

In 2014, a high-quality sequence was announced for the genome of *Homo neanderthalensis* (Neanderthals), an extinct species closely related to present-day humans. These genomes are of great interest in their own right, but they also provide important insights into evolution as well as other biological processes. Broadening the human-chimpanzee comparison to the genomes of other primates and more distantly related animals should reveal the sets of genes that control group-defining characteristics. Beyond that, comparisons with the genomes of bacteria, archaea, fungi, protists, and plants should enlighten us about the long evolutionary history of the ancient genes we all share.

With the genomes of many species fully sequenced, scientists can study whole sets of genes and their interactions, an approach called **genomics**. The sequencing efforts that feed this approach have generated, and continue to generate, enormous volumes of data. The need to deal with this ever-increasing flood of information has spawned the field of **bioinformatics**, the application of computational methods to store and analyze biological data.

We will begin this chapter by discussing two approaches to genome sequencing and some of the advances in bioinformatics and its applications. We will then summarize what has been learned from the genomes that have been sequenced thus far. Next, we will describe the composition of the human genome as a representative genome of a complex multicellular eukaryote. Finally, we will explore current ideas about how genomes evolve and about how the evolution of developmental mechanisms could have generated the great diversity of life on Earth today.

CONCEPT 21.1

The Human Genome Project fostered development of faster, less expensive sequencing techniques

Sequencing of the human genome, an ambitious undertaking, officially began as the **Human Genome Project** in 1990. Organized by an international, publicly funded consortium of scientists at universities and research institutes, the project involved 20 large sequencing centres in six countries plus a host of other labs working on smaller parts of the project.

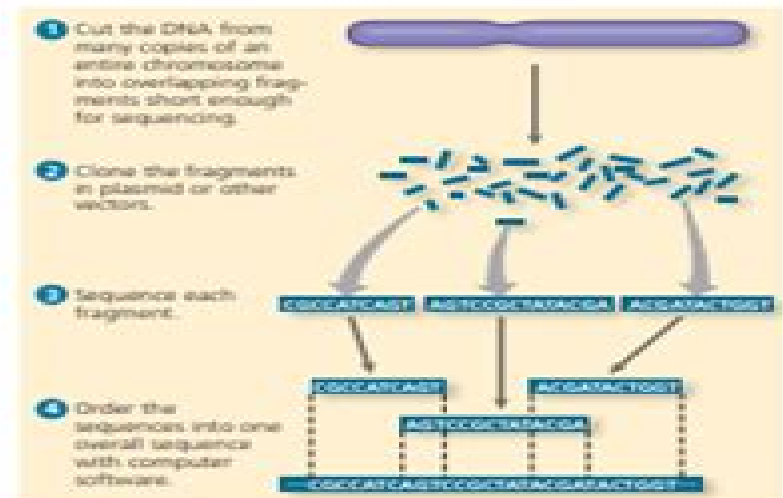
After the human genome sequence was largely completed in 2003, the sequence of each chromosome was analyzed and described in a series of papers, the last of which covered chromosome 1 and was published in 2006. At this point, the sequencing was declared “virtually complete.”

The ultimate goal in mapping any genome is to determine the complete nucleotide sequence of each chromosome. For the human genome, this was accomplished by sequencing machines, using the dideoxy chain termination method mentioned in Concept 20.1. Even with automation, though, the sequencing of all 3 billion base pairs in a haploid set of human chromosomes presented a formidable challenge. In fact, a major thrust of the Human Genome Project was the development of

technology for faster sequencing. Improvements over the years chipped away at each time-consuming step, enabling the rate of sequencing to accelerate impressively: Whereas a productive lab could typically sequence 1000 base pairs a day in the 1980s, by the year 2000 each research centre working on the Human Genome Project was sequencing 1000 base pairs per second. As of 2016, the most widely used automated machines can sequence nearly 25 million base pairs per second, while developers of some newer techniques claim they can achieve a rate of 66 billion base pairs per second. Methods that can analyze biological materials very rapidly and produce enormous volumes of data are said to be “high-throughput.” Sequencing machines are an example of high-throughput devices.

Two approaches complemented each other in obtaining the complete sequence. The initial approach was a methodical one that built on an earlier storehouse of human genetic information. In 1998, however, molecular biologist J. Craig Venter set up a company (Celera Genomics) and declared his intention to sequence the entire human genome using an alternative strategy. The **whole-genome shotgun approach** starts with the cloning and sequencing of DNA fragments from randomly cut DNA. Powerful computer programs then assemble the resulting very large number of overlapping short sequences into a single continuous sequence (**Figure 21.2**).

Y Figure 21.2 Whole-genome shotgun approach to sequencing. In this approach, developed by Craig Venter and colleagues at Celera Genomics, random DNA fragments are cloned, sequenced and then ordered relative to each other.



VISUAL SKILLS ▶ The fragments in step 2 of this figure are depicted as scattered, rather than being in an ordered array. How does this depiction reflect the approach?



HHMI Animation: Shotgun Sequencing



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1. Understanding the eBook Campbell Practicing Biology 3rd Edition Answers
 - The Rise of Digital Reading Campbell Practicing Biology 3rd Edition Answers
 - Advantages of eBooks Over Traditional Books
2. Identifying Campbell Practicing Biology 3rd Edition Answers
 - Exploring Different Genres
 - Considering Fiction vs. Non-Fiction
 - Determining Your Reading Goals
3. Choosing the Right eBook Platform
 - Popular eBook Platforms
 - Features to Look for in an Campbell Practicing Biology 3rd Edition Answers
 - User-Friendly Interface
4. Exploring eBook Recommendations from Campbell Practicing Biology 3rd Edition Answers

- Personalized Recommendations
- Campbell Practicing Biology 3rd Edition Answers User Reviews and Ratings
- Campbell Practicing Biology 3rd Edition Answers and Bestseller Lists
- 5. Accessing Campbell Practicing Biology 3rd Edition Answers Free and Paid eBooks
 - Campbell Practicing Biology 3rd Edition Answers Public Domain eBooks
 - Campbell Practicing Biology 3rd Edition Answers eBook Subscription Services
 - Campbell Practicing Biology 3rd Edition Answers Budget-Friendly Options
- 6. Navigating Campbell Practicing Biology 3rd Edition Answers eBook Formats
 - ePub, PDF, MOBI, and More
 - Campbell Practicing Biology 3rd Edition Answers Compatibility with Devices
 - Campbell Practicing Biology 3rd Edition Answers Enhanced eBook Features
- 7. Enhancing Your Reading Experience
 - Adjustable Fonts and Text Sizes of Campbell Practicing Biology 3rd Edition Answers
 - Highlighting and Note-Taking Campbell Practicing Biology 3rd Edition Answers
 - Interactive Elements Campbell Practicing Biology 3rd Edition Answers
- 8. Staying Engaged with Campbell Practicing Biology 3rd Edition Answers
 - Joining Online Reading Communities
 - Participating in Virtual Book Clubs
 - Following Authors and Publishers Campbell Practicing Biology 3rd Edition Answers
- 9. Balancing eBooks and Physical Books Campbell Practicing Biology 3rd Edition Answers
 - Benefits of a Digital Library
 - Creating a Diverse Reading Collection Campbell Practicing Biology 3rd Edition Answers
- 10. Overcoming Reading Challenges
 - Dealing with Digital Eye Strain
 - Minimizing Distractions
 - Managing Screen Time
- 11. Cultivating a Reading Routine Campbell Practicing Biology 3rd Edition Answers
 - Setting Reading Goals Campbell Practicing Biology 3rd Edition Answers
 - Carving Out Dedicated Reading Time
- 12. Sourcing Reliable Information of Campbell Practicing Biology 3rd Edition Answers

- Fact-Checking eBook Content of Campbell Practicing Biology 3rd Edition Answers
 - Distinguishing Credible Sources
13. Promoting Lifelong Learning
- Utilizing eBooks for Skill Development
 - Exploring Educational eBooks
14. Embracing eBook Trends
- Integration of Multimedia Elements
 - Interactive and Gamified eBooks

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