Within the Department of Cell Biology at Albert Einstein College of Medicine, each student is required to present a research article of his or her choosing for the department journal club. As new students entering the Department, it was unclear to us (Sabrina Volpi and Sandeep Wontakal) whether there were any rules for choosing the papers we would present. Should the paper relate to work performed within the Department? Did the paper have to be published within the last year, or five years, or could we select a “classic” paper from the early 1900s? While pondering these questions, we realized we shared a great interest in reading the original “landmark” papers we had once learned about in our introductory biology courses, the papers that laid the foundation of what we know as biology today.

As we continued to discuss this idea, we became increasingly excited at the thought of reading these classic papers. We decided to solicit the graduate student body to gauge general interest in this topic. After receiving an overwhelmingly positive response from our peers, we, along with our colleague Michelle Maxson, established “Bio 101,” the first student-run journal club at Einstein. We planned for Bio 101 to meet on a monthly basis, and to invite to each session an expert faculty member who was familiar with either the work or the scientists involved in the landmark paper. In this way, the faculty members could provide us with their unique perspectives on the historical discoveries.

The first meeting was held in October 2007; we discussed one of the initial studies that generated a knockout mouse (Thomas and Capecchi, 1990). This seminal paper contributed to Mario Capecchi being awarded the 2007 Nobel Prize in Physiology or Medicine, for the “discoveries of principles for introducing specific gene modifications in mice by the use of embryonic stem cells.” We were joined by Drs. Arthur Skoultchi and Winfried Edelman, who were both intimately involved in developing these techniques and had close ties to the Nobel laureates. During this first meeting, the student participants voted on which papers they would like to discuss over the course of the academic year from a list of potential papers we generated from the fields of biochemistry/biophysics, cancer biology, cell biology, developmental biology, genetics, immunology, microbiology, molecular biology, and neuroscience. After this inaugural meeting, “Bio 101” continued to have consistent participation from the student body, and the journal club ran successfully for two academic years.

We witnessed the continued enthusiasm of the students for the subject matter and were encouraged by several of the faculty participants to convert “Bio 101” into a course. One faculty member, Dr. Scott Emmons, suggested that we pilot the course the following semester, under the auspices of his Special Topics in Molecular Genetics course. Encouraged by this positive feedback, we began to design and organize what would become the first student-run course at Einstein. Our goal was to develop a course that would enhance the educational experience of Einstein graduate students and fill a specific niche within the graduate curriculum. At that time, no course was offered in which the history of science and the evolution of scientific ideas were discussed.

We also hoped to provide students with an opportunity to gain valuable teaching experience, something not easily accessible at Einstein. Statistics show that as graduate students, scientists have little formal training in education (Markowitz and DuPre, 2007; Tanner and Allen, 2006; Gough, 2010), and that teaching skills are (mistakenly) considered of minor importance to career success (Gentile and Boehlert, 2010). New academic faculty members often describe feeling ill-prepared for teaching responsibilities and curriculum development (Tanner and Allen, 2006; Ortlieb et al., 2010). However, a National Science Foundation survey (2008) reports that 48.7% of all recipients of life-science doctorates plan to work in academia, and a second survey (2006) concludes that 39.7% of academic faculty members indicate teaching as their primary work activity, with another 19.4% reporting it as a secondary work activity. Hence, a major part of the duties of academic faculty is pedagogical in nature, and some believe that a focus on teaching experience during graduate education is important and complements research training (Harland and Planker, 2004). With these ambitious objectives in mind, we designed the course so that during the first half of each class session, a student enrolled in the course would elicit discussion on the findings of a landmark paper and place the discovery in its proper historical context. During the second half of the session, a senior student or postdoc teaching-facilitator would update the class on the advances that have taken place since the publication of the landmark paper. We implemented these ideas and piloted the course under Dr. Emmons’ Special Topics in Molecular Genetics in the Fall of 2009. At the first class session, the enrolled students voted on which papers would be discussed that semester from a list of
potential papers we had assembled. As student course leaders, once we identified the final papers (Table 1; see superscript †), we arranged for an expert faculty member to be present at each class. Before the semester began, we solicited teaching-facilitators for each of the 12 class sessions. Prior to each class, teaching-facilitators met with the student presenters to mentor them and assist with their presentations.

After receiving positive feedback from the eight enrolled students and the faculty participants, we presented our ideas to the Einstein curriculum committee in order to incorporate the course into the official graduate school curriculum. The committee unanimously approved our proposal, and thus “Pillars of Biology: Classic Problems and Modern Concepts” was born. “Pillars” commenced during the Fall semester of 2010 and consisted of nine students who discussed 12 landmark papers (Table 1; see superscript ‡). This initial course ran successfully, and continue to be offered to Einstein students in the future. We are happy to announce that the Pillars baton has been passed to Michael Goldberg, Wendy McKimpson, and Arthur Ruiz—three former teaching-facilitators, one of whom was also a former enrolled student—who have been the course leaders in the Fall of 2011. Following this, Jean Masterson, Jason McCarthy and Lola McRae will be the course leaders in the Fall of 2012.

To assist the future course leaders in integrating new material into the “Pillars” course, we assembled a master list of landmark papers in numerous biological fields. Table 1, which summarizes this master list, gives a glimpse into what may be discussed in future semesters. We see “Pillars” as an evolving, developing, and unique opportunity for student initiative and interaction, and we encourage all students to provide suggestions and feedback for the course. We hope that the inaugural semester of “Pillars” will have been its most inexpert, and we trust that the course will continue to improve on our initial model.

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### TABLE 1. MASTER LIST OF PAPERS (CITATIONS AND TITLES, ORGANIZED BY SUBJECT) FOR THE PILLARS OF BIOLOGY COURSE

#### Biochemistry and Biophysics

| Citation | Title |
|----------|-------|
| A.V. Hill, *J Physiol* 1910 | The possible effects of the aggregation of the molecules of haemoglobin on its dissociation curves. |
| L. Pauling, *J Am Chem Soc* 1931 | The nature of the chemical bond: Application of results obtained from the quantum mechanics and from a theory of paramagnetic susceptibility to the structure of molecules. |
| H.A. Krebs et al., *Enzymologia* 1937 | LXXVII: Metabolism of ketonic acids in animal tissues. |
| W.A. Englehardt et al., *Nature* 1939 | Myosine and adenosinetriphosphatase. |
| M. Calvin et al., *Science* 1948 | The path of carbon in photosynthesis. |
| F.M. Richards et al., *JBC* 1959 | The preparation of subtilisin-modified ribonuclease and the preparation of the peptide and protein components. |
| J.H. Matthaei et al., *PNAS* 1962 | Characteristics and composition of RNA coding units. |
| J. Monod et al., *J Mol Biol* 1965 | On the nature of allosteric transitions: A plausible model. |
| J.A. McCammon et al., *Nature* 1977 | Dynamics of folded proteins. |
| K. Kruger et al., *Cell* 1982 | Self splicing RNA: Autoexcision and autocyclization of the ribosomal RNA intervening sequence of Tetrahymena. |
| T. Evans et al., *Cell* 1983 | Cyclin: A protein specified by maternal mRNA in sea urchin eggs that is destroyed at each cleavage division. |
| D.A. Doyle et al., *Science* 1998 | The structure of the potassium channel: Molecular basis of K+ conduction and selectivity. |
| N. Ban et al., *Science* 2000 | The complete atomic structure of the large ribosomal subunit at 2.4 Å resolution. |

#### Biomedical Sciences

| Citation | Title |
|----------|-------|
| J. Snow, London: Churchill, 1855 | *On the Mode of Communication of Cholera.* |
| V.M. Ingram, *Nature* 1956 | A specific chemical difference between globins of normal and sickle-cell anemia hemoglobins. |
| E.D. Thomas et al., *N Engl J Med* 1957 | Intravenous infusion of bone marrow in patients receiving radiation and chemotherapy. |
| T.R. Dawber et al., *Am J Public Health* 1959 | Some factors associated with the development of coronary heart disease. |
| P.B. Schiff et al., *Nature* 1979 | Promotion of microtubule assembly in vitro by taxol. |
| R.G.L. Shorr et al., *JBC* 1981 | Purification of the beta-adrenergic receptor: Identification of the hormone binding subunit. |
| S.B. Prusiner, *Science* 1982 | Novel proteinaceous infectious particles cause scrapie. |
| F. Barre-Sinoussi et al., *Science* 1983 | Isolation of a T-lymphotropic retrovirus from a patient at risk for Acquired Immune Deficiency Syndrome (AIDS). |
| T.C. Sudhof et al., *Science* 1985 | Cassette of eight exons shared by genes for LDL receptor and EGF precursor. |
| Y. Zhang et al., *Nature* 1994 | Positional cloning of the mouse obese gene and its human homologue. |
| B.J. Druker et al., *Nat Med* 1996 | Effects of a selective inhibitor of the Abl tyrosine kinase on the growth of Bcr-Abl positive cells. |
### Cancer Biology

| Author(s) | Journal/Publication Year |
|-----------|--------------------------|
| P. Rous | *JEM* 1910 |
| J. Furth et al. | *Am J Cancer* 1937 |
| H. Eagle | *Science* 1955 |
| J. Folkman et al. | *JEM* 1971 |
| A.G. Knudson, Jr. | *PNAS* 1971 |
| C. Shih et al. | *Nature* 1981 |
| A. de Klein et al. | *Nature* 1982 |
| W.K. Cavenee et al. | *Nature* 1983 |
| A.P. Feinberg et al. | *Nature* 1983 |
| A. de Klein et al. | *Nature* 1982 |
| W.K. Cavenee et al. | *Nature* 1983 |
| A.P. Feinberg et al. | *Nature* 1983 |
| D.S. Dolberg et al. | *Nature* 1984 |

- An experimental comparison of transplanted tumor and a transplanted normal tissue capable of growth.
- The transmission of leukaemia of mice with a single cell.
- Nutrition needs of mammalian cells in tissue culture.
- Isolation of a tumor factor responsible for angiogenesis.
- Mutation and cancer: Statistical study of retinoblastoma.
- Transforming genes of carcinomas and neuroblastomas introduced into mouse fibroblasts.
- A cellular oncogene is translocated to the Philadelphia chromosome in chronic myelocytic leukemia.
- Expression of recessive alleles by chromosomal mechanisms in retinoblastoma.
- Hypomethylation distinguishes genes of some human cancers from their normal counterparts.
- Inability of Rous sarcoma virus to cause sarcomas in the avian embryo.

### Cell Biology

| Author(s) | Journal/Publication Year |
|-----------|--------------------------|
| E. Metschnikoff | *Archiv f. pathol. Anatomie und klinische Medizin* 1884 |
| M.F. Lyon | *Nature* 1961 |
| R.D. Kornberg et al. | *Science* 1974 |
| A.B. Pardee | *PNAS* 1974 |
| P. Novick et al. | *Cell* 1980 |
| D. Kalderon et al. | *Cell* 1984 |
| C.W. Greider et al. | *Cell* 1985 |
| C. Schindler et al. | *Science* 1992 |
| T. Sollner et al. | *Nature* 1993 |
| M. Chalfie et al. | *Science* 1994 |

- A disease of Daphnia caused by a yeast: A contribution to the theory of phagocytes as agents of attack on disease-causing organisms.
- Gene action in the X chromosome of the mouse (*Mus musculus*).
- Chromatin structure: Oligomers of the histones.
- A restriction point for control of normal animal cell proliferation.
- Identification of 23 complementation groups required for post-translational events in the yeast secretory pathway.
- A short amino acid sequence able to specify nuclear location.
- Identification of a specific telomere terminal transferase activity in *Tetrahymena* extracts.
- Interferon-dependent tyrosine phosphorylation of a latent cytoplasmic transcription factor.
- SNAP receptors implicated in vesicle targeting and fusion.
- Green fluorescent protein as a marker for gene expression.

### Developmental Biology

| Author(s) | Journal/Publication Year |
|-----------|--------------------------|
| S. Gluecksohn-Schoenheimer | *Genetics* 1938 |
| R. Briggs et al. | *PNAS* 1952 |
| A.J. Becker et al. | *Nature* 1963 |
| P.D. Nieuwkoop | *Wilhem Roux Archiv* 1969 |
| E.B. Lewis | *Nature* 1978 |

- The development of two tailless mutants in the house mouse.
- Transplantation of living nuclei from blastula cells into enucleated frogs’ eggs.
- Cytological demonstration of the clonal nature of spleen colonies derived from transplanted mouse marrow cells.
- The formation of the mesoderm in urodelean amphibia.
- A gene complex controlling segmentation in *Drosophila*. 
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|---|
| **Evolutionary Biology** |
| S. Wright, *Proceedings of the Sixth International Congress on Genetics* 1932 | The roles of mutation, inbreeding, crossbreeding, and selection in evolution. |
| C.H. Waddington, *Nature* 1942 | Canalization of development and the inheritance of acquired characters. |
| †S.E. Luria et al., *Genetics* 1943 | Mutations of bacteria from virus sensitivity to virus resistance. |
| R. Holliday, *Gen Res* 1964 | A mechanism for gene conversion in fungi. |
| L. Sagan, *J Theor Bio* 1967 | On the origin of mitosing cells. |
| M.C. King et al., *Science* 1975 | Evolution at two levels in humans and chimpanzees. |
| †C.R. Woese, *PNAS* 1977 | Phylogenetic structure of the prokaryotic domain: The primary kingdoms. |
| J.J. Yunis et al., *Science* 1982 | The origin of man: A chromosomal pictorial legacy. |
| R.L. Cann et al., *Nature* 1987 | Mitochondrial DNA and human evolution. |
| S.B. Carroll et al., *Science* 1994 | Pattern formation and eyespot determination in butterfly wings. |
| M. Krings et al., *Cell* 1997 | Neandertal DNA sequences and the origin of modern humans. |
| **Genetics** |
| T.H. Morgan, *Science* 1910 | Sex limited inheritance in *Drosophila*. |
| H.J. Muller, *PNAS* 1928 | Production of mutations by X-rays. |
| †B. McClintock, *PNAS* 1950 | The origin and behavior of mutable loci in maize. |
| †R.J. Britten et al., *Science* 1968 | Repeated sequences in DNA: Hundreds of thousands of copies of DNA sequences have been incorporated into the genomes of higher organisms. |
| R.J. Konopka et al., *PNAS* 1971 | Clock mutants of *Drosophila melanogaster*. |
| L. Hartwell et al., *Science* 1974 | Genetic control of the cell division cycle in yeast. |
| P.C. Wensink et al., *Cell* 1974 | A system for mapping DNA sequences in the chromosomes of *Drosophila melanogaster*. |
| C. Nusslein-Volhard et al., *Nature* 1980 | Mutations affecting segment number and polarity in *Drosophila*. |
| F.S. Collins et al., *PNAS* 1984 | Directional cloning of DNA fragments at a large distance from an initial probe: A circularization method. |
| M.A.H. Surani et al., *Nature* 1984 | Development of reconstituted mouse eggs suggests imprinting of the genome during gametogenesis. |
| †O. Smithies et al., *Nature* 1985 | Insertion of DNA sequences into the human chromosomal beta-globin locus by homologous recombination. |
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| Authors          | Year | Citation                                                                 |
|------------------|------|---------------------------------------------------------------------------|
| K.R. Thomas et al. | 1987 | Site-directed mutagenesis by gene targeting in mouse embryo-derived stem cells. |
| R.C. Lee et al.  | 1993 | The *C. elegans* heterochronic gene lin-4 encodes small RNAs with antisense complementarity to lin-14. |
| ‡M. Kaeblerlein et al. | 1999 | The Sir2/3/4 complex and Sir2 alone promote longevity in *Saccharomyces cerevisiae* by two different mechanisms. |

### Immunology

| Authors          | Year | Citation                                                                 |
|------------------|------|---------------------------------------------------------------------------|
| E. Jenner, London: Sampson Low 1789 | | An Inquiry into the Causes and Effects of Variolae Vaccinæ, a Disease Discovered in Some Western Counties of England. |
| P. Ehrlich et al., *J Berlin Klin Wochenschr* 1899 | | Contributions to the theory of lysis action. |
| R.E.Billingham et al., *Nature* 1953 | | Actively acquired tolerance of foreign cells. |
| B. Glick et al., *Poult Sci* 1956 | | The bursa of Fabricius and antibody production. |
| ‡F.M. Burnet, *Austr J Sci* 1957 | | A modification of Jerne’s theory of antibody production using the concept of clonal selection. |
| G.M. Edelman et al., *J Exp Med* 1961 | | Studies on the structural units of the gamma-globulins. |
| ‡J.L. Gowans et al., *Nature* 1962 | | Initiation of immune responses by small lymphocytes. |
| E.V. Hersh et al., *J Immunol* 1968 | | Macrophage-lymphocyte interaction in the antigen-induced blastogenic response of human peripheral blood leukocytes. |
| J.F. Miller et al., *J Exp Med* 1968 | | Cell to cell interaction in the immune response: I. Hemolysin forming cells in neonatally thymectomized mice reconstituted with thymus or thoracic duct lymphocytes. |
| K.J. Lafferty et al., *Aust J Exp Biol Med Sci* 1969 | | Reactions of the graft versus host (gvh) type. |
| R.M. Steinman et al., *J Exp Med* 1973 | | Identification of a novel cell type in peripheral lymphoid organs of mice: I. Morphology, quantitation, tissue distribution. |
| R.M. Zinkernagel et al., *Nature* 1974 | | Restriction of in vitro T cell-mediated cytotoxicity in lymphocytic choriomeningitis within a syngeneic or semiallogeneic system. |
| N. Hozumi et al., *PNAS* 1976 | | Evidence for somatic rearrangement of immunoglobulin genes coding for variable and constant regions. |
| P. Early et al., *Cell* 1980 | | An immunoglobulin heavy chain variable region gene is generated from three segments of DNA: \( V_\kappa \), D and \( J_\kappa \). |
| J.P. Allison et al., *J Immunol* 1982 | | Tumor-specific antigen of murine T-lymphoma defined with monoclonal antibody. |
| T.R. Mosmann et al., *J Immunol* 1986 | | Two types of murine helper T cell clone: I. Definition according to profiles of lymphokine activities and secreted proteins. |
| ‡R. Medzhitov et al., *Nature* 1997 | | A human homologue of the *Drosophila* Toll protein signals activation of adaptive immunity. |
| M. Muramatsu et al., *Cell* 2000 | | Class switch recombination and hypermutation require activation-induced cytidine deaminase (AID), a potential RNA editing enzyme. |

### Microbiology

| Authors          | Year | Citation                                                                 |
|------------------|------|---------------------------------------------------------------------------|
| C.L.A. Laveran, *Bulletin de l’Academie de Medicine* 1880 | | A newly discovered parasite in the blood of patients suffering from malaria: Parasitic etiology of attacks of malaria. |
| R. Koch, *Berliner Klinischen Wochenschrift* 1882 | | The etiology of tuberculosis. |
| ‡A. Fleming, *Brit J Exp Pathol* 1929 | | On the antibacterial action of cultures of a *Penicillium*, with special reference to their use in the isolation of B. Influenzae. |
| E.L. Ellis et al., *JGP* 1939 | | The growth of bacteriophage. |
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| J. Lederberg et al., *Nature* 1946 | Gene recombination in *Escherichia coli*. Data for this announcement provided in “Novel genotypes in mixed cultures of biochemical mutants of bacteria.” *CSH Symposia on Quantitative Biology* 1946. |
| E.M. Witkin, *PNAS* 1946 | Inherited differences in sensitivity to radiation in *Escherichia coli*. |
| A. Gierer et al., *Nature* 1956 | Infectivity of ribonucleic acid from tobacco mosaic virus. |
| A.B. Pardee et al., *J Mol Biol* 1959 | The genetic control of cytoplasmic expression of “inducibility” in the synthesis of beta-galactosidase by *E. coli*. |
| H. Yoshikawa et al., *PNAS* 1963 | Sequential replication of *Bacillus subtilis* chromosome: I. Comparison of marker frequencies in exponential and stationary growth patterns. |
| T.D. Brock, *Nature* 1967 | Microorganisms adapted to high temperature. |
| *D. Baltimore, *Nature* 1970 | RNA-dependent DNA polymerase in virions of RNA tumour viruses. |
| K.H. Nealon et al., *J Bact* 1970 | Cellular control of the synthesis and activity of the bacterial luminescent system. |
| R.D. Fleischmann et al., *Science* 1995 | Whole genome random sequencing and assembly of *Haemophilus influenzae* Rd. |

**Molecular Biology**

| S. Benzer, *PNAS* 1958 | Fine structure of a genetic region in bacteriophage. |
| F.H. Crick, *Symp Soc Exp Biol* 1958 | On protein synthesis. |
| M. Meselson et al., *PNAS* 1958 | The replication of DNA in *Escherichia coli*. |
| P. Doty et al., *PNAS* 1960 | Strand separation and specific recombination in deoxyribonucleic acids: Physical and chemical studies. |
| S. Brenner et al., *Nature* 1961 | An unstable intermediate carrying information from genes to ribosomes for protein synthesis. |
| F.H. Crick et al., *Nature* 1961 | General nature of the genetic code for proteins. |
| F. Jacob et al., *J Mol Biol* 1961 | Genetic regulatory mechanisms in the synthesis of proteins. |
| S. Cohen et al., *PNAS* 1973 | Construction of biologically functional bacterial plasmids in vitro. |
| S.M. Berget et al., *PNAS* 1977 | Spliced segments at the 5' terminus of adenovirus 2 late mRNA. |
| M. Wigler et al., *PNAS* 1979 | DNA-mediated transfer of the adenine phosphoribosyltransferase locus into mammalian cells. |

**Neuroscience**

| J.M. Harlow, *Publications of the Massachusetts Medical Society* 1868 | Recovery from the passage of an iron bar through the head. |
| B. Scharrer, *J Comp Neurol* 1941 | Neurosecretion: II. Neurosecretory cells in the central nervous system of cockroaches. |
| A.L. Hodgkin et al., *J Physiol* 1945 | Resting and action potentials in single nerve fibres. |
| G. Moruzzi et al., *Electroencephalogr Clin Neurophysiol* 1949 | Brain stem reticular formation and activation of the EEG. |
| K.S. Lashley, *Society of Exp Biol Symp, No. 4: Psych Mech in Animal* 1950 | In search of the engram. |
| J. Del Castillo et al., *J Physiol* 1954 | Quantal components of the end-plate potential. |
| W.B. Scoville et al., *J Neurol Neurosurg Psychiatry* 1957 | Loss of recent memory after bilateral hippocampal lesions. |
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| Author(s)                      | Journal/Year | Title                                                                 |
|--------------------------------|--------------|----------------------------------------------------------------------|
| E.J. Furshpan et al.           | *J Physiol* 1959 | Transmission at the giant motor synapses of the crayfish.             |
| D.H. Hubel et al.              | *J Physiol* 1962 | Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. |
| R.W. Sperry, *PNAS* 1963       |              | Chemoaffinity in the orderly growth of nerve fiber patterns and connections. |
| T. Bliss et al.                | *J Physiol* 1973 | Long-lasting potentiation of synaptic transmission in the dentate area of the anaesthetized rabbit following stimulation of the prefrontal path. |
| C.B. Pert et al.               | *Science* 1973 | Opiate receptors: Demonstration in nervous tissue.                    |
| T. Poggio et al.               | *Nature* 1985 | Computational vision and regularization theory.                       |

**Systems and Computational Biology**

| Author(s)                      | Journal/Year | Title                                                                 |
|--------------------------------|--------------|----------------------------------------------------------------------|
| A.M. Turing, *Phil Trans R Soc Lond B* 1952 |              | The chemical basis of morphogenesis.                                 |
| A. Novick et al.               | *PNAS* 1957  | Enzyme induction as an all-or-none phenomenon.                       |
| J. Monod et al.                | *CSH Symp Quant Biol* 1961 | On the regulation of gene activity.                                |
| J.L. Spudich et al.            | *Nature* 1976 | Non-genetic individuality: Chance in the single cell.                |
| J.E. Sulston et al.            | *Dev Biol* 1977 | Postembryonic lineages of the nematode *Caenorhabditis elegans*. |
| J. Felsenstein                 | *J Mol Evol* 1981 | Evolutionary trees from DNA sequences: A maximum likelihood approach. |
| T.F. Smith et al.              | *J Mol Biol* 1981 | Identification of common molecular subsequences.                    |
| ‡M. Schena et al.              | *Science* 1995 | Quantitative monitoring of gene expression patterns with a complementary DNA microarray. |
| T. Ideker et al.               | *Science* 2001 | Integrated genomic and proteomic analyses of a systematically perturbed metabolic network. |

*Papers affiliated with Albert Einstein College of Medicine.*

†Papers covered in the fall 2009–2010 Landmark Papers course.

‡Papers covered in the fall 2010–2011 Pillars of Biology course.