Evolution

Monroe W. Strickberger SECOND EDITION

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Monroe W. Strickberger

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For Ursula

PREFACE

All biological phenomena derive from evolutionary relationships and past interactions. As the great evolutionary geneticist Theodosius Dobzhansky remarked, "Nothing in biology makes sense except in the light of evolution." Yet unifying all biology under an evolutionary theme is still difficult, although the explosive increase in molecular, organismic, and populational information makes the realization of this goal more possible now than ever before.

The purpose of this book is to bring together some prevailing knowledge and ideas about evolution, to provide an informed framework of thought for undergraduates. It is based on a course I have given for many years to biology majors who have had prior introductory biology courses. (Reviews of some basic biological and genetic concepts are nevertheless included.)

Academic biology is heavily partitioned, and biology majors not only take a variety of specialty courses such as development, ecology, genetics, microbiology, and physiology, but also must concentrate in specific areas. Thus the evolutionary theme that runs through all biology is often fragmented, or entirely ignored. In many courses and in many institutions, evolution is little more than a curricular afterthought, and biologists emerge from such programs with little grasp of such topics as

- *Philosophical and religious issues in evolution theory:* Why did scientists propose and welcome evolution theory, and why do so many others still find the concept unacceptable or highly questionable?
- *General events in cosmological and geological evolution:* What was the "beginning" of the universe, how did it develop, and how did it lead to those features that affected life on earth?
- *The origin and early development of life:* How did biological organisms come into being, and from what sources?
- *General features in the evolution of major life forms:* What characteristics did biological organisms assume, how did they change, and why?
- *The use of systematics and the influence of modern molecular phylogenies:* How can we determine and characterize evolutionary relationships among biological forms, morphologically and molecularly?
- *Current findings in human evolution:* From where did our species originate, and how does evolution explain our features and our behavior?
- *General mechanisms that underlie evolutionary changes:* What laws and concepts help explain why and how differences among populations develop?

Should the modern biology major have at least a modest understanding of these topics? The answer is an unequivocal *Yes*! To "make sense" of biology demands more than a short mention of a few evolutionary events in courses mainly focused on more specialized fields.

In general, I have considered evolution from a historical viewpoint, both biologically and conceptually. On the biological level, historical information passed on by transmitted genetic material connects the biology of organisms to past events–a modern organism derives from earlier organisms. On the ideological level, evolutionary concepts derive from previous cultural concepts. In both these forms of transmitted information, "like" not only produces "like" but also produces "unlike" because of (1) genetic changes in hereditary material and (2) conceptual changes in the ideas of evolution. Almost every aspect of existence has an evolutionary background and framework, and knowledge of the past is essential for fully understanding the present. In fact, what makes biology unique in contrast to chemistry or physics is that biological forms and functions, in all their many variations, originated through historical events and continue to do so–an understanding of biology is inseparable from its history, and evolutionary predictability cannot escape from contingency.

The realm of evolutionary science therefore includes both chronology and mechanisms–we seek concepts that explain both the sequence of events and their causes. For this purpose, evolutionary scientists have developed, and continue to develop, methods that reconstruct evolutionary events and let us understand not only biological chronology but also its genetic connections. That is, we conceive that evolution follows a sequence of logically understandable causes that give us rational explanations and reliable knowledge of the past.

Because it combines both history and mechanism, evolution is an exciting subject, and I have found over the years that students often respond best when the text is generously illustrated. I have therefore provided close to 450 figures, tables, and diagrams. To further help the student master the material, the text includes boxed reviews of special topics, end-of-chapter summaries, lists of key terms, discussion questions, and a glossary. For research and reference, complete chapter bibliographies as well as separate author and subject indexes are provided. Some added points of interest, not crucial to understanding the text, are given in footnotes.

Although the order of topics offered here has worked well for my own classes, I know there are different ways to organize this material, and the chapters have therefore generally been written to allow considerable flexibility. I have avoided an overly theoretical treatment of the subject. Nothing beyond elementary algebra is needed to understand the mathematics used.

Since evolution is the broadest of biological fields, covering the greatest range of disciplines, even the brief survey of evolution offered here has errors and ambiguities. To the extent that this book has been spared many such failings, I owe thanks to many reviewers, who commented on one or more sections of this new edition:

Robert Carroll, McGill University

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BRIEF CONTENTS

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PART IV: THE MECHANISMS

P A R T I

The Historical Framework

CHAPTER

1

Before Darwin

BIOLOGICAL EVOLUTION ENTAILS inherited changes in populations of organisms, over a period of time, that lead to differences among them. Essential to our present concept of evolution are the notions that a group of organisms is bound together by its common inheritance; that the past has been long enough for inherited changes to accumulate; and perhaps most essential of all, that discoverable natural events and relationships explain the phenomena of evolution. Although people studied and discussed each of these aspects at various times in human history, it is only during this last century, since the work of Charles Darwin, that biological evolution became socially accepted. This acceptance was based on many changes in how people view the world and explain natural phenomena. The purpose of this chapter and the three that follow is to provide a review of some of the underpinnings that enabled the modern Darwinian concept of evolution to unfold.[1]

[1]The term "evolution" actually had a seventeenth-century embryological origin, defined as the "unfolding" of parts and organs during development. It was only in the nineteenth century that people came to generally use *evolution* to mean the transformation of species.

Idealism and the Species

Attempts to understand the world in a rational way–that is, by commonly accepted methods of thought and logic–began about the fifth century B.C. in Greece. Plato (428–348 B.C.), the philosopher who along with Aristotle (384–322 B.C.) had the greatest impact on Western thought, suggested that the observable world–our experience–is no more than a shadowy reflection of underlying "ideals" that are true and eternal for all time. Most things, according to Plato, were originally in the form of such eternal ideals, and any change represents disharmony. The Platonic goal for human society was to analyze experience in order to understand and strive for ideal perfection. The notions of "perfect circles" to explain the motions of the heavenly bodies (Fig. 1-1), "perfect numbers" such as 6 (1 + 2 + 3) and 10 (1 + 2 + 3 + 4), and the four "elements" (earth, water, fire, and air) to which all matter could be reduced were among the results of the search for perfection.[2] What are the sources of such **idealism**?

[2]Variations on this theme were not uncommon. To the four elements Empedocles (c. 490–430 B.C.) added two active principles: love, which binds elements together, and hate, which

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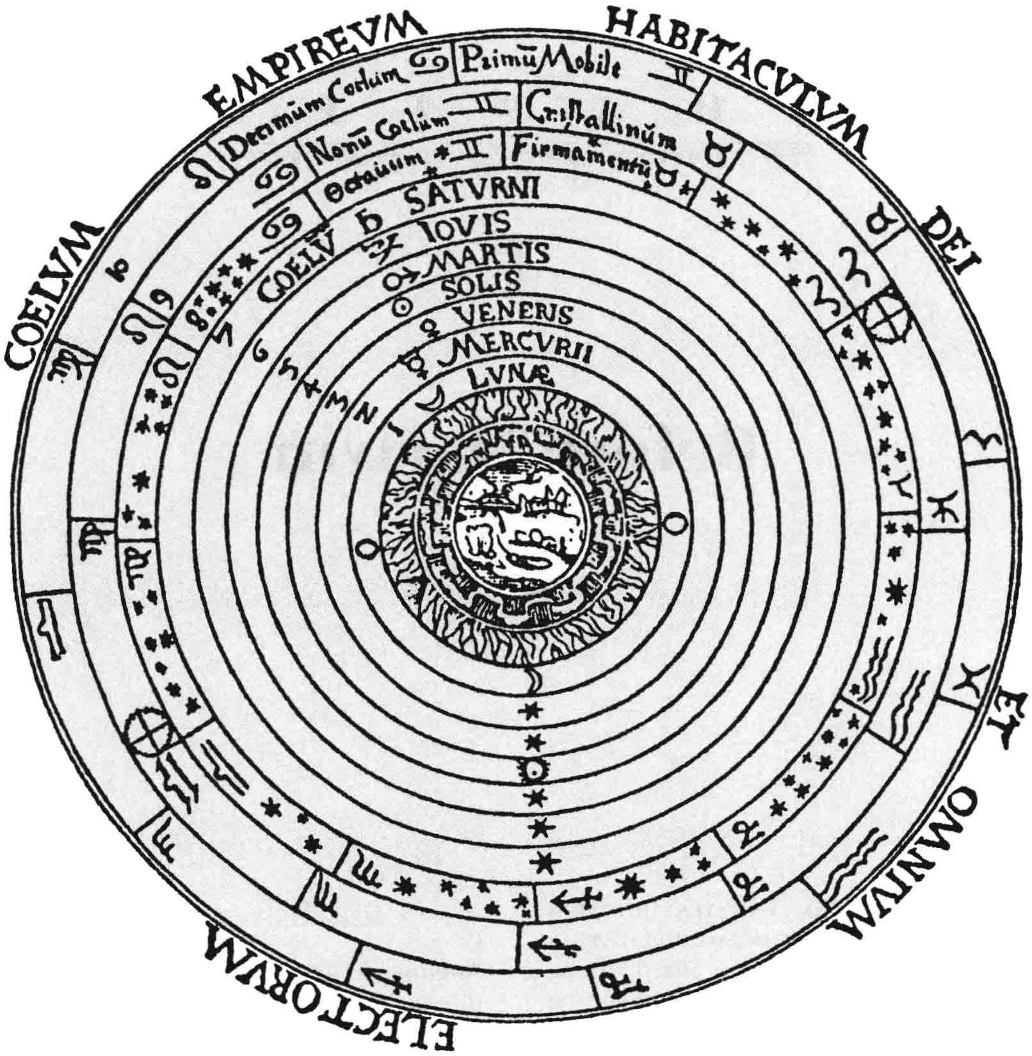

Figure 1–1

A medieval concept of the ten spheres of the universe with Earth and its four elements (earth, air, fire, water) at the center, according to Apian's Cosmographia *(published 1539 in Antwerp). Surrounding Earth are transparent crystal spheres containing in succession the moon, Mercury, Venus, the sun, Mars, Jupiter, Saturn, the fixed stars, and spheres involved in the motion of the stars and of the entire universe ("Primū Mobile"). Beyond these spheres lies Heaven ("The Empire and Habitation of God and All the Elect").*

To a large extent, idealism originates from our often-used ability to abstract concepts from experience–to think, for example, of "cat" rather than one particular animal of specific size and head shape, with claws, tail, fur, and so on. Such abstraction lets us generalize our experience, to differentiate between cat and tiger, to pet the cat and run away from the tiger, and to communicate these general concepts or universals to others through our symbolic language. Despite these advantages, however, generalizations are not always reliable, because our experiences may modify the generalizations: not all cats or tigers are the same.

In fact, the struggle between generalization and particularization is continual, because only by generalizing can we conceive of regularity in nature and thereby consciously adapt to its needs, but only by particularizing can we contact and observe reality. No sooner do we conceive of some new generality than we often discover further details and may thereby be forced to modify our original conception. Experience

separates them. A further element, the "quintessence," was presumed by Aristotle and others to be the component of heavenly bodies. In respect to mystical numbers, Oken (1779–1851), one of the German Natural Philosophers, proposed that the highest mathematical idea is zero, and God, or the "primal idea," is therefore zero.