the information in this prospectus or in the documents incorporated by reference is accurate as of any date other than the date on the front of this prospectus or those documents.

We advise that there have been no material changes in our affairs that have occurred since the end of the latest fiscal period for which audited financial statements were included in the latest Form 10-K and that have not been described in a Form 10-Q or Form 8-K filed under the Exchange Act.

This prospectus is part of a registration statement we filed with the SEC. We have incorporated exhibits into this registration statement. You should read the exhibits carefully for provisions that may be important to you.

PROSPECTUS



Common Stock
Preferred Stock
Debt Securities
Warrants
Units

We and/or selling stockholders may from time to time issue, in one or more series or classes, our common stock, preferred stock, debt securities, warrants and/or units. We and/or selling stockholders may offer these securities separately or together in units. We and/or selling stockholders will specify in the accompanying prospectus supplement the terms of the securities being offered. We and/or selling stockholders may sell these securities to or through underwriters and also to other purchasers or through agents. We and/or selling stockholders will set forth the names of any underwriters or agents, and any fees, conversions, or discount arrangements, in the accompanying prospectus supplement. We and/or selling stockholders may not sell any securities under this prospectus without delivery of the applicable prospectus supplement.

You should read this document and any prospectus supplement or amendment carefully before you invest in our securities.

Our common stock is listed on The Nasdaq Global Select Market under the symbol "SRRK." On October 4, 2024, the closing price for our common stock, as reported on The Nasdaq Global Select Market, was $7.42 per share. Our principal executive offices are located at 301 Binney Street, 3rd Floor, Cambridge, MA 02142.

Investing in our securities involves a high degree of risk. You should review carefully the risks and uncertainties described under the heading "*Risk Factors*" contained in this prospectus beginning on page 2 and any applicable prospectus supplement, and under similar headings in the other documents that are incorporated by reference into this prospectus.

Neither the Securities and Exchange Commission nor any state securities commission has approved or disapproved of these securities or determined if this prospectus is truthful or complete. Any representation to the contrary is a criminal offense.

The date of this Prospectus is October 7, 2024.

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ABOUT THIS PROSPECTUS

This prospectus is a part of an automatic registration statement on Form S-3 that we filed with the Securities and Exchange Commission, or the SEC, as a "well-known seasoned issuer" as defined in Rule 405 under the Securities Act of 1933, as amended, or the Securities Act, using a "shelf" registration process. Under this shelf registration process, we and/or selling stockholders may from time to time sell any combination of the securities described in this prospectus in one or more offerings.

This prospectus provides you with a general description of the securities we and/or selling stockholders may offer. Each time we sell securities, we will provide one or more prospectus supplements that will contain specific information about the terms of the offering. The applicable prospectus supplement may also add, update or change information contained in this prospectus. You should read both this prospectus and the accompanying prospectus supplement together with the additional information described under the heading "Where You Can Find More Information" beginning on page 42 of this prospectus.

You should rely only on the information contained in or incorporated by reference in this prospectus, any accompanying prospectus supplement or in any related free writing prospectus filed by us with the SEC. We have not authorized anyone to provide you with different information. This prospectus and the accompanying prospectus supplement do not constitute an offer to sell or the solicitation of an offer to buy any securities other than the securities described in the accompanying prospectus supplement or an offer to sell or the solicitation of an offer to buy such securities in any circumstances in which such offer or solicitation is unlawful. You should assume that the information appearing in this prospectus, any prospectus supplement, the documents incorporated by reference and any related free writing prospectus is accurate only as of their respective dates. Our business, financial condition, results of operations and prospects may have changed materially since those dates.

Unless the context otherwise indicates, references in this prospectus or the accompanying prospectus supplement to "Scholar Rock", "we", "our", "us" and "the Company" refer, collectively, to Scholar Rock Holding Corporation and its subsidiaries.

We own various U.S. federal trademark applications and unregistered trademarks, including "Scholar Rock" and our corporate logo. All other trademarks or trade names referred to in this prospectus are the property of their respective owners. Solely for convenience, the trademarks and trade names in this prospectus are referred to without the symbols ® and ™, but such references should not be construed as any indicator that their respective owners will not assert, to the fullest extent under applicable law, their rights thereto. We do not intend our use or display of other companies' trademarks and trade names to imply a relationship with, or endorsement or sponsorship of us by, any other companies.

RISK FACTORS

Investing in our securities involves a high degree of risk. You should carefully consider the risks described in the documents incorporated by reference in this prospectus and any prospectus supplement, as well as other information we include or incorporate by reference into this prospectus and any applicable prospectus supplement, before making an investment decision. Our business, financial condition or results of operations could be materially adversely affected by the materialization of any of these risks. The trading price of our securities could decline due to the materialization of any of these risks, and you may lose all or part of your investment. This prospectus and the documents incorporated herein by reference also contain forward-looking statements that involve risks and uncertainties. Actual results could differ materially from those anticipated in these forward-looking statements as a result of certain factors, including the risks described below and in the documents incorporated herein by reference, including our Annual Report on Form 10-K for the fiscal year ended December 31, 2023, which is on file with the SEC and is incorporated herein by reference, and our subsequent Quarterly Reports on Form 10-Q for the quarters ended March 31, 2024 and June 30, 2024, which are on file with the SEC and incorporated herein by reference, and other documents we file with the SEC that are deemed incorporated by reference into this prospectus. See "Where You Can Find More Information" for information about how to obtain a copy of these documents. The risks and uncertainties described in the documents we incorporate by reference are not the only ones we face. Additional risks and uncertainties not presently known to us or that we currently deem immaterial may also impair our business operations. If any of these risks or uncertainties actually occur, they could materially and adversely affect our business, financial condition, results of operations, cash flows or prospects, which in turn could materially and adversely affect the price of our securities and might cause you to lose all or part of your investment in the offered securities.

CAUTIONARY STATEMENT REGARDING FORWARD-LOOKING STATEMENTS

This prospectus, including the documents that we incorporate by reference contains forward-looking statements within the meaning of Section 27A of the Securities Act and Section 21E of the Securities Exchange Act of 1934, as amended, or the Exchange Act. Any statements about our expectations, beliefs, plans, objectives, assumptions or future events or performance are not historical facts and may be forward-looking. These statements are often, but are not always, made through the use of words or phrases such as "anticipate," "believe," "contemplate," "continue," "could," "estimate," "expect," "intend," "may," "plan," "potential," "predict," "project," "seek," "should," "target," "will," "would," and similar expressions, or the negative of these terms, or similar expressions. Accordingly, these statements involve estimates, assumptions and uncertainties which could cause actual results to differ materially from those expressed in them. Any forward-looking statements are qualified in their entirety by reference to the factors discussed throughout this prospectus, and in particular those factors referenced in the section "Risk Factors."

This prospectus contains forward-looking statements that are based on our management's belief and assumptions and on information currently available to our management. These statements relate to future events or our future financial performance, and involve known and unknown risks, uncertainties and other factors that may cause our actual results, levels of activity, performance or achievements to be materially different from any future results, levels of activity, performance or achievements expressed or implied by these forward-looking statements. Forward-looking statements include, but are not limited to, statements about:

- the success, cost and timing of clinical trials for apitegromab (such as our Phase 2 EMBRAZE clinical trial) and SRK-181, including the progress, completion, timing of results, and actual results of our clinical trials;
- the timing, scope, or likelihood of our ability to obtain and maintain regulatory approval from the U.S. Food and Drug Administration ("FDA"), the European Commission ("EC") and other regulatory authorities for apitegromab following completion of our Phase 3 SAPPHIRE clinical trial, and any related restrictions, limitations or warnings in the label of any approval for apitegromab;
- our success in identifying and executing a development program for our preclinical product candidates, including SRK-439 and identifying additional product candidates from our preclinical programs and research pipeline;
- our success in identifying and executing development programs for additional indications for apitegromab and SRK-181;
- the clinical utility of our product candidates and their potential advantages over other therapeutic options;
- our ability to obtain, generally or on terms acceptable to us, funding for our operations, including funding necessary to complete further development and, upon successful development, if approved, commercialization of apitegromab, SRK-181, SRK-439 or any of our future product candidates;
- our ability to retain our executives and highly skilled technical and managerial personnel, which could be affected due to any transition in management, or if we fail to recruit additional highly skilled personnel;
- our expectations regarding our ability to obtain and maintain intellectual property protection for our product candidates and the duration of such protection and our ability to operate our business without infringing on the intellectual property rights of others;
- our ability, through third party manufacturers, to successfully manufacture our product candidates for clinical trials and for commercial use, if approved;
- our ability to successfully build a commercial infrastructure to launch and market apitegromab, or otherwise provide access to apitegromab, if and when it is approved or receives pricing or reimbursement approval;
- our ability to establish or maintain collaborations or strategic relationships;
- our expectations relating to the potential of our proprietary platform technology;

- the size and growth potential of the markets for our product candidates, and our ability to serve those markets, either alone or in combination with others;
- the impact of new laws and regulations or amendments to existing laws and regulations in the United States and foreign countries;
- risks associated with the impact of global economic and political developments on our business, including rising inflation and capital market disruptions, economic sanctions and economic slowdowns or recessions or public health pandemics;
- developments and projections relating to our competitors and our industry;
- our estimates and expectations regarding cash, cash reserves, and expense levels, future revenues, capital requirements and needs for additional financing, including our expected use of proceeds from our public offerings, and liquidity sources;
- our expectations regarding our ability to continue as a going concern;
- our estimates and expectations regarding cash and expense levels, future revenues, capital requirements and needs for additional financing, including our expected use of proceeds from our public offerings, and liquidity sources;
- our expectations regarding the period during which we qualify as a "smaller reporting company" as defined by Rule 12b-2 of the Exchange Act; and
- other risks and uncertainties, including those listed under the caption "Risk Factors."

We have included important factors in the cautionary statements included in this prospectus and the documents we incorporate by reference herein, particularly in the "Risk Factors" sections of these documents, that we believe could cause actual results or events to differ materially from the forward-looking statements that we make. Our forward-looking statements do not reflect the potential impact of any future acquisitions, mergers, dispositions, joint ventures or investments we may make. No forward-looking statement is a guarantee of future performance.

You should read this prospectus and the documents that we incorporate by reference in this prospectus completely and with the understanding that our actual future results may be materially different from what we expect. The forward-looking statements in this prospectus and the documents we incorporate by reference herein represent our views as of the date of this prospectus. We anticipate that subsequent events and developments will cause our views to change. However, while we may elect to update these forward-looking statements at some point in the future, we have no current intention of doing so except to the extent required by applicable law. You should, therefore, not rely on these forward-looking statements as representing our views as of any date subsequent to the date of this prospectus.

In addition, statements that "we believe" and similar statements reflect our beliefs and opinions on the relevant subject. These statements are based upon information available to us as of the date of this prospectus, and while we believe such information forms a reasonable basis for such statements, such information may be limited or incomplete, and our statements should not be read to indicate that we have conducted an exhaustive inquiry into, or review of, all potentially available relevant information.

THE COMPANY

The following highlights information about the Registrant and our business contained elsewhere or incorporated by reference in this prospectus. It is not complete and does not contain all of the information that you should consider before investing in any of our securities. You should carefully read this prospectus together with the more detailed information incorporated by reference in this prospectus.

Company Overview

We are a late-stage biopharmaceutical company focused on the discovery, development, and delivery of innovative medicines for the treatment of serious diseases in which signaling by protein growth factors plays a fundamental role. As a global leader in transforming growth factor beta (“TGFβ”) superfamily biology, our novel understanding of the molecular mechanisms of growth factor activation enabled us to develop a proprietary platform for the discovery and development of monoclonal antibodies that locally and selectively target the precursor, or latent, forms of growth factors. By targeting the signaling proteins at the cellular level and acting in the disease microenvironment, we believe we may avoid the historical dose-limiting safety challenges associated with inhibiting growth factors for therapeutic effect. We believe our focus on biologically validated growth factors may facilitate a more efficient development path.

Based on this proprietary and scalable technology platform, we are building a growing portfolio of novel product candidates with the aim of transforming the lives of patients suffering from a wide range of serious diseases, including neuromuscular disorders, cardiometabolic disorders, cancer, fibrosis and iron-restricted anemia. We have discovered and progressed the development of:

- Apitegromab, an investigational, fully human monoclonal antibody that inhibits myostatin activation by selectively binding the pro- and latent forms of myostatin in skeletal muscle and is being developed for the treatment of Spinal Muscular Atrophy (“SMA”). We also believe apitegromab could have potential in the treatment of other neuromuscular disorders where the inhibition of myostatin may be beneficial.
- SRK-439, a novel, preclinical, investigational myostatin inhibitor that has high in vitro affinity for pro- and latent myostatin and maintains myostatin specificity and is being developed for the treatment of cardiometabolic disorders.
- SRK-181, an inhibitor of the activation of latent transforming growth factor beta 1 (“TGFβ1”), that is being developed for the treatment of cancers that are resistant to anti-PD-(L)1 antibody therapies.
- Potent and selective inhibitors of the activation of TGFβ for the treatment of fibrotic diseases. We are advancing multiple antibody profiles toward product candidate selection including antibodies that selectively inhibit the activation of latent TGFβ1 in the context of fibrotic extracellular matrix and that avoid perturbing TGFβ1 presented by cells of the immune system.
- Additional discovery and early preclinical programs related to the selective modulation of growth factor signaling including bone morphogenic protein 6 and other growth factors.

Our first product candidate, apitegromab, is a highly selective, fully human, monoclonal antibody with a unique mechanism of action that results in inhibition of the activation of the growth factor, myostatin, in skeletal muscle. Apitegromab is being developed as a potential first muscle-targeted therapy for the treatment of SMA. We are conducting SAPPHIRE, a pivotal Phase 3 clinical trial to evaluate the efficacy and safety of apitegromab in patients with nonambulatory Type 2 and Type 3 SMA (which is estimated to represent the majority of the current prevalent SMA patient population in the U.S. and Europe). We completed enrollment of SAPPHIRE in 2023. We announced top-line data from SAPPHIRE on October 7, 2024. If apitegromab is approved, we expect to initiate a commercial product launch in 2025.

Apitegromab was evaluated in our Phase 2 TOPAZ proof-of-concept clinical trial for the treatment of patients with Type 2 and Type 3 SMA. Positive 12-month top-line results were initially announced in April 2021. We have subsequently presented data from the TOPAZ trial over 24-months (2022), 36-months (2023) and 48-months (2024). At 48-months over 90% of TOPAZ patients with nonambulatory Type 2 and 3 SMA receiving an SMN therapy remained on apitegromab treatment and showed sustained clinical

benefit, a continued favorable safety profile with no new safety findings. Additionally, we have a long-term extension study, ONYX, for patients from both the TOPAZ and SAPPHIRE studies, who are receiving apitegromab in conjunction with an approved SMN therapy. The FDA granted Fast Track designation, Rare Pediatric Disease designation and Orphan Drug designation to apitegromab for the treatment of SMA in May 2021, August 2020 and March 2018, respectively. The European Medicines Agency (''EMA") granted Priority Medicines designation in March 2021 and the EC granted Orphan Medicinal Product designation in December 2018 to apitegromab for the treatment of SMA.

In October 2023, we announced an expansion of our therapeutic focus into cardiometabolic disorders by advancing our anti-myostatin program with SRK-439, a novel, fully human anti-myostatin monoclonal antibody, for evaluation in cardiometabolic disorders, including obesity. We are developing SRK-439 towards a potential Investigational New Drug (''IND") submission in 2025. In June 2024, new preclinical data that support the potential of SRK-439 to increase lean mass and contribute to a favorable body composition following withdrawal from GLP-1 RA treatment were presented at the American Diabetes Association's 84th Scientific Sessions. To inform the development of SRK-439, in May 2024 we initiated the Phase 2 EMBRAZE proof-of-concept trial, designed to assess the safety and efficacy of apitegromab to preserve muscle mass in individuals living with obesity and on background therapy of a GLP-1 RA. In September 2024, we announced that we completed enrollment in the Phase 2 EMBRAZE proof-of-concept trial. Results from this trial are expected in the second quarter of 2025.

We believe that apitegromab has the potential to be the first muscle-targeted therapy which is aimed at improving motor function in patients with SMA who are receiving an SMN therapy. We have identified multiple other diseases for which the selective inhibition of the activation of myostatin may offer therapeutic benefit, including additional patient populations in SMA (such as patients under the age of two with SMA and ambulatory patients with SMA) and indications for other neuromuscular disorders beyond SMA.

Our second product candidate, SRK-181, a highly selective inhibitor of the activation of latent TGFβ, is being developed for the treatment of cancers that are resistant to checkpoint inhibitor therapies, such as anti-PD-1 or anti-PD-L1 antibody therapies (referred to together as anti-PD-(L)1 antibody therapies). SRK-181 is being evaluated in our Phase 1 DRAGON proof-of-concept clinical trial in patients with locally advanced or metastatic solid tumors that exhibit resistance to anti-PD-(L)1 antibody therapies. We completed enrollment of the DRAGON trial in December 2023 and continue to treat patients who remain on study. This two-part clinical trial consists of a dose escalation portion (Part A) and a dose expansion portion evaluating SRK-181 in combination with an approved anti-PD-(L)1 antibody therapy (Part B). Part B commenced in 2021 and includes the following active cohorts: urothelial carcinoma, cutaneous melanoma, non-small cell lung cancer, clear cell renal cell carcinoma ("ccRCC"), and head and neck squamous cell carcinoma. Safety, efficacy and biomarker data were presented in November 2023 at the Society for Immunotherapy of Cancer 38th Annual Meeting and in June 2024 at the ASCO annual meeting. The data showed encouraging responses in heavily pretreated and anti-PD-(L)1 resistant patients across multiple tumor types. We believe that the DRAGON trial achieved its study objectives by showing objective, durable clinical responses in patients with ccRCC resistant to PD-1 therapy above what is expected from continuing PD-1 alone. We anticipate that emerging data from the DRAGON trial will be presented at medical meetings in the future.

Using our innovative approach and proprietary platform, we are creating a pipeline of novel product candidates that selectively modulate the activation of growth factors implicated in a variety of serious diseases, including neuromuscular disorders, cardiometabolic disorders, cancer, fibrosis, and iron-restricted anemia. Our proprietary platform is designed to generate highly selective antibodies that target the growth factor's latent precursor form prior to its activation within the disease microenvironment, or tissue where it is localized. Our structural insights and unique antibody discovery capabilities can also be applied to other protein classes beyond growth factors, with an aim of generating differentiated candidates targeting cell surface receptors such as immune cell receptors or G-protein coupled receptors, where selectivity remains challenging.

Since inception, we have incurred significant operating losses. Our net losses were $115.4 million for the six months ended June 30, 2024. As of June 30, 2024, we had an accumulated deficit of $791.8 million. We expect to continue to incur significant expenses and operating losses for the foreseeable future in performing our ongoing activities, as we:

- continue development activities for apitegromab, including the conduct of our Phase 3 SAPPHIRE pivotal clinical trial in SMA, ONYX, our long-term extension study for patients from both the TOPAZ and SAPPHIRE studies and the associated drug supply;
- continue research and development activities for SRK-181, including the conduct of our Phase 1 DRAGON proof-of-concept clinical trial;
- continue research and development activities for our cardiometabolic program, including EMBRAZE, our Phase 2 proof-of-concept trial with apitegromab and advancing SRK-439 towards a potential IND submission in 2025;
- continue to discover, validate and develop additional product candidates through the use of our proprietary platform;
- maintain, expand and protect our intellectual property portfolio;
- hire additional research, development, commercial and other business personnel; and
- continue to build the infrastructure to support our operations as a public company.

To date, we have not generated any revenue from product sales. If we successfully complete clinical development and obtain regulatory approval for apitegromab, SRK-181, SRK-439 or any of our future product candidates, we may generate revenue in the future from product sales. In addition, if we obtain regulatory approval for apitegromab, SRK-181, SRK-439 or any of our future product candidates, we expect to incur significant expenses related to developing our commercialization capabilities to support product sales, marketing and distribution activities. Based on current operating plans and excluding any contribution from revenues or external financing, we may not have sufficient cash, cash equivalents and marketable securities to fund our operating expenses and capital requirements beyond one year from the date of this filing, and therefore, we have concluded that there is substantial doubt about our ability to continue as a going concern.

Company Information

We were incorporated in 2017 under the laws of the State of Delaware as the holding company for Scholar Rock, Inc. Scholar Rock, Inc. is a wholly owned subsidiary of Scholar Rock Holding Corporation. On December 22, 2017, we completed a series of transactions pursuant to which Scholar Rock Merger Sub, LLC, a wholly owned subsidiary of Scholar Rock Holding Corporation, was merged with and into Scholar Rock, LLC, or the Reorganization. The purpose of the Reorganization was to reorganize our corporate structure so that we would continue as a corporation and so that our investors prior to the Reorganization would own our capital stock after the Reorganization rather than equity interests in a limited liability company. All of our convertible preferred stock converted into shares of common stock upon the completion of our initial public offering at the then effective conversion ratio. Our operations to date have been limited to organizing and staffing our company, business planning, raising capital, developing our technology, identifying potential product candidates, producing drug substance and drug product material for use in preclinical studies and clinical trials, conducting preclinical studies of our product candidates and conducting clinical trials for our product candidates, apitegromab (formerly SRK-015) and SRK-181, and preparing our commercialization capabilities in anticipation of a potential approval and commercial launch of apitegromab. We do not have any products approved for sale and have not generated any product revenue to date.

Our principal executive offices are located at 301 Binney Street, Cambridge, MA 02142, and our phone number is (857) 259-3860. Our website address is www.scholarrock.com. The information contained on our website or social media accounts, or that can be accessed through our website or social media accounts, is not a part of this prospectus and is not incorporated by reference into this prospectus. You should not rely on any such information in deciding whether to purchase our common stock.

USE OF PROCEEDS

Unless otherwise described in the applicable prospectus supplement, we intend to use the net proceeds from the sale of any securities described in this prospectus for general corporate purposes. General corporate purposes may include research and development and commercialization costs, including the conduct of clinical trials and process development and manufacturing of our product candidates, preparing our commercialization capabilities for potential approval and commercial launch of our product candidates, services or technologies, expansion of our technology infrastructure and capabilities, working capital and capital expenditures.

We may set forth additional information concerning our expected use of net proceeds from sales of securities in the applicable prospectus supplement relating to the specific offering. Pending use of net proceeds as described above, we may temporarily invest the net proceeds in a variety of capital preservation instruments, including investment grade, interest bearing instruments and U.S. government securities, or we may hold such proceeds as cash, until they are used for their stated purpose. We have not determined the amount of net proceeds to be used specifically for such purposes. As a result, management will retain broad discretion over the allocation of net proceeds.

SECURITIES WE MAY OFFER AND/OR SELLING STOCKHOLDERS MAY OFFER OR SELL

This prospectus contains summary descriptions of the securities we and/or selling stockholders may offer from time to time. These summary descriptions are not meant to be complete descriptions of each security. The particular terms of any security will be described in the applicable prospectus supplement. This prospectus provides you with a general description of the securities we may offer. Each time we sell securities described herein, we will provide prospective investors with a supplement to this prospectus that will contain specific information about the terms of that offering, including the specific amounts, prices and terms of the securities offered. We may sell the securities to or through underwriters, dealers or agents, directly to purchasers or through a combination of any of these methods of sale or as otherwise set forth below under "Plan of Distribution." We, as well as any agents acting on our behalf, reserve the sole right to accept and to reject in whole or in part any proposed purchase of securities. Any prospectus supplement will set forth the names of any underwriters, dealers, agents or other entities involved in the sale of securities described in that prospectus supplement and any applicable fee, commission or discount arrangements with them.

DESCRIPTION OF CAPITAL STOCK

The following summary description of our common stock and preferred stock, together with the additional information we include in any applicable prospectus supplements, summarizes the material terms and provisions of the common stock and preferred stock that we may offer under this prospectus. The following description of our capital stock is intended as a summary only, does not purport to be complete and is subject to, and qualified in its entirety by, our Amended and Restated Certificate of Incorporation, as amended to date, and our Amended and Restated Bylaws, which are exhibits to the registration statement of which this prospectus forms a part, and by applicable law. We refer in this section to our Amended and Restated Certificate of Incorporation, as amended to date, as our "certificate of incorporation," and we refer to our Amended and Restated Bylaws as our "bylaws." The terms of our common stock and preferred stock may also be affected by Delaware law.

Authorized Capital Stock

Our authorized capital stock consists of 300,000,000 shares of common stock, par value $0.001 per share, and 10,000,000 shares of preferred stock, par value $0.001 per share, all of which preferred stock is undesignated.

As of June 30, 2024, 79,992,068 shares of our common stock were outstanding and held by approximately 7 stockholders of record. In addition, as of June 30, 2024, we had outstanding options to purchase 9,167,552 shares of our common stock, at a weighted average exercise price of $14.96 per share, 4,473,458 of which were exercisable, 2,984,663 shares of unvested restricted stock units, 17,008,164 pre-funded warrants to purchase shares of our common stock and 9,157,496 warrants to purchase shares of our common stock at a weighted-average exercise price of $7.35 per share.

Common Stock

The holders of our common stock are entitled to one vote for each share held on all matters submitted to a vote of the stockholders. The holders of our common stock do not have any cumulative voting rights. Holders of our common stock are entitled to receive ratably any dividends declared by the board of directors out of funds legally available for that purpose, subject to any preferential dividend rights of any outstanding preferred stock. Our common stock has no preemptive rights, conversion rights or other subscription rights or redemption or sinking fund provisions.

In the event of our liquidation, dissolution or winding up, holders of our common stock will be entitled to share ratably in all assets remaining after payment of all debts and other liabilities and any liquidation preference of any outstanding preferred stock. When we issue shares of common stock under this prospectus, when issued and paid for, the shares will be validly issued, fully paid and non-assessable.

Exchange Listing

Our common stock is listed on The Nasdaq Global Select Market under the symbol "SRRK." On October 4, 2024, the closing price for our common stock, as reported on The Nasdaq Global Select Market, was $7.42 per share.

Transfer Agent and Registrar

The transfer agent and registrar for our common stock is Computershare Trust Company, N.A**.** The transfer agent and registrar's address is P.O. Box 43006, Providence, Rhode Island 02940-3006, and its telephone number within the U.S. is (800) 736-3001 and outside the U.S. is (781) 575-3100.

Prefunded Warrants for Common Stock

November 2020 Pre-Funded Warrants

In November 2020, we sold pre-funded warrants to purchase 2,179,487 shares of common stock.

Form. The pre-funded warrants are issued as individual warrant agreements to each individual purchaser of a pre-funded warrant.

Term. The pre-funded warrants do not expire.

Exercisability. The pre-funded warrants are exercisable at any time after their original issuance. The pre-funded warrants will be exercisable, at the option of each holder, in whole or in part, by delivering to us a duly executed exercise notice and by payment in full of the exercise price in immediately available funds for the number of shares of our common stock purchased upon such exercise. As an alternative to payment of the exercise price in immediately available funds, the holder may elect to exercise the pre-funded warrant through a cashless exercise, in which case the holder would receive upon such exercise the net number of shares of our common stock determined according to the formula set forth in the pre-funded warrants. No fractional shares of our common stock will be issued in connection with the exercise of a pre-funded warrant. In lieu of fractional shares, we will pay the holder an amount in cash equal to the fractional amount multiplied by the last closing trading price of our common stock on the exercise date.

Exercise limitations. Under the pre-funded warrants, we may not effect the exercise of any pre-funded warrant, and a holder will not be entitled to exercise any portion of any pre-funded warrant, which, upon giving effect to such exercise, would cause (i) the aggregate number of shares of our common stock beneficially owned by the holder (together with its affiliates) to exceed 9.99% of the number of shares of our common stock outstanding immediately after giving effect to the exercise, or (ii) the combined voting power of our securities beneficially owned by the holder (together with its affiliates) to exceed 9.99% of the combined voting power of all of our securities then outstanding immediately after giving effect to the exercise, as such percentage ownership is determined in accordance with the terms of the pre-funded warrants. However, any holder may increase or decrease such percentage to any other percentage not in excess of 19.99% upon at least 61 days' prior notice from the holder to us.

Exercise price. The exercise price per whole share of our common stock purchasable upon the exercise of the pre-funded warrants is $0.0001 per share of our common stock. The exercise price of the prefunded warrants and the number of shares of our common stock issuable upon exercise of the pre-funded warrants are subject to appropriate adjustment in the event of certain stock dividends and distributions, stock splits, stock combinations, reclassifications or similar events affecting our common stock and also upon any distributions of assets, including cash, stock or other property to our stockholders. The exercise price will not be adjusted below the par value of our common stock.

Transferability. Subject to applicable laws, the pre-funded warrants may be offered for sale, sold, transferred or assigned without our consent. The pre-funded warrants will be held in definitive form by the warrant agent. The ownership of the pre-funded warrants and any transfers of the pre-funded warrants will be registered in a warrant register maintained by the warrant agent. We will initially act as warrant agent.

June 2022 Pre-Funded Warrants

In June 2022, we sold pre-funded warrants to purchase 25,510,205 shares of common stock.

Form. The pre-funded warrants are issued as individual warrant agreements to each individual purchaser of a pre-funded warrant.

Term. The pre-funded warrants do not expire.

Exercise price. Each pre-funded warrant offered has an initial exercise price per share equal to $0.0001. The exercise price and number of shares of common stock issuable upon exercise is subject to appropriate adjustment in the event of stock dividends, stock splits, reorganizations or similar events affecting our common stock and the exercise price.

Exercisability. The pre-funded warrants are exercisable, at the option of each holder, in whole or in part, by delivering to us a duly executed exercise notice accompanied by payment in full for the number of shares of our common stock purchased upon such exercise (except in the case of a cashless exercise as discussed below). A holder (together with its affiliates) may not exercise any portion of such holder's pre-funded warrant to the extent that the holder would own more than 9.99% (or, at the election of the purchaser, 4.99%,

14.99% or 19.99%) of the outstanding shares of common stock immediately after exercise, except that upon at least 61 days' written prior notice from the holder to us, the holder may increase or decrease the amount of ownership of outstanding shares of common stock after exercising the holder's pre-funded warrants up to 19.99% of the number of shares of common stock outstanding immediately after giving effect to the exercise, as such percentage ownership is determined in accordance with the terms of the pre-funded warrants. No fractional shares of common stock will be issued in connection with the exercise of a pre-funded warrant. In lieu of fractional shares, we will either pay the holder an amount in cash equal to the fractional amount multiplied by the exercise price or round up to the next whole share.

Cashless exercise. In lieu of making the cash payment otherwise contemplated to be made to us upon such exercise in payment of the aggregate exercise price, the holder may elect instead to receive upon such exercise (either in whole or in part) the net number of shares of common stock determined according to a formula set forth in the pre-funded warrants.

Fundamental transactions. In the event of any fundamental transaction, as described in the pre-funded warrants and generally including any merger with or into another entity, sale of all or substantially all of our assets, tender offer or exchange offer, or reclassification of our shares of common stock, then upon any subsequent exercise of a pre-funded warrant, the holder will have the right to receive as alternative consideration, for each share of common stock that would have been issuable upon such exercise immediately prior to the occurrence of such fundamental transaction, the number of shares of common stock of the successor or acquiring corporation or of our company, if it is the surviving corporation, and any additional consideration receivable upon or as a result of such transaction by a holder of the number of shares of common stock for which the Pre-funded Warrant is exercisable immediately prior to such event.

Transferability. Subject to applicable laws, the pre-funded warrants may be offered for sale, sold, transferred or assigned without our consent. The pre-funded warrants will be held in definitive form by the warrant agent. The ownership of the pre-funded warrants and any transfers of the pre-funded warrants will be registered in a warrant register maintained by the warrant agent. We act as warrant agent.

Exchange listing. There is no established trading market for the pre-funded warrants. We do not intend to list the pre-funded warrants on any securities exchange or nationally recognized trading system.

Right as a stockholder. Except as otherwise provided in the pre-funded warrants or by virtue of such holder's ownership of shares of our common stock, the holders of the pre-funded warrants do not have the rights or privileges of holders of our common stock, including any voting rights, until such pre-funded warrant holders exercise their pre-funded warrants.

Common Stock Purchase Warrants

June 2022 Common Warrants

In June 2022, we sold warrants to purchase 10,459,181 shares of common stock.

Form. The common warrants are issued as individual warrant agreements to each individual purchaser of a common warrant.

Duration and exercise price. Each warrant has an initial exercise price per share equal to $7.35 The warrants are immediately exercisable and will expire upon December 31, 2025. The exercise price and number of shares of common stock issuable upon exercise is subject to appropriate adjustment in the event of stock dividends, stock splits, reorganizations or similar events affecting our common stock and the exercise price.

Exercisability. The warrants are exercisable, at the option of each holder, in whole or in part, by delivering to us a duly executed exercise notice accompanied by payment in full for the number of shares of our common stock purchased upon such exercise (except in the case of a cashless exercise as discussed below). A holder (together with its affiliates) may not exercise any portion of such holder's warrant to the extent that the holder would own more than 4.99% (or, at the election of the purchaser, 9.99%, 14.99% or 19.99%) of the outstanding shares of common stock immediately after exercise, except that upon at least 61 days' prior notice from the holder to us, the holder may increase the amount of ownership of outstanding

shares of common stock after exercising the holder's warrants up to 9.99%, 14.99% or 19.99% of the number of shares of common stock outstanding immediately after giving effect to the exercise, as such percentage ownership is determined in accordance with the terms of the warrants. No fractional shares of common stock will be issued in connection with the exercise of a warrant. In lieu of fractional shares, we will either pay the holder an amount in cash equal to the fractional amount multiplied by the exercise price or round up to the next whole share.

Cashless exercise. If at the time of exercise hereof there is no effective registration statement registering, or the prospectus contained therein is not available for the issuance of the shares of common stock issuable upon exercise of the warrants, then in lieu of making the cash payment otherwise contemplated to be made to us upon such exercise in payment of the aggregate exercise price, the holder may elect instead to receive upon such exercise (either in whole or in part) the net number of shares of common stock determined according to a formula set forth in the warrants.

Fundamental transactions. In the event of any fundamental transaction, as described in the warrants and generally including any merger with or into another entity, sale of all or substantially all of our assets, tender offer or exchange offer, or reclassification of our shares of common stock, then upon any subsequent exercise of a warrant, the holder will have the right to receive as alternative consideration, for each share of common stock that would have been issuable upon such exercise immediately prior to the occurrence of such fundamental transaction, the number of shares of common stock of the successor or acquiring corporation or of our company, if it is the surviving corporation, and any additional consideration receivable upon or as a result of such transaction by a holder of the number of shares of common stock for which the warrant is exercisable immediately prior to such event.

Transferability. Subject to applicable laws, a warrant or the rights thereunder may not be transferred or assigned, in whole or in part unless such transfer is to the warrant holder's successors and Affiliates (as defined in the warrant). The ownership of the warrants and any transfers of the warrants will be registered in a warrant register maintained by the warrant agent. We will initially act as warrant agent.

Exchange listing. There is no trading market available for the warrants on any securities exchange or nationally recognized trading system. We do not intend to list the warrants on any securities exchange or nationally recognized trading system.

Right as a stockholder. Except as otherwise provided in the warrants or by virtue of such holder's ownership of shares of our common stock, the holders of the warrants do not have the rights or privileges of holders of our common stock, including any voting rights, until they exercise their warrants.

Preferred Stock

Undesignated Preferred Stock

Our board of directors or any authorized committee thereof has the authority, without further action by our stockholders, to issue up to 10,000,000 shares of preferred stock in one or more series and to fix the rights, preferences, privileges, and restrictions thereof. No shares of preferred stock are outstanding, and we have no present plans to issue any shares of preferred stock.

The purpose of authorizing our board of directors to issue preferred stock in one or more series and determine the number of shares in the series and its rights and preferences is to eliminate delays associated with a shareholder vote on specific issuances. Examples of rights and preferences that the board of directors may fix are:

- dividend rights;
- dividend rates;
- conversion rights;
- voting rights;
- terms of redemption; and

- liquidation preferences.

The existence of authorized but unissued shares of preferred stock may enable our board of directors to render more difficult or to discourage an attempt to obtain control of us by means of a merger, tender offer, proxy contest or otherwise. For example, if in the due exercise of its fiduciary obligations, our board of directors were to determine that a takeover proposal is not in the best interests of us or our stockholders, our board of directors could cause shares of preferred stock to be issued without stockholder approval in one or more private offerings or other transactions that might dilute the voting or other rights of the proposed acquirer, stockholder or stockholder group. The rights of holders of our common stock described above will be subject to, and may be adversely affected by, the rights of any preferred stock that we may designate and issue in the future. The issuance of shares of preferred stock could decrease the amount of earnings and assets available for distribution to holders of shares of common stock. The issuance may also adversely affect the rights and powers, including voting rights, of these holders and may have the effect of delaying, deterring or preventing a change in control of us.

Additional Series of Preferred Stock

We will incorporate by reference as an exhibit to the registration statement, which includes this prospectus, the form of any certificate of designation that describes the terms of the series of preferred stock we are offering. This description and the applicable prospectus supplement will include:

- the title and stated value;
- the number of shares authorized;
- the liquidation preference per share;
- the purchase price;
- the dividend rate, period and payment date, and method of calculation for dividends;
- whether dividends will be cumulative or non-cumulative and, if cumulative, the date from which dividends will accumulate;
- the procedures for any auction and remarketing, if any;
- the provisions for a sinking fund, if any;
- the provisions for redemption or repurchase, if applicable, and any restrictions on our ability to exercise those redemption and repurchase rights;
- any listing of the preferred stock on any securities exchange or market;
- whether the preferred stock will be convertible into our common stock, and, if applicable, the conversion price, or how it will be calculated, and the conversion period;
- whether the preferred stock will be exchangeable into debt securities, and, if applicable, the exchange price, or how it will be calculated, and the exchange period;
- voting rights, if any, of the preferred stock;
- preemptive rights, if any;
- restrictions on transfer, sale or other assignment, if any;
- whether interests in the preferred stock will be represented by depositary shares;
- a discussion of any material United States federal income tax considerations applicable to the preferred stock;
- the relative ranking and preferences of the preferred stock as to dividend rights and rights if we liquidate, dissolve or wind up our affairs;
- any limitations on issuance of any class or series of preferred stock ranking senior to or on a parity with the series of preferred stock as to dividend rights and rights if we liquidate, dissolve or wind up our affairs; and

- any other specific terms, preferences, rights or limitations of, or restrictions on, the preferred stock.

When we issue shares of preferred stock under this prospectus, the shares will fully be paid and nonassessable and will not have, or be subject to, any preemptive or similar rights.

Registration Rights

Gilead Sciences, Inc., or Gilead, is entitled to rights with respect to the registration of certain shares under the Securities Act pursuant to a registration rights agreement, or Registration Rights Agreement, and include demand registration rights, short-form and shelf registration rights and piggyback registration rights. All fees, costs and expenses of underwritten registrations, subject to certain restrictions, will be borne by us and all selling expenses, including underwriting discounts and selling commissions, will be borne by Gilead.

Demand Registration Rights

Under the terms of the Registration Rights Agreement with Gilead, beginning on December 19, 2020, we are required, upon the written request of the stockholder to register securities with an aggregate value of at least $10.0 million based on then-current value of the securities, to use reasonable best efforts to effect the registration of such shares on Form S-1, subject to certain exceptions. Under the terms of the Registration Rights Agreement, we are required to effect up to two registrations pursuant to this provision, and the short-form and shelf registration rights provisions of the Registration Rights Agreement, except that the number of shelf takedowns that are not underwritten offerings are not limited.

An aggregate of 490,196 shares of common stock are entitled to the demand registration rights under the Registration Rights Agreement.

Short-Form and Shelf Registration Rights

Under the terms of the Registration Rights Agreement, beginning on December 19, 2020, if we are eligible to file a registration statement on Form S-3, upon the written request of the stockholder to register securities with an aggregate value of at least $3.0 million based on then-current value of the securities, we will use reasonable best efforts to cause registration of the securities on Form S-3. In addition, under the terms of the Registration Rights Agreement, upon the written request of the stockholder, we will be required to file a shelf registration statement on Form S-3 to register the securities pursuant to Securities Act Rule 415 and use our reasonable best efforts to cause such shelf registration statement to become effective, subject to certain exceptions.

The right to have such shares registered on Form S-3 is further subject to other specified conditions and limitations in each case.

An aggregate of 490,196 shares of common stock are entitled to the Form S-3 registration rights under the Registration Rights Agreement.

Piggyback Registration Rights

If we propose to register any of our securities, either for our own account or for the account of other security holders, under the Registration Rights Agreement, we will use reasonable best efforts to include the stockholder's shares in the registration.

Under the Registration Rights Agreement, subject to certain exceptions, the underwriters may limit the number of shares included in the underwritten offering to the number of shares which the underwriters determine in their sole discretion will not jeopardize the success of the offering, including, specifically, where the underwriter has determined that in their opinion there is a risk that the price of the securities will be reduced or the number of securities intended to be included on our behalf will be reduced.

An aggregate of 490,196 shares of common stock are entitled to these piggyback registration rights under the Registration Rights Agreement.

Indemnification

The Registration Rights Agreement contains customary cross-indemnification provisions, under which we are obligated to indemnify the stockholder in the event of material misstatements or omissions in the registration statement attributable to us, and the stockholder is obligated to indemnify us for material misstatements or omissions attributable to it.

Expiration of Registration Rights

The registration rights granted under the Registration Rights Agreement will terminate on December 19, 2024.

Anti-Takeover Effects of Our Certificate of Incorporation and Our Bylaws

Our certificate of incorporation and bylaws contain certain provisions that are intended to enhance the likelihood of continuity and stability in the composition of the board of directors and which may have the effect of delaying, deferring or preventing a future takeover or change in control of the company unless such takeover or change in control is approved by the board of directors.

These provisions include:

Classified Board. Our certificate of incorporation provides that our board of directors is divided into three classes of directors, with the classes as nearly equal in number as possible. As a result, approximately one-third of our board of directors will be elected each year. The classification of directors has the effect of making it more difficult for stockholders to change the composition of our board. Our certificate of incorporation provides that, subject to any rights of holders of preferred stock to elect additional directors under specified circumstances, the number of directors will be fixed exclusively pursuant to a resolution adopted by our board of directors. Our board of directors has eight members. Our certificate of incorporation provides that the affirmative vote of at least two-thirds of the outstanding shares of capital stock entitled to vote, and the affirmative vote of at least two-thirds of the outstanding shares of each class entitled to vote as a class, is required to amend or repeal the foregoing provision. This requirement of a supermajority vote to amend or repeal that provision of our bylaws could enable a minority of our stockholders to prevent a declassification of our Board.

Action by Written Consent; Special Meetings of Stockholders. Our certificate of incorporation provides that stockholder action can be taken only at an annual or special meeting of stockholders and cannot be taken by written consent in lieu of a meeting. This limit may lengthen the amount of time required to take stockholder actions and would prevent the amendment of our bylaws or removal of directors by our stockholders without holding a meeting of stockholders. Our certificate of incorporation provides that the affirmative vote of at least two-thirds of the outstanding shares of capital stock entitled to vote, and the affirmative vote of at least two-thirds of the outstanding shares of each class entitled to vote as a class, is required to amend or repeal the foregoing provision. Our certificate of incorporation and bylaws provide that, except as otherwise required by law, special meetings of the stockholders can be called only by or at the direction of the board of directors pursuant to a resolution adopted by a majority of the total number of directors, and only those matters set forth in the notice of the special meeting may be considered or acted upon at a special meeting of stockholders. Our bylaws limit the business that may be conducted at an annual meeting of stockholders to those matters properly brought before the meeting. Stockholders are not permitted to call a special meeting or to require the board of directors to call a special meeting. Our bylaws provide that the affirmative vote of at least two thirds of the outstanding shares entitled to vote, and of each class entitled to vote, respectively, is required to amend the or repeal the provision in our bylaws that provides that special meetings of the stockholders can be called only by or at the direction of the board of directors pursuant to a resolution adopted by a majority of the total number of directors, unless the Board first recommends such amendment or repeal to stockholders. This requirement of a supermajority vote to amend or repeal that provision of our bylaws could enable a minority of our stockholders to prevent a change to such provision and has the effect of making it more difficult for stockholders to call a special meeting of stockholders.

Removal of Directors. Our certificate of incorporation provides that our directors may be removed only for cause and then only by the affirmative vote of the holders of two-thirds or more of the shares then

entitled to vote at an election of directors, at a meeting of the stockholders called for that purpose. Furthermore, any vacancy on our board of directors, however occurring, including a vacancy resulting from an increase in the size of our board, may only be filled by the affirmative vote of a majority of our directors then in office even if less than a quorum. This requirement of a supermajority vote to remove directors could enable a minority of our stockholders to prevent a change in the composition of our board, and the treatment of vacancies also has the effect of making it more difficult for stockholders to change the composition of our board.

Advance Notice Procedures. Our bylaws establish an advance notice procedure for stockholder proposals to be brought before an annual meeting of our stockholders, including proposed nominations of persons for election to the board of directors. These procedures provide that notice of stockholder proposals must be timely given in writing to our corporate secretary prior to the meeting at which the action is to be taken. Generally, to be timely, notice must be received at our principal executive offices not less than 90 days nor more than 120 days prior to the first anniversary date of the annual meeting for the preceding year. Our bylaws specify the requirements as to form and content of all stockholders' notices. Stockholders at an annual meeting will only be able to consider proposals or nominations specified in the notice of meeting or brought before the meeting by or at the direction of the board of directors or by a stockholder who was a stockholder of record on the record date for the meeting, who is entitled to vote at the meeting and who has given our secretary timely written notice, in proper form, of the stockholder's intention to bring that business before the meeting. Although the bylaws do not give the board of directors the power to approve or disapprove stockholder nominations of candidates or proposals regarding other business to be conducted at a special or annual meeting, the bylaws may have the effect of precluding the conduct of certain business at a meeting if the proper procedures are not followed or may discourage or deter a potential acquirer from conducting a solicitation of proxies to elect its own slate of directors or otherwise attempting to obtain control of the company.

Super Majority Approval Requirements and Amendment to Certificate of Incorporation and Bylaws. Any amendment of our certificate of incorporation must first be approved by a majority of our board of directors, and if required by law or our certificate of incorporation, must thereafter be approved by a majority of the outstanding shares entitled to vote on the amendment and a majority of the outstanding shares of each class entitled to vote thereon as a class, except that the amendment of the provisions relating to stockholder action, board composition, limitation of liability and the amendment of our bylaws and certificate of incorporation must be approved by not less than two-thirds of the outstanding shares entitled to vote on the amendment, and not less than two-thirds of the outstanding shares of each class entitled to vote thereon as a class. Our bylaws may be amended by the affirmative vote of a majority of the directors then in office, subject to any limitations set forth in the bylaws, and may also be amended by the affirmative vote of at least two-thirds of the outstanding shares entitled to vote on the amendment, or, if our board of directors recommends that the stockholders approve the amendment, by the affirmative vote of the majority of the outstanding shares entitled to vote on the amendment, in each case voting together as a single class.

Authorized but Unissued Shares. Our authorized but unissued shares of common stock and preferred stock are available for future issuance without stockholder approval. These additional shares may be utilized for a variety of corporate purposes, including future public offerings to raise additional capital and corporate acquisitions. The existence of authorized but unissued shares of common stock and preferred stock could render more difficult or discourage an attempt to obtain control of a majority of our common stock by means of a proxy contest, tender offer, merger or otherwise. For example, if in the due exercise of its fiduciary obligations, our board of directors were to determine that a takeover proposal is not in the best interests of our stockholders, our board of directors could cause shares of convertible preferred stock to be issued without stockholder approval in one or more private offerings or other transactions that might dilute the voting or other rights of the proposed acquirer or insurgent stockholder or stockholder group. In this regard, our certificate of incorporation grants our board of directors broad power to establish the rights and preferences of authorized and unissued shares of convertible preferred stock. The issuance of shares of convertible preferred stock could decrease the amount of earnings and assets available for distribution to holders of shares of common stock. The issuance may also adversely affect the rights and powers, including voting rights, of these holders and may have the effect of delaying, deterring or preventing a change in control of us.

Choice of Forum. Our bylaws provide that, unless we consent in writing to the selection of an alternative forum, the Court of Chancery of the State of Delaware will be the sole and exclusive forum for: (1) any derivative action or proceeding brought on our behalf; (2) any action asserting a claim of breach of a fiduciary duty or other wrongdoing by any of our directors, officers, employees or agents to us or our stockholders; (3) any action asserting a claim against us arising pursuant to any provision of the General Corporation Law of the State of Delaware or our certificate of incorporation or bylaws; (4) any action to interpret, apply, enforce or determine the validity of our certificate of incorporation or bylaws; or (5) any action asserting a claim governed by the internal affairs doctrine.

In addition, our bylaws contain a provision by virtue of which, unless we consent in writing to the selection of an alternative forum, the United States District Court for the District of Massachusetts will be the exclusive forum for any complaint asserting a cause of action arising under the Securities Act. In addition, our bylaws provide that any person or entity purchasing or otherwise acquiring any interest in shares of our common stock is deemed to have notice of and consented to the foregoing provisions.

This exclusive forum provision would not apply to suits brought to enforce any liability or duty created by the Securities Act or the Exchange Act or any other claim for which the federal courts have exclusive jurisdiction. To the extent that any such claims may be based upon federal law claims, Section 27 of the Exchange Act creates exclusive federal jurisdiction over all suits brought to enforce any duty or liability created by the Exchange Act or the rules and regulations thereunder. Furthermore, Section 22 of the Securities Act creates concurrent jurisdiction for federal and state courts over all suits brought to enforce any duty or liability created by the Securities Act or the rules and regulations thereunder. Although our certificate of incorporation contains the choice of forum provision described above, it is possible that a court could rule that such a provision is inapplicable for a particular claim or action or that such provision is unenforceable.

We have chosen the United States District Court for the District of Massachusetts as the exclusive forum for such causes of action because our principal executive offices are located in Cambridge, Massachusetts. Some companies that have adopted similar federal district court forum selection provisions are currently subject to a suit in the Court of Chancery of the State of Delaware brought by stockholders who assert that the federal district court forum selection provision is not enforceable. While the Delaware Supreme Court ruled in March 2020 that federal forum selection provisions purporting to require claims under the Securities Act be brought in federal court are "facially valid" under Delaware law, there is uncertainty as to whether other courts will enforce our federal forum selection provision, and we may incur additional costs of litigation should such enforceability be challenged.

Section 203 of the Delaware General Corporation Law

We are subject to the provisions of Section 203 of the Delaware General Corporation Law, or Section 203. In general, Section 203 prohibits a publicly-held Delaware corporation from engaging in a "business combination" with an "interested stockholder" for a three-year period following the time that this stockholder becomes an interested stockholder, unless the business combination is approved in a prescribed manner. A "business combination" includes, among other things, a merger, asset or stock sale or other transaction resulting in a financial benefit to the interested stockholder. An "interested stockholder" is a person who, together with affiliates and associates, owns, or did own within three years prior to the determination of interested stockholder status, 15% or more of the corporation's voting stock.

Under Section 203, a business combination between a corporation and an interested stockholder is prohibited unless it satisfies one of the following conditions: before the stockholder became interested, the board of directors approved either the business combination or the transaction which resulted in the stockholder becoming an interested stockholder; upon consummation of the transaction which resulted in the stockholder becoming an interested stockholder, the interested stockholder owned at least 85% of the voting stock of the corporation outstanding at the time the transaction commenced, excluding for purposes of determining the voting stock outstanding, shares owned by persons who are directors and also officers, and employee stock plans, in some instances; or at or after the time the stockholder became interested, the business combination was approved by the board of directors of the corporation and authorized at an annual or special meeting of the stockholders by the affirmative vote of at least two-thirds of the outstanding voting stock which is not owned by the interested stockholder.

A Delaware corporation may "opt out" of these provisions with an express provision in its original certificate of incorporation or an express provision in its certificate of incorporation or bylaws resulting from a stockholders' amendment approved by at least a majority of the outstanding voting shares. We have not opted out of these provisions. As a result, mergers or other takeover or change in control attempts of us may be discouraged or prevented.

DESCRIPTION OF DEBT SECURITIES

The paragraphs below describe the general terms and provisions of the debt securities we may issue. When we offer to sell a particular series of debt securities, we will describe the specific terms of the securities in a supplement to this prospectus, including any additional covenants or changes to existing covenants relating to such series. The prospectus supplement also will indicate whether the general terms and provisions described in this prospectus apply to a particular series of debt securities. You should read the actual indenture if you do not fully understand a term or the way we use it in this prospectus.

We may offer senior or subordinated debt securities. Each series of debt securities may have different terms. The senior debt securities will be issued under one or more senior indentures, dated as of a date prior to such issuance, between us and the trustee identified in the applicable prospectus supplement, as amended or supplemented from time to time. We will refer to any such indenture throughout this prospectus as the "senior indenture." Any subordinated debt securities will be issued under one or more separate indentures, dated as of a date prior to such issuance, between us and the trustee identified in the applicable prospectus supplement, as amended or supplemented from time to time. We will refer to any such indenture throughout this prospectus as the "subordinated indenture" and to the trustee under the senior or subordinated indenture as the "trustee." The senior indenture and the subordinated indenture are sometimes collectively referred to in this prospectus as the "indentures." The indentures will be subject to and governed by the Trust Indenture Act of 1939, as amended. We included copies of the forms of the indentures as exhibits to our registration statement and they are incorporated into this prospectus by reference.

If we issue debt securities at a discount from their principal amount, then, for purposes of calculating the aggregate initial offering price of the offered securities issued under this prospectus, we will include only the initial offering price of the debt securities and not the principal amount of the debt securities.

We have summarized below the material provisions of the indentures and the debt securities, or indicated which material provisions will be described in the related prospectus supplement. The prospectus supplement relating to any particular securities offered will describe the specific terms of the securities, which may be in addition to or different from the general terms summarized in this prospectus. Because the summary in this prospectus and in any prospectus supplement does not contain all of the information that you may find useful, you should read the documents relating to the securities that are described in this prospectus or in any applicable prospectus supplement. Please read "Where You Can Find More Information" to find out how you can obtain a copy of those documents. Except as otherwise indicated, the terms of the indentures are identical. As used under this caption, the term "debt securities" includes the debt securities being offered by this prospectus and all other debt securities issued by us under the indentures.

General

The indentures:

- do not limit the amount of debt securities that we may issue;
- allow us to issue debt securities in one or more series;
- do not require us to issue all of the debt securities of a series at the same time;
- allow us to reopen a series to issue additional debt securities without the consent of the holders of the debt securities of such series; and
- provide that the debt securities will be unsecured, except as may be set forth in the applicable prospectus supplement.

Unless we give you different information in the applicable prospectus supplement, the senior debt securities will be unsubordinated obligations and will rank equally with all of our other senior unsecured and unsubordinated indebtedness. Payments on the subordinated debt securities will be subordinated to the prior payment in full of all of our senior indebtedness, as described under "Description of Debt Securities — Subordination" and in the applicable prospectus supplement.

Each indenture provides that we may, but need not, designate more than one trustee under an indenture. Any trustee under an indenture may resign or be removed and a successor trustee may be appointed to act

with respect to the series of debt securities administered by the resigning or removed trustee. If two or more persons are acting as trustee with respect to different series of debt securities, each trustee shall be a trustee of a trust under the applicable indenture separate and apart from the trust administered by any other trustee. Except as otherwise indicated in this prospectus, any action described in this prospectus to be taken by each trustee may be taken by each trustee with respect to, and only with respect to, the one or more series of debt securities for which it is trustee under the applicable indenture.

The prospectus supplement for each offering will provide the following terms, where applicable:

- the title of the debt securities and whether they are senior or subordinated;
- the aggregate principal amount of the debt securities being offered, the aggregate principal amount of the debt securities outstanding as of the most recent practicable date and any limit on their aggregate principal amount, including the aggregate principal amount of debt securities authorized;
- the price at which the debt securities will be issued, expressed as a percentage of the principal and, if other than the principal amount thereof, the portion of the principal amount thereof payable upon declaration of acceleration of the maturity thereof or, if applicable, the portion of the principal amount of such debt securities that is convertible into common stock or other securities of ours or the method by which any such portion shall be determined;
- if convertible, the terms on which such debt securities are convertible, including the initial conversion price or rate and the conversion period and any applicable limitations on the ownership or transferability of common stock or other securities of ours received on conversion;
- the date or dates, or the method for determining the date or dates, on which the principal of the debt securities will be payable;
- the fixed or variable interest rate or rates of the debt securities, or the method by which the interest rate or rates is determined;
- the date or dates, or the method for determining the date or dates, from which interest will accrue;
- the dates on which interest will be payable;
- the record dates for interest payment dates, or the method by which such dates will be determined;
- the persons to whom interest will be payable;
- the basis upon which interest will be calculated if other than that of a 360-day year of twelve 30-day months;
- any make-whole amount, which is the amount in addition to principal and interest that is required to be paid to the holder of a debt security as a result of any optional redemption or accelerated payment of such debt security, or the method for determining the make-whole amount;
- the place or places where the principal of, and any premium or make-whole amount, and interest on, the debt securities will be payable;
- where the debt securities may be surrendered for registration of transfer or conversion or exchange;
- where notices or demands to or upon us in respect of the debt securities and the applicable indenture may be served;
- the times, prices and other terms and conditions upon which we may redeem the debt securities;
- any obligation we have to redeem, repay or purchase the debt securities pursuant to any sinking fund or analogous provision or at the option of holders of the debt securities, and the times and prices at which we must redeem, repay or purchase the debt securities as a result of such obligation;
- the currency or currencies in which the debt securities are denominated and payable if other than United States dollars, which may be a foreign currency or units of two or more foreign currencies or a composite currency or currencies and the terms and conditions relating thereto, and the manner of determining the equivalent of such foreign currency in United States dollars;

- whether the principal of, and any premium or make-whole amount, or interest on, the debt securities of the series are to be payable, at our election or at the election of a holder, in a currency or currencies other than that in which the debt securities are denominated or stated to be payable, and other related terms and conditions;
- whether the amount of payments of principal of, and any premium or make-whole amount, or interest on, the debt securities may be determined according to an index, formula or other method and how such amounts will be determined;
- whether the debt securities will be in registered form, bearer form, or both, and (i) if in registered form, the person to whom any interest shall be payable, if other than the person in whose name the security is registered at the close of business on the regular record date for such interest, or (ii) if in bearer form, the manner in which, or the person to whom, any interest on the security shall be payable if otherwise than upon presentation and surrender upon maturity;
- any restrictions applicable to the offer, sale or delivery of securities in bearer form and the terms upon which securities in bearer form of the series may be exchanged for securities in registered form of the series and vice versa, if permitted by applicable laws and regulations;
- whether any debt securities of the series are to be issuable initially in temporary global form and whether any debt securities of the series are to be issuable in permanent global form with or without coupons and, if so, whether beneficial owners of interests in any such permanent global security may, or shall be required to, exchange their interests for other debt securities of the series, and the manner in which interest shall be paid;
- the identity of the depositary for securities in registered form, if such series are to be issuable as a global security;
- the date as of which any debt securities in bearer form or in temporary global form shall be dated if other than the original issuance date of the first security of the series to be issued;
- the applicability, if any, of the defeasance and covenant defeasance provisions described in this prospectus or in the applicable indenture;
- whether and under what circumstances we will pay any additional amounts on the debt securities in respect of any tax, assessment or governmental charge and, if so, whether we will have the option to redeem the debt securities in lieu of making such a payment;
- whether and under what circumstances the debt securities being offered are convertible into common stock or other securities of ours, as the case may be, including the conversion price or rate and the manner or calculation thereof;
- the circumstances, if any, specified in the applicable prospectus supplement, under which beneficial owners of interests in the global security may obtain definitive debt securities and the manner in which payments on a permanent global debt security will be made if any debt securities are issuable in temporary or permanent global form;
- any provisions granting special rights to holders of securities upon the occurrence of such events as specified in the applicable prospectus supplement;
- if the debt securities of such series are to be issuable in definitive form only upon receipt of certain certificates or other documents or satisfaction of other conditions, then the form and/or terms of such certificates, documents or conditions;
- the name of the applicable trustee and the nature of any material relationship with us or any of our affiliates, and the percentage of debt securities of the class necessary to require the trustee to take action;
- any deletions from, modifications of or additions to our events of default or covenants with regard to such debt securities and any change in the right of any trustee or any of the holders to declare the principal amount of any of such debt securities due and payable;
- applicable CUSIP numbers; and

- any other terms of such debt securities not inconsistent with the provisions of the applicable indenture.

We may issue debt securities that provide for less than the entire principal amount thereof to be payable upon declaration of acceleration of the maturity of the debt securities. We refer to any such debt securities throughout this prospectus as "original issue discount securities." The applicable prospectus supplement will describe the United States federal income tax consequences and other relevant considerations applicable to original issue discount securities.

We also may issue indexed debt securities. Payments of principal of, and premium and interest on, indexed debt securities are determined with reference to the rate of exchange between the currency or currency unit in which the debt security is denominated and any other currency or currency unit specified by us, to the relationship between two or more currencies or currency units or by other similar methods or formulas specified in the prospectus supplement.

Except as described under "— Merger, Consolidation or Sale of Assets" or as may be set forth in any prospectus supplement, the debt securities will not contain any provisions that (i) would limit our ability to incur indebtedness or (ii) would afford holders of debt securities protection in the event of (a) a highly leveraged or similar transaction involving us, or (b) a change of control or reorganization, restructuring, merger or similar transaction involving us that may adversely affect the holders of the debt securities. In the future, we may enter into transactions, such as the sale of all or substantially all of our assets or a merger or consolidation, that may have an adverse effect on our ability to service our indebtedness, including the debt securities, by, among other things, substantially reducing or eliminating our assets.

Our governing instruments do not define the term "substantially all" as it relates to the sale of assets. Additionally, Delaware cases interpreting the term "substantially all" rely upon the facts and circumstances of each particular case. Consequently, to determine whether a sale of "substantially all" of our assets has occurred, a holder of debt securities must review the financial and other information that we have disclosed to the public.

We will provide you with more information in the applicable prospectus supplement regarding any deletions, modifications, or additions to the events of default or covenants that are described below, including any addition of a covenant or other provision providing event risk or similar protection.

Payment

Unless we give you different information in the applicable prospectus supplement, the principal of, and any premium or make-whole amount, and interest on, any series of the debt securities will be payable at the corporate trust office of the trustee. We will provide you with the address of the trustee in the applicable prospectus supplement. We may also pay interest by mailing a check to the address of the person entitled to it as it appears in the applicable register for the debt securities or by wire transfer of funds to that person at an account maintained within the United States.

All monies that we pay to a paying agent or a trustee for the payment of the principal of, and any premium or make-whole amount, or interest on, any debt security will be repaid to us if unclaimed at the end of two years after the obligation underlying payment becomes due and payable. After funds have been returned to us, the holder of the debt security may look only to us for payment, without payment of interest for the period which we hold the funds.

Denomination, Interest, Registration and Transfer

Unless otherwise described in the applicable prospectus supplement, the debt securities of any series will be issuable in denominations of $1,000 and integral multiples of $1,000.

Subject to the limitations imposed upon debt securities that are evidenced by a computerized entry in the records of a depository company rather than by physical delivery of a note, a holder of debt securities of any series may:

- exchange them for any authorized denomination of other debt securities of the same series and of a like aggregate principal amount and kind upon surrender of such debt securities at the corporate trust office of the applicable trustee or at the office of any transfer agent that we designate for such purpose; and
- surrender them for registration of transfer or exchange at the corporate trust office of the applicable trustee or at the office of any transfer agent that we designate for such purpose.

Every debt security surrendered for registration of transfer or exchange must be duly endorsed or accompanied by a written instrument of transfer satisfactory to the applicable trustee or transfer agent. Payment of a service charge will not be required for any registration of transfer or exchange of any debt securities, but we or the trustee may require payment of a sum sufficient to cover any tax or other governmental charge payable in connection therewith. If in addition to the applicable trustee, the applicable prospectus supplement refers to any transfer agent initially designated by us for any series of debt securities, we may at any time rescind the designation of any such transfer agent or approve a change in the location through which any such transfer agent acts, except that we will be required to maintain a transfer agent in each place of payment for such series. We may at any time designate additional transfer agents for any series of debt securities.

Neither we, nor any trustee, will be required to:

- issue, register the transfer of or exchange debt securities of any series during a period beginning at the opening of business 15 days before the day that the notice of redemption of any debt securities selected for redemption is mailed and ending at the close of business on the day of such mailing;
- register the transfer of or exchange any debt security, or portion thereof, so selected for redemption, in whole or in part, except the unredeemed portion of any debt security being redeemed in part; and
- issue, register the transfer of or exchange any debt security that has been surrendered for repayment at the option of the holder, except the portion, if any, of such debt security not to be so repaid.

Merger, Consolidation or Sale of Assets

The indentures provide that we may, without the consent of the holders of any outstanding debt securities, (i) consolidate with, (ii) sell, lease or convey all or substantially all of our assets to, or (iii) merge with or into, any other entity provided that:

- either we are the continuing entity, or the successor entity, if other than us, assumes the obligations (a) to pay the principal of, and any premium or make-whole amount, and interest on, all of the debt securities and (b) to duly perform and observe all of the covenants and conditions contained in each indenture;
- after giving effect to the transaction, there is no event of default under the indentures and no event which, after notice or the lapse of time, or both, would become such an event of default, occurs and continues; and
- an officers' certificate and legal opinion covering such conditions are delivered to each applicable trustee.

Covenants

Existence. Except as described under "— Merger, Consolidation or Sale of Assets," the indentures require us to do or cause to be done all things necessary to preserve and keep in full force and effect our existence, rights and franchises. However, the indentures do not require us to preserve any right or franchise if we determine that any right or franchise is no longer desirable in the conduct of our business.

Payment of taxes and other claims. The indentures require us to pay, discharge or cause to be paid or discharged, before they become delinquent (i) all taxes, assessments and governmental charges levied or imposed on us, and (ii) all lawful claims for labor, materials and supplies which, if unpaid, might by law become a lien upon our property. However, we will not be required to pay, discharge or cause to be paid or

discharged any such tax, assessment, charge or claim whose amount, applicability or validity is being contested in good faith by appropriate proceedings.

Provision of financial information. The indentures require us to (i) within 15 days of each of the respective dates by which we are required to file our annual reports, quarterly reports and other documents with the SEC, file with the trustee copies of the annual report, quarterly report and other documents that we file with the SEC under Section 13 or 15(d) of the Exchange Act, (ii) file with the trustee and the SEC any additional information, documents and reports regarding compliance by us with the conditions and covenants of the indentures, as required, (iii) within 30 days after the filing with the trustee, mail to all holders of debt securities, as their names and addresses appear in the applicable register for such debt securities, without cost to such holders, summaries of any documents and reports required to be filed by us pursuant to (i) and (ii) above, and (iv) supply, promptly upon written request and payment of the reasonable cost of duplication and delivery, copies of such documents to any prospective holder.

Additional covenants. The applicable prospectus supplement will set forth any of our additional covenants relating to any series of debt securities.

Events of Default, Notice and Waiver

Unless the applicable prospectus supplement states otherwise, when we refer to "events of default" as defined in the indentures with respect to any series of debt securities, we mean:

- default in the payment of any installment of interest on any debt security of such series continuing for 30 days;
- default in the payment of principal of, or any premium or make-whole amount on, any debt security of such series for five business days at its stated maturity;
- default in making any sinking fund payment as required for any debt security of such series for five business days;
- default in the performance or breach of any covenant or warranty in the debt securities or in the indenture by us continuing for 60 days after written notice as provided in the applicable indenture, but not of a covenant added to the indenture solely for the benefit of a series of debt securities issued thereunder other than such series;
- a default under any bond, debenture, note, mortgage, indenture or instrument:
  - having an aggregate principal amount of at least $30,000,000; or
  - under which there may be issued, secured or evidenced any existing or later created indebtedness for money borrowed by us, if we are directly responsible or liable as obligor or guarantor,

  if the default results in the indebtedness becoming or being declared due and payable prior to the date it otherwise would have, without such indebtedness having been discharged, or such acceleration having been rescinded or annulled, within 30 days after notice to the issuing company specifying such default. Such notice shall be given to us by the trustee, or to us and the trustee by the holders of at least 10% in principal amount of the outstanding debt securities of that series. The written notice shall specify such default and require us to cause such indebtedness to be discharged or cause such acceleration to be rescinded or annulled and shall state that such notice is a "Notice of Default" under such indenture;
- bankruptcy, insolvency or reorganization, or court appointment of a receiver, liquidator or trustee of us; and
- any other event of default provided with respect to a particular series of debt securities.

If an event of default occurs and is continuing with respect to debt securities of any series outstanding, then the applicable trustee or the holders of 25% or more in principal amount of the debt securities of that series will have the right to declare the principal amount of all the debt securities of that series to be due and payable. If the debt securities of that series are original issue discount securities or indexed securities, then the applicable trustee or the holders of 25% or more in principal amount of the debt securities of that series

will have the right to declare the portion of the principal amount as may be specified in the terms thereof to be due and payable. However, at any time after such a declaration of acceleration has been made, but before a judgment or decree for payment of the money due has been obtained by the applicable trustee, the holders of at least a majority in principal amount of outstanding debt securities of such series or of all debt securities then outstanding under the applicable indenture may rescind and annul such declaration and its consequences if:

- we have deposited with the applicable trustee all required payments of the principal, any premium or make-whole amount, interest and, to the extent permitted by law, interest on overdue installment of interest, plus applicable fees, expenses, disbursements and advances of the applicable trustee; and
- all events of default, other than the non-payment of accelerated principal, or a specified portion thereof, and any premium or make-whole amount, have been cured or waived.

The indentures also provide that the holders of at least a majority in principal amount of the outstanding debt securities of any series or of all debt securities then outstanding under the applicable indenture may, on behalf of all holders, waive any past default with respect to such series and its consequences, except a default:

- in the payment of the principal, any premium or make-whole amount, or interest;
- in respect of a covenant or provision contained in the applicable indenture that cannot be modified or amended without the consent of the holders of the outstanding debt security that is affected by the default; or
- in respect of a covenant or provision for the benefit or protection of the trustee, without its express written consent.

The indentures require each trustee to give notice to the holders of debt securities within 90 days of a default unless such default has been cured or waived. However, the trustee may withhold notice if specified persons of such trustee consider such withholding to be in the interest of the holders of debt securities. The trustee may not withhold notice of a default in the payment of principal, any premium or interest on any debt security of such series or in the payment of any sinking fund installment in respect of any debt security of such series.

The indentures provide that holders of debt securities of any series may not institute any proceedings, judicial or otherwise, with respect to such indenture or for any remedy under the indenture, unless the trustee fails to act for a period of 60 days after the trustee has received a written request to institute proceedings in respect of an event of default from the holders of 25% or more in principal amount of the outstanding debt securities of such series, as well as an offer of indemnity reasonably satisfactory to the trustee. However, this provision will not prevent any holder of debt securities from instituting suit for the enforcement of payment of the principal of, and any premium or make-whole amount, and interest on, such debt securities at the respective due dates thereof.

The indentures provide that, subject to provisions in each indenture relating to its duties in the case of a default, a trustee has no obligation to exercise any of its rights or powers at the request or direction of any holders of any series of debt securities then outstanding under the indenture, unless the holders have offered to the trustee reasonable security or indemnity. The holders of at least a majority in principal amount of the outstanding debt securities of any series or of all debt securities then outstanding under an indenture shall have the right to direct the time, method and place of conducting any proceeding for any remedy available to the applicable trustee, or of exercising any trust or power conferred upon such trustee. However, a trustee may refuse to follow any direction which:

- is in conflict with any law or the applicable indenture;
- may involve the trustee in personal liability; or
- may be unduly prejudicial to the holders of debt securities of the series not joining the proceeding.

Within 120 days after the close of each fiscal year, we will be required to deliver to each trustee a certificate, signed by one of our several specified officers, stating whether or not that officer has knowledge

of any default under the applicable indenture. If the officer has knowledge of any default, the notice must specify the nature and status of the default.

Modification of the Indentures

The indentures provide that modifications and amendments may be made only with the consent of the affected holders of a majority in principal amount of all outstanding debt securities issued under that indenture. However, no such modification or amendment may, without the consent of the holders of the debt securities affected by the modification or amendment:

- change the stated maturity of the principal of, or any premium or make-whole amount on, or any installment of principal of or interest on, any such debt security;
- reduce the principal amount of, the rate or amount of interest on, or any premium or make-whole amount payable on redemption of, any such debt security;
- reduce the amount of principal of an original issue discount security that would be due and payable upon declaration of acceleration of the maturity thereof or would be provable in bankruptcy, or adversely affect any right of repayment of the holder of any such debt security;
- change the place of payment or the coin or currency for payment of principal of, or any premium or make-whole amount, or interest on, any such debt security;
- impair the right to institute suit for the enforcement of any payment on or with respect to any such debt security;
- reduce the percentage in principal amount of any outstanding debt securities necessary to modify or amend the applicable indenture with respect to such debt securities, to waive compliance with particular provisions thereof or defaults and consequences thereunder or to reduce the quorum or voting requirements set forth in the applicable indenture; and
- modify any of the foregoing provisions or any of the provisions relating to the waiver of particular past defaults or covenants, except to increase the required percentage to effect such action or to provide that some of the other provisions may not be modified or waived without the consent of the holder of such debt security.

The holders of a majority in aggregate principal amount of the outstanding debt securities of each series may, on behalf of all holders of debt securities of that series, waive, insofar as that series is concerned, our compliance with material restrictive covenants of the applicable indenture.

We and our respective trustee may make modifications and amendments of an indenture without the consent of any holder of debt securities for any of the following purposes:

- to evidence the succession of another person to us as obligor under such indenture;
- to add to our covenants for the benefit of the holders of all or any series of debt securities or to surrender any right or power conferred upon us in such indenture;
- to add events of default for the benefit of the holders of all or any series of debt securities;
- to add or change any provisions of an indenture (i) to change or eliminate restrictions on the payment of principal of, or premium or make-whole amount, or interest on, debt securities in bearer form, or (ii) to permit or facilitate the issuance of debt securities in uncertificated form, provided that such action shall not adversely affect the interests of the holders of the debt securities of any series in any material respect;
- to change or eliminate any provisions of an indenture, provided that any such change or elimination shall become effective only when there are no debt securities outstanding of any series created prior thereto which are entitled to the benefit of such provision;
- to secure the debt securities;
- to establish the form or terms of debt securities of any series;

- to provide for the acceptance of appointment by a successor trustee or facilitate the administration of the trusts under an indenture by more than one trustee;
- to cure any ambiguity, defect or inconsistency in an indenture, provided that such action shall not adversely affect the interests of holders of debt securities of any series issued under such indenture; and
- to supplement any of the provisions of an indenture to the extent necessary to permit or facilitate defeasance and discharge of any series of such debt securities, provided that such action shall not adversely affect the interests of the holders of the outstanding debt securities of any series.

Voting

The indentures provide that in determining whether the holders of the requisite principal amount of outstanding debt securities of a series have given any request, demand, authorization, direction, notice, consent or waiver under the indentures or whether a quorum is present at a meeting of holders of debt securities:

- the principal amount of an original issue discount security that shall be deemed to be outstanding shall be the amount of the principal thereof that would be due and payable as of the date of such determination upon declaration of acceleration of the maturity thereof;
- the principal amount of any debt security denominated in a foreign currency that shall be deemed outstanding shall be the United States dollar equivalent, determined on the issue date for such debt security, of the principal amount or, in the case of an original issue discount security, the United States dollar equivalent on the issue date of such debt security of the amount determined as provided in the preceding bullet point;
- the principal amount of an indexed security that shall be deemed outstanding shall be the principal face amount of such indexed security at original issuance, unless otherwise provided for such indexed security under such indenture; and
- debt securities owned by us or any other obligor upon the debt securities or by any affiliate of ours or of such other obligor shall be disregarded.

The indentures contain provisions for convening meetings of the holders of debt securities of a series. A meeting will be permitted to be called at any time by the applicable trustee, and also, upon request, by us or the holders of at least 25% in principal amount of the outstanding debt securities of such series, in any such case upon notice given as provided in such indenture. Except for any consent that must be given by the holder of each debt security affected by the modifications and amendments of an indenture described above, any resolution presented at a meeting or adjourned meeting duly reconvened at which a quorum is present may be adopted by the affirmative vote of the holders of a majority of the aggregate principal amount of the outstanding debt securities of that series represented at such meeting.

Notwithstanding the preceding paragraph, except as referred to above, any resolution relating to a request, demand, authorization, direction, notice, consent, waiver or other action that may be made, given or taken by the holders of a specified percentage, which is less than a majority of the aggregate principal amount of the outstanding debt securities of a series, may be adopted at a meeting or adjourned meeting duly reconvened at which a quorum is present by the affirmative vote of such specified percentage.

Any resolution passed or decision taken at any properly held meeting of holders of debt securities of any series will be binding on all holders of such series. The quorum at any meeting called to adopt a resolution, and at any reconvened meeting, will be persons holding or representing a majority in principal amount of the outstanding debt securities of a series. However, if any action is to be taken relating to a consent or waiver which may be given by the holders of at least a specified percentage in principal amount of the outstanding debt securities of a series, the persons holding such percentage will constitute a quorum.

Notwithstanding the foregoing provisions, the indentures provide that if any action is to be taken at a meeting with respect to any request, demand, authorization, direction, notice, consent, waiver or other action that such indenture expressly provides may be made, given or taken by the holders of a specified percentage

in principal amount of all outstanding debt securities affected by such action, or of the holders of such series and one or more additional series:

- there shall be no minimum quorum requirement for such meeting; and
- the principal amount of the outstanding debt securities of such series that vote in favor of such request, demand, authorization, direction, notice, consent, waiver or other action shall be taken account in determining whether such request, demand, authorization, direction, notice, consent, waiver or other action has been made, given or taken under such indenture.

Subordination

Unless otherwise provided in the applicable prospectus supplement, subordinated debt securities will be subject to the following subordination provisions.

Upon any distribution to our creditors in a liquidation, dissolution or reorganization, the payment of the principal of and interest on any subordinated debt securities will be subordinated to the extent provided in the applicable indenture in right of payment to the prior payment in full of all senior debt. However, our obligation to make payments of the principal of and interest on such subordinated debt securities otherwise will not be affected. No payment of principal or interest will be permitted to be made on subordinated debt securities at any time if a default on senior debt exists that permits the holders of such senior debt to accelerate its maturity and the default is the subject of judicial proceedings or we receive notice of the default. After all senior debt is paid in full and until the subordinated debt securities are paid in full, holders of subordinated debt securities will be subrogated to the rights of holders of senior debt to the extent that distributions otherwise payable to holders of subordinated debt securities have been applied to the payment of senior debt. The subordinated indenture will not restrict the amount of senior debt or other indebtedness of ours. As a result of these subordination provisions, in the event of a distribution of assets upon insolvency, holders of subordinated debt securities may recover less, ratably, than our general creditors.

The term “senior debt” will be defined in the applicable indenture as the principal of and interest on, or substantially similar payments to be made by us in respect of, other outstanding indebtedness, whether outstanding at the date of execution of the applicable indenture or subsequently incurred, created or assumed. The prospectus supplement may include a description of additional terms implementing the subordination feature.

No restrictions will be included in any indenture relating to subordinated debt securities upon the creation of additional senior debt.

If this prospectus is being delivered in connection with the offering of a series of subordinated debt securities, the accompanying prospectus supplement or the information incorporated in this prospectus by reference will set forth the approximate amount of senior debt outstanding as of the end of our most recent fiscal quarter.

Discharge, Defeasance and Covenant Defeasance

Unless otherwise indicated in the applicable prospectus supplement, the indentures allow us to discharge our obligations to holders of any series of debt securities issued under any indenture when:

- either (i) all securities of such series have already been delivered to the applicable trustee for cancellation; or (ii) all securities of such series have not already been delivered to the applicable trustee for cancellation but (a) have become due and payable, (b) will become due and payable within one year, or (c) if redeemable at our option, are to be redeemed within one year, and we have irrevocably deposited with the applicable trustee, in trust, funds in such currency or currencies, currency unit or units or composite currency or currencies in which such debt securities are payable, an amount sufficient to pay the entire indebtedness on such debt securities in respect of principal and any premium or make-whole amount, and interest to the date of such deposit if such debt securities have become due and payable or, if they have not, to the stated maturity or redemption date;
- we have paid or caused to be paid all other sums payable; and

- an officers' certificate and an opinion of counsel stating the conditions to discharging the debt securities have been satisfied has been delivered to the trustee.

Unless otherwise indicated in the applicable prospectus supplement, the indentures provide that, upon our irrevocable deposit with the applicable trustee, in trust, of an amount, in such currency or currencies, currency unit or units or composite currency or currencies in which such debt securities are payable at stated maturity, or government obligations, or both, applicable to such debt securities, which through the scheduled payment of principal and interest in accordance with their terms will provide money in an amount sufficient to pay the principal of, and any premium or make-whole amount, and interest on, such debt securities, and any mandatory sinking fund or analogous payments thereon, on the scheduled due dates therefor, the issuing company may elect either:

- to defease and be discharged from any and all obligations with respect to such debt securities; or
- to be released from its obligations with respect to such debt securities under the applicable indenture or, if provided in the applicable prospectus supplement, its obligations with respect to any other covenant, and any omission to comply with such obligations shall not constitute an event of default with respect to such debt securities.

Notwithstanding the above, we may not elect to defease and be discharged from the obligation to pay any additional amounts upon the occurrence of particular events of tax, assessment or governmental charge with respect to payments on such debt securities and the obligations to register the transfer or exchange of such debt securities, to replace temporary or mutilated, destroyed, lost or stolen debt securities, to maintain an office or agency in respect of such debt securities, or to hold monies for payment in trust.

The indentures only permit us to establish the trust described in the paragraph above if, among other things, we have delivered to the applicable trustee an opinion of counsel to the effect that the holders of such debt securities will not recognize income, gain or loss for United States federal income tax purposes as a result of such defeasance or covenant defeasance and will be subject to United States federal income tax on the same amounts, in the same manner and at the same times as would have been the case if such defeasance or covenant defeasance had not occurred. Such opinion of counsel, in the case of defeasance, will be required to refer to and be based upon a ruling received from or published by the Internal Revenue Service or a change in applicable United States federal income tax law occurring after the date of the indenture. In the event of such defeasance, the holders of such debt securities would be able to look only to such trust fund for payment of principal, any premium or make-whole amount, and interest.

When we use the term "government obligations," we mean securities that are:

- direct obligations of the United States or the government that issued the foreign currency in which the debt securities of a particular series are payable, for the payment of which its full faith and credit is pledged; or
- obligations of a person controlled or supervised by and acting as an agency or instrumentality of the United States or other government that issued the foreign currency in which the debt securities of such series are payable, the payment of which is unconditionally guaranteed as a full faith and credit obligation by the United States or such other government, which are not callable or redeemable at the option of the issuer thereof and shall also include a depository receipt issued by a bank or trust company as custodian with respect to any such government obligation or a specific payment of interest on or principal of any such government obligation held by such custodian for the account of the holder of a depository receipt. However, except as required by law, such custodian is not authorized to make any deduction from the amount payable to the holder of such depository receipt from any amount received by the custodian in respect of the government obligation or the specific payment of interest on or principal of the government obligation evidenced by such depository receipt.

Unless otherwise provided in the applicable prospectus supplement, if after we have deposited funds and/or government obligations to effect defeasance or covenant defeasance with respect to debt securities of any series, (i) the holder of a debt security of such series is entitled to, and does, elect under the terms of the applicable indenture or the terms of such debt security to receive payment in a currency, currency unit or composite currency other than that in which such deposit has been made in respect of such debt security,

or (ii) a conversion event occurs in respect of the currency, currency unit or composite currency in which such deposit has been made, the indebtedness represented by such debt security will be deemed to have been, and will be, fully discharged and satisfied through the payment of the principal of, and premium or make-whole amount, and interest on, such debt security as they become due out of the proceeds yielded by converting the amount so deposited in respect of such debt security into the currency, currency unit or composite currency in which such debt security becomes payable as a result of such election or such cessation of usage based on the applicable market exchange rate.

When we use the term "conversion event," we mean the cessation of use of:

- a currency, currency unit or composite currency both by the government of the country that issued such currency and for the settlement of transactions by a central bank or other public institutions of or within the international banking community;
- the European Currency Unit both within the European Monetary System and for the settlement of transactions by public institutions of or within the European Communities; or
- any currency unit or composite currency other than the European Currency Unit for the purposes for which it was established.

Unless otherwise provided in the applicable prospectus supplement, all payments of principal of, and any premium or make-whole amount, and interest on, any debt security that is payable in a foreign currency that ceases to be used by its government of issuance shall be made in United States dollars.

In the event that (i) we effect covenant defeasance with respect to any debt securities and (ii) those debt securities are declared due and payable because of the occurrence of any event of default, the amount in the currency, currency unit or composite currency in which such debt securities are payable, and government obligations on deposit with the applicable trustee, will be sufficient to pay amounts due on such debt securities at the time of their stated maturity but may not be sufficient to pay amounts due on such debt securities at the time of the acceleration resulting from such event of default. However, the issuing company would remain liable to make payments of any amounts due at the time of acceleration.

The applicable prospectus supplement may further describe the provisions, if any, permitting such defeasance or covenant defeasance, including any modifications to the provisions described above, with respect to the debt securities of or within a particular series.

Conversion Rights

The terms and conditions, if any, upon which the debt securities are convertible into common stock or other securities of ours will be set forth in the applicable prospectus supplement. The terms will include whether the debt securities are convertible into shares of common stock or other securities of ours, the conversion price, or manner of calculation thereof, the conversion period, provisions as to whether conversion will be at the issuing company's option or the option of the holders, the events requiring an adjustment of the conversion price and provisions affecting conversion in the event of the redemption of the debt securities and any restrictions on conversion.

Global Securities

The debt securities of a series may be issued in whole or in part in the form of one or more global securities that will be deposited with, or on behalf of, a depository identified in the applicable prospectus supplement relating to such series. Global securities, if any, issued in the United States are expected to be deposited with The Depository Trust Company, or DTC, as depository. We may issue global securities in either registered or bearer form and in either temporary or permanent form. We will describe the specific terms of the depository arrangement with respect to a series of debt securities in the applicable prospectus supplement relating to such series. We expect that unless the applicable prospectus supplement provides otherwise, the following provisions will apply to depository arrangements.

Once a global security is issued, the depository for such global security or its nominee will credit on its book-entry registration and transfer system the respective principal amounts of the individual debt securities represented by such global security to the accounts of participants that have accounts with such depository.

Such accounts shall be designated by the underwriters, dealers or agents with respect to such debt securities or by us if we offer such debt securities directly. Ownership of beneficial interests in such global security will be limited to participants with the depository or persons that may hold interests through those participants.

We expect that, under procedures established by DTC, ownership of beneficial interests in any global security for which DTC is the depository will be shown on, and the transfer of that ownership will be effected only through, records maintained by DTC or its nominee, with respect to beneficial interests of participants with the depository, and records of participants, with respect to beneficial interests of persons who hold through participants with the depository. Neither we nor the trustee will have any responsibility or liability for any aspect of the records of DTC or for maintaining, supervising or reviewing any records of DTC or any of its participants relating to beneficial ownership interests in the debt securities. The laws of some states require that certain purchasers of securities take physical delivery of such securities in definitive form. Such limits and laws may impair the ability to own, pledge or transfer beneficial interest in a global security.

So long as the depository for a global security or its nominee is the registered owner of such global security, such depository or such nominee, as the case may be, will be considered the sole owner or holder of the debt securities represented by the global security for all purposes under the applicable indenture. Except as described below or in the applicable prospectus supplement, owners of beneficial interest in a global security will not be entitled to have any of the individual debt securities represented by such global security registered in their names, will not receive or be entitled to receive physical delivery of any such debt securities in definitive form and will not be considered the owners or holders thereof under the applicable indenture. Beneficial owners of debt securities evidenced by a global security will not be considered the owners or holders thereof under the applicable indenture for any purpose, including with respect to the giving of any direction, instructions or approvals to the trustee under the indenture. Accordingly, each person owning a beneficial interest in a global security with respect to which DTC is the depository must rely on the procedures of DTC and, if such person is not a participant with the depository, on the procedures of the participant through which such person owns its interests, to exercise any rights of a holder under the applicable indenture. We understand that, under existing industry practice, if DTC requests any action of holders or if an owner of a beneficial interest in a global security desires to give or take any action which a holder is entitled to give or take under the applicable indenture, DTC would authorize the participants holding the relevant beneficial interest to give or take such action, and such participants would authorize beneficial owners through such participants to give or take such actions or would otherwise act upon the instructions of beneficial owners holding through them.

Payments of principal of, and any premium or make-whole amount, and interest on, individual debt securities represented by a global security registered in the name of a depository or its nominee will be made to or at the direction of the depository or its nominee, as the case may be, as the registered owner of the global security under the applicable indenture. Under the terms of the applicable indenture, we and the trustee may treat the persons in whose name debt securities, including a global security, are registered as the owners thereof for the purpose of receiving such payments. Consequently, neither we nor the trustee have or will have any responsibility or liability for the payment of such amounts to beneficial owners of debt securities including principal, any premium or make-whole amount, or interest. We believe, however, that it is currently the policy of DTC to immediately credit the accounts of relevant participants with such payments, in amounts proportionate to their respective holdings of beneficial interests in the relevant global security as shown on the records of DTC or its nominee. We also expect that payments by participants to owners of beneficial interests in such global security held through such participants will be governed by standing instructions and customary practices, as is the case with securities held for the account of customers in bearer form or registered in street name, and will be the responsibility of such participants. Redemption notices with respect to any debt securities represented by a global security will be sent to the depository or its nominee. If less than all of the debt securities of any series are to be redeemed, we expect the depository to determine the amount of the interest of each participant in such debt securities to be redeemed to be determined by lot. Neither we, the trustee, any paying agent nor the security registrar for such debt securities will have any responsibility or liability for any aspect of the records relating to or payments made on account of beneficial ownership interests in the global security for such debt securities or for maintaining any records with respect thereto.

Neither we nor the trustee will be liable for any delay by the holders of a global security or the depository in identifying the beneficial owners of debt securities, and we and the trustee may conclusively rely on, and will be protected in relying on, instructions from the holder of a global security or the depository for all purposes. The rules applicable to DTC and its participants are on file with the SEC.

If a depository for any debt securities is at any time unwilling, unable or ineligible to continue as depository and we do not appoint a successor depository within 90 days, we will issue individual debt securities in exchange for the global security representing such debt securities. In addition, we may at any time and at our sole discretion, subject to any limitations described in the applicable prospectus supplement relating to such debt securities, determine not to have any of such debt securities represented by one or more global securities and in such event will issue individual debt securities in exchange for the global security or securities representing such debt securities. Individual debt securities so issued will be issued in denominations of $1,000 and integral multiples of $1,000.

The debt securities of a series may also be issued in whole or in part in the form of one or more bearer global securities that will be deposited with a depository, or with a nominee for such depository, identified in the applicable prospectus supplement. Any such bearer global securities may be issued in temporary or permanent form. The specific terms and procedures, including the specific terms of the depositary arrangement, with respect to any portion of a series of debt securities to be represented by one or more bearer global securities will be described in the applicable prospectus supplement.

No Recourse

There is no recourse under any obligation, covenant or agreement in the applicable indenture or with respect to any security against any of our or our successor's past, present or future shareholders, employees, officers or directors.

DESCRIPTION OF WARRANTS

The following description, together with the additional information we may include in any applicable prospectus supplements, summarizes the material terms and provisions of the warrants that we may offer under this prospectus and the related warrant agreements and warrant certificates. While the terms summarized below will apply generally to any warrants that we may offer, we will describe the particular terms of any series of warrants in more detail in the applicable prospectus supplement. If we indicate in the prospectus supplement, the terms of any warrants offered under that prospectus supplement may differ from the terms described below. Specific warrant agreements will contain additional important terms and provisions and will be incorporated by reference as an exhibit to the registration statement, which includes this prospectus.

General

We may issue warrants for the purchase of common stock, preferred stock and/or debt securities in one or more series. We may issue warrants independently or together with common stock, preferred stock and/or debt securities, and the warrants may be attached to or separate from these securities.

We will evidence each series of warrants by warrant certificates that we will issue under a separate warrant agreement. We will enter into the warrant agreement with a warrant agent. We will indicate the name and address of the warrant agent and any other depositaries, execution or paying agents, transfer agents, registrars or other agents in the applicable prospectus supplement relating to a particular series of warrants.

We will describe in the applicable prospectus supplement the terms of the series of warrants, including:

- the offering price and aggregate number of warrants offered;
- the currency for which the warrants may be purchased;
- if applicable, the designation and terms of the securities with which the warrants are issued and the number of warrants issued with each such security or each principal amount of such security;
- if applicable, the date on and after which the warrants and the related securities will be separately transferable;
- in the case of warrants to purchase debt securities, the principal amount of debt securities purchasable upon exercise of one warrant and the price at, and currency in which, this principal amount of debt securities may be purchased upon such exercise;
- in the case of warrants to purchase common stock or preferred stock, the number of shares of common stock or preferred stock, as the case may be, purchasable upon the exercise of one warrant and the price at which these shares may be purchased upon such exercise;
- the effect of any merger, consolidation, sale or other disposition of our business on the warrant agreement and the warrants;
- the terms of any rights to redeem or call the warrants;
- any provisions for changes to or adjustments in the exercise price or number of securities issuable upon exercise of the warrants;
- the periods during which, and places at which, the warrants are exercisable;
- if applicable, the minimum or maximum amount of the warrants that may be exercised at any one time;
- the manner of exercise, including information with respect to book-entry procedures, if any;
- the antidilution provisions of, and other provisions for changes to or adjustment in the exercise price of, the warrants, if any;
- any redemption or call provisions;
- the dates on which the right to exercise the warrants will commence and expire;

- the manner in which the warrant agreement and warrants may be modified;
- federal income tax consequences of holding or exercising the warrants;
- the terms of the securities issuable upon exercise of the warrants; and
- any other specific terms, preferences, rights or limitations of or restrictions on the warrants.

Specific warrant agreements will contain additional important terms and provisions and will be incorporated by reference as an exhibit to the registration statement of which this prospectus forms a part.

Governing Law

The warrant agreement and the warrants will be governed by and construed in accordance with the laws of the State of New York.

DESCRIPTION OF UNITS

We may issue units comprised of shares of common stock, shares of preferred stock, debt securities and warrants in any combination. We may issue units in such amounts and in as many distinct series as we wish. This section outlines certain provisions of the units that we may issue. If we issue units, they will be issued under one or more unit agreements to be entered into between us and a bank or other financial institution, as unit agent. The information described in this section may not be complete in all respects and is qualified entirely by reference to the unit agreement with respect to the units of any particular series. The specific terms of any series of units offered will be described in the applicable prospectus supplement. If so described in a particular supplement, the specific terms of any series of units may differ from the general description of terms presented below. We urge you to read any prospectus supplement related to any series of units we may offer, as well as the complete unit agreement and unit certificate that contain the terms of the units. If we issue units, forms of unit agreements and unit certificates relating to such units will be incorporated by reference as exhibits to the registration statement, which includes this prospectus.

Each unit that we may issue will be issued so that the holder of the unit is also the holder of each security included in the unit. Thus, the holder of a unit will have the rights and obligations of a holder of each included security. The unit agreement under which a unit is issued may provide that the securities included in the unit may not be held or transferred separately, at any time or at any time before a specified date. The applicable prospectus supplement may describe:

- the designation and terms of the units and of the securities comprising the units, including whether and under what circumstances those securities may be held or transferred separately;
- any provisions of the governing unit agreement;
- the price or prices at which such units will be issued;
- the applicable United States federal income tax considerations relating to the units;
- any provisions for the issuance, payment, settlement, transfer or exchange of the units or of the securities comprising the units; and
- any other terms of the units and of the securities comprising the units.

The provisions described in this section, as well as those described under “Description of Capital Stock,” “Description of Debt Securities” and “Description of Warrants” will apply to the securities included in each unit, to the extent relevant and as may be updated in any prospectus supplements.

Issuance in Series

We may issue units in such amounts and in as many distinct series as we wish. This section summarizes terms of the units that apply generally to all series. Most of the financial and other specific terms of your series will be described in the applicable prospectus supplement.

Unit Agreements

We will issue the units under one or more unit agreements to be entered into between us and a bank or other financial institution, as unit agent. We may add, replace or terminate unit agents from time to time. We will identify the unit agreement under which each series of units will be issued and the unit agent under that agreement in the applicable prospectus supplement.

The following provisions will generally apply to all unit agreements unless otherwise stated in the applicable prospectus supplement:

Modification without Consent

We and the applicable unit agent may amend any unit or unit agreement without the consent of any holder:

- to cure any ambiguity, including modifying any provisions of the governing unit agreement that differ from those described below;

- to correct or supplement any defective or inconsistent provision; or
- to make any other change that we believe is necessary or desirable and will not adversely affect the interests of the affected holders in any material respect.

We do not need any approval to make changes that affect only units to be issued after the changes take effect. We may also make changes that do not adversely affect a particular unit in any material respect, even if they adversely affect other units in a material respect. In those cases, we do not need to obtain the approval of the holder of the unaffected unit; we need only obtain any required approvals from the holders of the affected units.

Modification with Consent

We may not amend any particular unit or a unit agreement with respect to any particular unit unless we obtain the consent of the holder of that unit, if the amendment would:

- impair any right of the holder to exercise or enforce any right under a security included in the unit if the terms of that security require the consent of the holder to any changes that would impair the exercise or enforcement of that right; or
- reduce the percentage of outstanding units or any series or class the consent of whose holders is required to amend that series or class, or the applicable unit agreement with respect to that series or class, as described below.

Any other change to a particular unit agreement and the units issued under that agreement would require the following approval:

- If the change affects only the units of a particular series issued under that agreement, the change must be approved by the holders of a majority of the outstanding units of that series; or
- If the change affects the units of more than one series issued under that agreement, it must be approved by the holders of a majority of all outstanding units of all series affected by the change, with the units of all the affected series voting together as one class for this purpose.

These provisions regarding changes with majority approval also apply to changes affecting any securities issued under a unit agreement, as the governing document.

In each case, the required approval must be given by written consent.

Unit Agreements Will Not Be Qualified under Trust Indenture Act

No unit agreement will be qualified as an indenture, and no unit agent will be required to qualify as a trustee, under the Trust Indenture Act. Therefore, holders of units issued under unit agreements will not have the protections of the Trust Indenture Act with respect to their units.

Mergers and Similar Transactions Permitted; No Restrictive Covenants or Events of Default

The unit agreements will not restrict our ability to merge or consolidate with, or sell our assets to, another corporation or other entity or to engage in any other transactions. If at any time we merge or consolidate with, or sell our assets substantially as an entirety to, another corporation or other entity, the successor entity will succeed to and assume our obligations under the unit agreements. We will then be relieved of any further obligation under these agreements.

The unit agreements will not include any restrictions on our ability to put liens on our assets, nor will they restrict our ability to sell our assets. The unit agreements also will not provide for any events of default or remedies upon the occurrence of any events of default.

Governing Law

The unit agreements and the units will be governed by and construed in accordance with the laws of the State of Delaware.

Form, Exchange and Transfer

Unless the accompanying prospectus supplement states otherwise, we will issue each unit in global — i.e., book-entry — form only. Units in book-entry form will be represented by a global security registered in the name of a depositary, which will be the holder of all the units represented by the global security. Those who own beneficial interests in a unit will do so through participants in the depositary's system, and the rights of these indirect owners will be governed solely by the applicable procedures of the depositary and its participants. We will describe book-entry securities, and other terms regarding the issuance and registration of the units in the applicable prospectus supplement.

Unless the accompanying prospectus supplement states otherwise, each unit and all securities comprising the unit will be issued in the same form.

If we issue any units in registered, non-global form, the following will apply to them.

The units will be issued in the denominations stated in the applicable prospectus supplement. Holders may exchange their units for units of smaller denominations or combined into fewer units of larger denominations, as long as the total amount is not changed.

- Holders may exchange or transfer their units at the office of the unit agent. Holders may also replace lost, stolen, destroyed or mutilated units at that office. We may appoint another entity to perform these functions or perform them ourselves.
- Holders will not be required to pay a service charge to transfer or exchange their units, but they may be required to pay for any tax or other governmental charge associated with the transfer or exchange. The transfer or exchange, and any replacement, will be made only if our transfer agent is satisfied with the holder's proof of legal ownership. The transfer agent may also require an indemnity before replacing any units.
- If we have the right to redeem, accelerate or settle any units before their maturity, and we exercise our right as to less than all those units or other securities, we may block the exchange or transfer of those units during the period beginning 15 days before the day we mail the notice of exercise and ending on the day of that mailing, in order to freeze the list of holders to prepare the mailing. We may also refuse to register transfers of or exchange any unit selected for early settlement, except that we will continue to permit transfers and exchanges of the unsettled portion of any unit being partially settled. We may also block the transfer or exchange of any unit in this manner if the unit includes securities that are or may be selected for early settlement.

Only the depositary will be entitled to transfer or exchange a unit in global form, since it will be the sole holder of the unit.

Payments and Notices

In making payments and giving notices with respect to our units, we will follow the procedures as described in the applicable prospectus supplement.

PLAN OF DISTRIBUTION

We may sell securities:

- through underwriters;
- through dealers;
- through agents;
- directly to purchasers; or
- through a combination of any of these methods or any other method permitted by law.

In addition, we may issue the securities as a dividend or distribution or in a subscription rights offering to our existing security holders.

We may directly solicit offers to purchase securities, or agents may be designated to solicit such offers. In the prospectus supplement relating to such offering, we will name any agent that could be viewed as an underwriter under the Securities Act and describe any commissions that we must pay to any such agent. Any such agent will be acting on a best efforts basis for the period of its appointment or, if indicated in the applicable prospectus supplement, on a firm commitment basis. This prospectus may be used in connection with any offering of our securities through any of these methods or other methods described in the applicable prospectus supplement.

The distribution of the securities may be effected from time to time in one or more transactions:

- at a fixed price, or prices, which may be changed from time to time;
- at market prices prevailing at the time of sale;
- at prices related to such prevailing market prices; or
- at negotiated prices.

Each prospectus supplement will describe the method of distribution of the securities and any applicable restrictions.

The prospectus supplement with respect to the securities of a particular series will describe the terms of the offering of the securities, including the following:

- the name of the agent or any underwriters;
- the public offering or purchase price;
- any discounts and commissions to be allowed or paid to the agent or underwriters;
- all other items constituting underwriting compensation;
- any discounts and commissions to be allowed or paid to dealers; and
- any exchanges on which the securities will be listed.

If any underwriters or agents are used in the sale of the securities in respect of which this prospectus is delivered, we will enter into an underwriting agreement, sales agreement or other agreement with them at the time of sale to them, and we will set forth in the prospectus supplement relating to such offering the names of the underwriters or agents and the terms of the related agreement with them.

In connection with the offering of securities, we may grant to the underwriters an option to purchase additional securities with an additional underwriting commission, as may be set forth in the accompanying prospectus supplement. If we grant any such option, the terms of such option will be set forth in the prospectus supplement for such securities.

If a dealer is used in the sale of the securities in respect of which the prospectus is delivered, we will sell such securities to the dealer, as principal. The dealer, who may be deemed to be an “underwriter” as that term

is defined in the Securities Act, may then resell such securities to the public at varying prices to be determined by such dealer at the time of resale.

If we offer securities in a subscription rights offering to our existing security holders, we may enter into a standby underwriting agreement with dealers, acting as standby underwriters. We may pay the standby underwriters a commitment fee for the securities they commit to purchase on a standby basis. If we do not enter into a standby underwriting arrangement, we may retain a dealer-manager to manage a subscription rights offering for us.

Agents, underwriters, dealers and other persons may be entitled under agreements which they may enter into with us to indemnification by us against certain civil liabilities, including liabilities under the Securities Act, and may be customers of, engage in transactions with or perform services for us in the ordinary course of business.

If so indicated in the applicable prospectus supplement, we will authorize underwriters or other persons acting as our agents to solicit offers by certain institutions to purchase securities from us pursuant to delayed delivery contracts providing for payment and delivery on the date stated in the prospectus supplement. Each contract will be for an amount not less than, and the aggregate amount of securities sold pursuant to such contracts shall not be less nor more than, the respective amounts stated in the prospectus supplement. Institutions with whom the contracts, when authorized, may be made include commercial and savings banks, insurance companies, pension funds, investment companies, educational and charitable institutions and other institutions, but shall in all cases be subject to our approval. Delayed delivery contracts will not be subject to any conditions except that:

- the purchase by an institution of the securities covered under that contract shall not at the time of delivery be prohibited under the laws of the jurisdiction to which that institution is subject; and
- if the securities are also being sold to underwriters acting as principals for their own account, the underwriters shall have purchased such securities not sold for delayed delivery. The underwriters and other persons acting as our agents will not have any responsibility in respect of the validity or performance of delayed delivery contracts.

Offered securities may also be offered and sold, if so indicated in the prospectus supplement, in connection with a remarketing upon their purchase, in accordance with a redemption or repayment pursuant to their terms, or otherwise, by one or more remarketing firms, acting as principals for their own accounts or as agents for us. Any remarketing firm will be identified and the terms of its agreement, if any, with us and its compensation will be described in the applicable prospectus supplement. Remarketing firms may be deemed to be underwriters in connection with their remarketing of offered securities.

Certain agents, underwriters and dealers, and their associates and affiliates, may be customers of, have borrowing relationships with, engage in other transactions with, or perform services, including investment banking services, for us or one or more of our respective affiliates in the ordinary course of business.

In order to facilitate the offering of the securities, any underwriters may engage in transactions that stabilize, maintain or otherwise affect the price of the securities or any other securities the prices of which may be used to determine payments on such securities. Specifically, any underwriters may overallot in connection with the offering, creating a short position for their own accounts. In addition, to cover overallotments or to stabilize the price of the securities or of any such other securities, the underwriters may bid for, and purchase, the securities or any such other securities in the open market. Finally, in any offering of the securities through a syndicate of underwriters, the underwriting syndicate may reclaim selling concessions allowed to an underwriter or a dealer for distributing the securities in the offering if the syndicate repurchases previously distributed securities in transactions to cover syndicate short positions, in stabilization transactions or otherwise. Any of these activities may stabilize or maintain the market price of the securities above independent market levels. Any such underwriters are not required to engage in these activities and may end any of these activities at any time.

We may engage in at the market offerings into an existing trading market in accordance with Rule 415(a)(4) under the Securities Act. In addition, we may enter into derivative transactions with third parties, or sell securities not covered by this prospectus to third parties in privately negotiated transactions.

If the applicable prospectus supplement so indicates, in connection with those derivatives, the third parties may sell securities covered by this prospectus and the applicable prospectus supplement, including in short sale transactions. If so, the third party may use securities pledged by us or borrowed from us or others to settle those sales or to close out any related open borrowings of stock, and may use securities received from us in settlement of those derivatives to close out any related open borrowings of stock. The third party in such sale transactions will be an underwriter and, if not identified in this prospectus, will be named in the applicable prospectus supplement (or a post-effective amendment). In addition, we may otherwise loan or pledge securities to a financial institution or other third party that in turn may sell the securities short using this prospectus and an applicable prospectus supplement. Such financial institution or other third party may transfer its economic short position to investors in our securities or in connection with a concurrent offering of other securities.

Under Rule 15c6-1 of the Exchange Act, trades in the secondary market generally are required to settle in two business days, unless the parties to any such trade expressly agree otherwise. The applicable prospectus supplement may provide that the original issue date for your securities may be more than two scheduled business days after the trade date for your securities. Accordingly, in such a case, if you wish to trade securities on any date prior to the second business day before the original issue date for your securities, you will be required, by virtue of the fact that your securities initially are expected to settle in more than two scheduled business days after the trade date for your securities, to make alternative settlement arrangements to prevent a failed settlement.

The securities may be new issues of securities and may have no established trading market. The securities may or may not be listed on a national securities exchange. We can make no assurance as to the liquidity of or the existence of trading markets for any of the securities.

The specific terms of any lock-up provisions in respect of any given offering will be described in the applicable prospectus supplement.

The underwriters, dealers and agents may engage in transactions with us, or perform services for us, in the ordinary course of business for which they receive compensation.

The anticipated date of delivery of offered securities will be set forth in the applicable prospectus supplement relating to each offer.

LEGAL MATTERS

Certain legal matters in connection with this offering will be passed upon for us by Goodwin Procter LLP, Boston, Massachusetts. Any underwriters will also be advised about the validity of the securities and other legal matters by their own counsel, which will be named in the prospectus supplement.

EXPERTS

Ernst & Young LLP, independent registered public accounting firm, has audited our consolidated financial statements included in our Annual Report on Form 10-K for the year ended December 31, 2023, as set forth in their report, which is incorporated by reference in this prospectus and elsewhere in the registration statement. Our financial statements are incorporated by reference in reliance on Ernst & Young LLP's report, given on their authority as experts in accounting and auditing.

WHERE YOU CAN FIND MORE INFORMATION

We are subject to the information requirements of the Exchange Act and, in accordance therewith, file annual, quarterly and special reports, proxy statements and other information with the SEC. These documents also may be accessed through the SEC's electronic data gathering, analysis and retrieval system, or EDGAR, via electronic means, including the SEC's home page on the Internet (*www.sec.gov*).

We have the authority to designate and issue more than one class or series of stock having various preferences, conversion and other rights, voting powers, restrictions, limitations as to dividends, qualifications, and terms and conditions of redemption. See "Description of Capital Stock." We will furnish a full statement of the relative rights and preferences of each class or series of our stock which has been so designated and any restrictions on the ownership or transfer of our stock to any shareholder upon request and without charge. Written requests for such copies should be directed to Investor Relations, Scholar Rock Holding Corporation, 301 Binney Street, 3rd Floor, Cambridge, MA 02142; telephone: (857) 259-3860. Our website is located at *www.scholarrock.com.* Information contained on our website is not incorporated by reference into this prospectus and, therefore, is not part of this prospectus or any accompanying prospectus supplement.

This prospectus is part of a registration statement that we have filed with the SEC. Certain information in the registration statement has been omitted from this prospectus in accordance with SEC rules and regulations. For more detail about us and any securities that may be offered by this prospectus, you may examine the registration statement on Form S-3 and the exhibits filed with it at the locations listed in the previous paragraph. Please be aware that statements in this prospectus referring to a contract or other document are summaries and you should refer to the exhibits that are part of the registration statement for a copy of the contract or document.

INCORPORATION BY REFERENCE

The SEC allows us to incorporate by reference the information and reports we file with it, which means that we can disclose important information to you by referring you to these documents. The information incorporated by reference is an important part of this prospectus, and information that we file later with the SEC will automatically update and supersede the information already incorporated by reference. We are incorporating by reference the documents listed below, which we have already filed with the SEC, and any future filings we make with the SEC under Sections 13(a), 13(c), 14 or 15(d) of the Exchange Act, including all filings made after the date of the filing of this registration statement and prior to the effectiveness of this registration statement, except as to any portion of any future report or document that is not deemed filed under such provisions, until we sell all of the securities:

- our Annual Report on Form 10-K for the year ended December 31, 2023, filed with the SEC on March 19, 2024;
- our Quarterly Reports on Form 10-Q for the quarters ended March 31, 2024 and June 30, 2024, filed with the SEC on May 7, 2024 and August 8, 2024;
- our Definitive Proxy Statement on Schedule 14A (other than information furnished rather than filed), filed with the SEC on April 29, 2024;
- our Current Reports on Form 8-K (other than information furnished rather than filed) filed with the SEC on January 8, 2024, February 15, 2024, May 14, 2024, May 22, 2024, June 3, 2024, June 24, 2024, June 28, 2024, August 8, 2024 and October 7, 2024; and
- the description of our common stock contained in our registration statement on Form 8-A filed with the SEC on May 21, 2018, as the description therein has been updated and superseded by the description of our common stock contained in Exhibit 4.4 to our Annual Report on Form 10-K for the fiscal year ended December 31, 2023, as filed with the SEC on March 19, 2024, including any amendments or reports filed for the purposes of updating this description.

Upon written or oral request, we will provide, without charge, to each person, including any beneficial owner, to whom a copy of this prospectus supplement is delivered, a copy of the documents incorporated by reference into this prospectus supplement but not delivered with the prospectus. You may request a copy of these filings, and any exhibits we have specifically incorporated by reference as an exhibit in this prospectus supplement, at no cost by writing us at the following address: Investor Relations, Scholar Rock Holding Corporation, 301 Binney Street, 3rd Floor, Cambridge, MA 02142. Our website is located at www.scholarrock.com. The reference to our website is intended to be an inactive textual reference and, except for the documents incorporated by reference as noted above, the information on, or accessible through, our website is not intended to be part of this prospectus supplement.

You may also access these documents, free of charge on the SEC's website at *www.sec.gov* or on our website at *www.scholarrock.com*. Information contained on our website is not incorporated by reference into this prospectus, and you should not consider any information on, or that can be accessed from, our website as part of this prospectus or any accompanying prospectus supplement.

This prospectus is part of a registration statement we filed with the SEC. We have incorporated exhibits into this registration statement. You should read the exhibits carefully for provisions that may be important to you.

You should rely only on the information incorporated by reference or provided in this prospectus or any prospectus supplement. We have not authorized anyone to provide you with different information. We are not making an offer of these securities in any state where the offer is not permitted. You should not assume that the information in this prospectus or in the documents incorporated by reference is accurate as of any date other than the date on the front of this prospectus or those documents.

Notwithstanding the foregoing, unless specifically stated to the contrary, information that we furnish (and that is not deemed "filed" with the SEC) under Items 2.02 and 7.01 of any Current Reports on Form 8-K, including the related exhibits under Item 9.01, is not incorporated by reference into this prospectus supplement or the registration statement of which this prospectus supplement is a part.



Up to $200,000,000

Common Stock

PROSPECTUS SUPPLEMENT

Jefferies

November 14, 2025

Calculation of Filing Fee Tables

S-3

Scholar Rock Holding Corp

Table 1: Newly Registered and Carry Forward Securities ☐Not Applicable

		Security Type	Security Class Title	Fee Calculation or Carry Forward Rule	Amount Registered	Proposed Maximum Offering Price Per Unit	Maximum Aggregate Offering Price	Fee Rate	Amount of Registration Fee	Carry Forward Form Type	Carry Forward File Number	Carry Forward Initial Effective Date	Filing Fee Previously Paid in Connection with Unsold Securities to be Carried Forward
Newly Registered Securities													
Fees to be Paid	1	Equity	Common Stock, par value $0.001 per share	457(o)			$ 200,000,000.00	0.0001381	$ 27,620.00				
Fees Previously Paid													
Carry Forward Securities													
Carry Forward Securities													
				Total Offering Amounts:			$ 200,000,000.00		$ 27,620.00				
				Total Fees Previously Paid:					$ 0.00				
				Total Fee Offsets:					$ 0.00				
				Net Fee Due:					$ 27,620.00				

Offering Note

1

The proposed maximum aggregate offering price is being used to calculate the registration fee pursuant to Rule 457(o) under the Securities Act of 1933, as amended.

Calculated in accordance with Rule 456(b) and Rule 457(r) of the Securities Act of 1933, as amended. This "Calculation of Registration Fee" table shall be deemed to update the "Calculation of Registration Fee" table in the registrant's registration statement on Form S-3ASR filed with the Securities and Exchange Commission on October 7, 2024 (File No. 333-282530).

Table 2: Fee Offset Claims and Sources ☑Not Applicable

		Registrant or Filer Name	Form or Filing Type	File Number	Initial Filing Date	Filing Date	Fee Offset Claimed	Security Type Associated with Fee Offset Claimed	Security Title Associated with Fee Offset Claimed	Unsold Securities Associated with Fee Offset Claimed	Unsold Aggregate Offering Amount Associated with Fee Offset Claimed	Fee Paid with Fee Offset Source
Rules 457(b) and 0-11(a)(2)												
Fee Offset Claims	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Fee Offset Sources	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Rule 457(p)												
Fee Offset Claims	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Fee Offset Sources	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

Table 3: Combined Prospectuses ☑Not Applicable

	Security Type	Security Class Title	Amount of Securities Previously Registered	Maximum Aggregate Offering Price of Securities Previously Registered	Form Type	File Number	Initial Effective Date
N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

Narrative Disclosure

The maximum aggregate offering price of the securities to which the prospectus relates is $200,000,000.00. The prospectus is a final prospectus for

the related offering.