

THE EVOLUTIONARY BIOLOGY OF SPECIES. *Oxford Series in Ecology and Evolution*.

By Timothy G. Barraclough. Oxford and New York: Oxford University Press. \$90.00 (hardcover); \$45.95 (paper). xii + 271 p.; ill.; index. ISBN: 978-0-19-874974-5 (hc); 978-0-19-874975-2 (pb). 2019.

In this volume, the author defends the view that species form a real unit in *rerum natura*, serving as a unit central to understanding the origin and dynamics of biological diversity. Barraclough argues that individuals within the same species interact and evolve interdependently, while individuals belonging to distinct species evolve independently. And he maintains that we observe this phenomenon in the discrete clustering of genetic and phenotypic variation. He refers to this discrete clustering as the “species pattern.” Acknowledging that the boundaries between species may diachronically be obscured, in virtue of the dynamics of ongoing formation and evolution, the author holds that the morphometric, single-locus, and multilocus data support the claim that species are more than conceptual instruments or artifacts created to classify diversity.

The first chapter provides a preliminary argument and introduces nomenclature. In the second chapter, Barraclough discusses the etiology responsible for diversification for lineages and independently evolving groups. The outlines of a testable account begin to emerge. The third and fourth chapters provide empirical evidence in support of the presence of species patterns in contrast to alternative hypotheses. Chapter 3 focuses upon theory and practice for species delimitation and Chapter 4 describes a method whereby species are delimited by criteria relating to reproductive isolation and divergent selection. The following chapter concerns speciation and evidence is gleaned from a variety of speciation patterns among clades. Gene flow and dispersal, it is argued, provide key indications in relation to the rates of speciation among different organisms. An issue concerning whether the rates of speciation rely primarily upon ecological opportunity or genetic traits is introduced. In Chapter 6, Barraclough discusses sex, recombination, and alternative lifestyle, as it relates to species and speciation. Thereafter, in the next three chapters, the author turns to the ramifications for species in terms of contemporary evolutionary theory. In the next chapter, he investigates the role of ecology and genetic barrier for the selection of a gene across species boundaries. In Chapter 8, Barraclough investigates further the effects of species interacting with ecology. Species are said to diversify in virtue of their distinct uses of resources in their habitat. In the ninth chapter, he argues that explanation and prediction in terms of evolutionary dynamics requires examining whole systems of interacting species. In the penultimate

chapter, the author considers how the processes he outlines shape diversity over expansive temporal and spatial dimensions, and he contrasts the approach he favors with more classical approaches. The final chapter provides a summary of the extended arguments and directions for future research.

The Evolutionary Biology of Species is aimed at graduate-level students and researchers. The work is, however, clearly written, and the author provides a glossary of important nomenclature. More generally, individuals with an interest in systematics will find much in Barraclough’s work, worthy of interest and critical thought.

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GAME THEORY IN BIOLOGY: CONCEPTS AND FRONTIERS. *Oxford Series in Ecology and Evolution*.

By John M. McNamara and Olof Leimar. Oxford and New York: Oxford University Press. \$95.00 (hardcover); \$45.95 (paper). xi + 328 p.; ill.; index. ISBN: 978-0-19-881577-8 (hc); 978-0-19-881578-5 (pb). [A companion website is available.] 2020.

Evolutionary game theory is used to predict the end-points of evolution when the fitness of a strategy (an action—coded by genes—taken by an individual, possibly depending upon its state) depends upon the frequency of other strategies in the population. This theory was given a firm grounding in the last quarter of the 20th century by William D. Hamilton (U. Segerstråle. 2013. *Nature’s Oracle: The Life and Work of W. D. Hamilton*. Oxford (U.K.): Oxford University Press) and John Maynard Smith (B. Charlesworth and P. Harvey. 2005. *Biographical Memoirs of Fellows of the Royal Society* 51:253–265). McNamara and Leimar show that they are justifiable heirs in the tradition of Hamilton and Maynard Smith.

There is much to like about this book. From the outset, the models are motivated by biological systems and observations. That is, the authors are using evolutionary theory to answer the question “why is nature like that?” rather than asserting that “this is how nature should be.” The focus of the models is on strategies, which are coded by genes but the relationship between them is not simple. That is, there may be many genetic ways to reach the same phenotypic solution (J. Giske et al. 2014. *Proceedings of the Royal Society B: Biological Sciences* 281:20141096) and McNamara and Leimar note that there may be large amounts of genetic variation at evolutionary stability. They are clear about the limitations of the models. For many situations, an analytical model is not feasible, so numerical methods are illustrated. They are also clear that they are modeling fitness proxies and that these proxies are associated with strategies.

The authors cover a wide range of topics, including contributing to a common benefit, helping others,

the tragedy of the commons, biparental care, contests over resources, signaling and interpretation of cues, coordination, sex allocation, dispersal, learning via Bayesian updating, coevolution, anisogamy, and specialization. At the same time, current challenges to inspire the next generation are provided. I especially liked viewing future directions of game theory through Tinbergen's four questions (N. Tinbergen. 1963. *Zeitschrift für Tierpsychologie* 20:410–433).

The authors go over the key tools (e.g., Nash equilibrium, invasion fitness, adaptive dynamics, replicator dynamics, reproductive value) of evolutionary game theory at a good level of complexity so that most of the volume is generally accessible. They give exercises at the end of each chapter and solutions for these exercises, which increases the pedagogic value of the book immensely. One warning: sometimes the level of mathematical training required shifts unexpectedly, as in the sudden appearance of Hessian matrices and the methods of linear algebra required for evolutionary games in structured populations or the explanation of dynamic programming in a less than half-page box.

It is rare to find a book that can be used effectively by both experts and neophytes, but this is one. Indeed, I can imagine teaching an upper-level undergraduate seminar with it, passing it to a new postdoctoral researcher who wants to learn the methods, and using it in my own research. Owning it will be a wise investment.

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PALEONTOLOGY

HOMININ POSTCRANIAL REMAINS FROM STERKFONTEIN, SOUTH AFRICA, 1936–1995. *Human Evolution Series*.

Edited by Bernhard Zipfel, Brian G. Richmond, and Carol V. Ward. Oxford and New York: Oxford University Press. \$95.00. xix + 367 p.; ill.; index. ISBN: 9780197507667 (hc); 9780197507681 (eb). 2020.

Sterkfontein is a large complex paleokarst cave system that opened to the surface in the Late Pliocene, allowing for its infilling by sediment and bones over a period of perhaps a million years into the Early Pleistocene. The size of the cave system and its lengthy exposure to the surface have resulted in a very rich assemblage of fossils that includes numerous hominin specimens. In addition to the abundant published cranial, mandibular, and dental remains

that are largely attributable to *Australopithecus*, excavations at Sterkfontein over a period of 60 years have yielded over 150 hominin postcranial elements. Although some of these—especially those recovered between 1936 and 1947—have been described and analyzed, the vast majority have remained unpublished. Almost all of the elements derive from the bulk of the Sterkfontein deposit that has been designated as “Member 4.” In 2008, the late Charles Lockwood began to organize a workshop of experts to rectify this and, after his untimely death, the workshop eventuated in Johannesburg in 2009 under the guidance of the editors of the volume under review.

The book comprises 18 chapters that run to 337 pages of text, with an additional five appendixes. The chapters are organized into three sections. The first contains three chapters that provide background to the history, geology, and geochronology of the site. The second section represents the corpus of the book and entails 12 chapters in which the descriptions and analyses of the individual elements are presented. The descriptions are clearly written and are accompanied by numerous good quality color photographs of the fossils together with numerous tables of mensural data. These chapters are separated along the lines of the anatomical components of the skeleton (e.g., scapula, clavicle, and proximal humerus; ulna and radius; carpals; metacarpals and manual phalanges). They will serve as rich sources of comparison for future fossil discoveries from Plio-Pleistocene of Africa. The third section comprises three chapters. The first provides a consideration of long bone cross-sectional geometry; the second an analysis of limb proportions and their implications for reconstructing locomotor adaptations. The third is a short summary and synthesis of the preceding 17 chapters.

Each of the chapters in the second and third sections addresses one or more of the key questions surrounding the postcranial remains from Sterkfontein: Is more than one hominin species represented in the Member 4 deposit? What do these fossils reveal about posture and locomotion in *Australopithecus africanus* and/or any other australopith species that might be represented there? What are the similarities and differences between the Sterkfontein elements and homologues from other Plio-Pleistocene African sites and taxa?

The analyses presented in each of the chapters arrive at a similar conclusion regarding the presence of more than one australopith taxon in Member 4. There is no good evidence that would serve to reject the principal null hypothesis that the entire assemblage can be attributed to a single species. However, this species (*A. africanus*) evinces considerable phenotypic variability that perhaps stems, at least in