Preface

This book is an investigation into processes associated with evolutionary divergence and diversification. The focus, as the title indicates, is on the role played by the exchange of genes between divergent lineages. This process has been given various monikers, the most recent being "divergence-with-gene-flow." I want to first express my profound relief concerning the degree to which evolutionary biologists in general have embraced a model of diversification that includes some measure of genetic exchange. Many research groups, including my own, have emphasized the important role of gene transfer events in evolution for decades. However, I would be remiss if I did not express some misgivings concerning some of the current research into these processes. As my friends and family members (and especially those people with whom I do not see eye-to-eye) know, I do not hesitate to mention when I think there is a lack of an appreciation of historical precedence. I would argue that often this newest terminology—used in place of what many before us described as natural hybridization, introgression, horizontal gene transfer, viral reassortment, parapatric and/or sympatric divergence, etc.—demonstrates an unfortunate lack of understanding of the rich history of studies of genetic exchange.

Notwithstanding this concern, I once again prefer to emphasize the fact that evolutionary biologists now appear to believe that testing for divergence accompanied by genetic exchange has merit. The order and structure of the various chapters, as with my previous texts, reflect the goal of illustrating the conceptual and biological breadth of genetic exchange-mediated evolutionary processes. I have thousands of Endnote references (10,851 at the time of this writing), most of which discuss web-of-life processes, from which I had to choose the following topics and examples. This means that not only was it necessary to be subjective, but also due to unintentional oversight, I will have minimized some extremely important research. However, as with my most recent two books, I include discussions of viruses, prokaryotes, and eukaryotes. My rationale for discussing clades from all the domains of life remains the same as before. Though the mechanisms by which organisms exchange genomic material differ widely, the outcomes others and I are interested in—adaptive evolution and the formation of new "hybrid" lineages—do not. Furthermore, there remains in some corners a biased outlook on the utility of different organismic groups in defining the "important" evolutionary processes. An interaction I had with a colleague at a Society for the Study of Evolution meeting, I believe, illustrates this point well. In discussing my intention to include organisms from all domains of life in a text like this one, he objected and stated: "Horizontal gene transfer occurs in micro-organisms and has nothing to do with animals. In contrast, natural hybridization affects the latter, but not the former." I addressed this colleague's concern by first reminding him that genetic exchange could produce similar, important evolutionary consequences, regardless of the underlying mechanism causing gene transfer. For example, the evolution of novel adaptations, at least partially via horizontal gene transfer, resulting in the bacterial agent of plague is analogous to the adaptive evolution through introgressive hybridization between annual sunflower species resulting in the formation of several new *Helianthus* species. Finally, I suggested that he keep in mind that natural hybridization *and* horizontal gene transfer have impacted both "higher" and "lower" organisms. In terms of so-called higher lineages, there is evidence

for introgressive hybridization between different species of *Homo*, as well as the repeated insertion of retroviral-like elements into the *H. sapiens* genome. On the other hand, the combined effects from natural hybridization and horizontal gene transfer in "lower" eukaryotic clades such as trypanosomes and yeast are now well substantiated.

As mentioned, I am wedded to the idea that we should reflect accurately what our scientific predecessors described, especially when it applies to our chosen field of study. Needless to say, I have not been able to achieve perfection in past books, reviews, and contributions to the primary literature. Neither will I have achieved this in this text. However, in Chapter 1, I attempt to establish what I perceive as some of the most important steps in the history of studies of divergence-with-genetic-exchange. In particular, I highlight work from those on either side of the cultural divide represented by such persons as Lotsy, Anderson, and Stebbins on the one hand and Mayr on the other. I also present a large proportion of definitions used in this book and the genetic exchange literature. I also provide a discussion of theoretical and empirical foundations for the central topic (at least for eukaryotic clades) of hybrid zones. I move on to a discussion of genetic exchange that affects adaptive evolution in plants and animals. I then turn my attention to the origin of plant and animal taxa through hybridization. Finally, I provide exemplars of genetic exchange between lineages from different domains of life.

Chapter 2 reflects a subject on which I have been teaching and writing for over 25 years. I still find it extremely difficult and frustrating. This reaction is because, to un-paraphrase Will Rogers, I have never met a species concept that I liked. Almost certainly this results from the fact that, as much as I want order in the biological world, it is instead extremely messy. This is nowhere more apparent than when we attempt to categorize biological objects into taxonomic categories. I know that humans can attempt this—my first publication (in 1978) was a paper describing a new plant species—but it does not necessarily mean that the organisms typified will fit well within whatever pigeon-hole we construct. In Chapter 2 I emphasize that one source of difficulty for defining species relates to estimates of genetic exchange. In this regard, I discuss some of the limitations and strengths of various conceptual frameworks upon which evolutionary biologists place their hypothesis testing.

One of the major (and well-justified) complaints by students in graduate courses I have taught, in which I used my previous books, was that there was no meaningful discussion of methodologies used to discern between incomplete lineage sorting (i.e. deep coalescence) and genetic exchange. Thus, though I had discussed ways in which reticulate evolution might be tested for, I had not explicitly provided illustrations of how this had been accomplished relative to the contribution of shared ancestral polymorphisms. In Chapter 3 (and elsewhere), I provide a sample of the methodologies that have begun to be used. An obvious caveat is that by the time this text appears the current methodologies will have likely evolved into many, divergent iterations. In addition to analytical means by which alternative hypotheses may be tested, Chapter 3 also contains a number of other approaches (e.g. examining hybrid zones) by which genetic exchange may be inferred.

I begin Chapter 4 with the following statement, "I often use the analogy of genetic exchange and reproductive isolation as occupying either side of the same coin. In seminars on this topic, I also often show a photo of two North American Rocky Mountain bull elk with their antlers locked in a sparring match to illustrate this analogy. I believe that both the analogy and the photo illustrate the conclusions to be drawn from the accumulated evidence of the past several decades regarding both the observation of the semipermeability of reproductive barriers between divergent lineages (Key 1968) and the processes that cause this semipermeability." This sums up the concept of this chapter. In almost every lineage, genetic exchange is possible, and likely. This is because organisms are highly unlikely to be separated geographically from related lineages until complete reproductive isolation is achieved. This probably should have been obvious in the light of climate change throughout the biological record. In other words, what is the likelihood that two populations somehow isolated geographically would remain so for more than several thousand years or so? This might happen in some regions (i.e. some

portion of the tropical latitudes?), and possibly for island migrants from a mainland source, but otherwise the allopatric model of diversification remains unlikely. For example, glacial refugia end and the members of different refugia overlap thus providing opportunities for genetic exchange. Based on the expanding number of genomic data sets, this appears representative for viruses, prokaryotes, and eukaryotes. However, when members of divergent lineages meet and exchange genes, recombination has been shown to be limited to only certain portions of the genome. This is an obvious expectation given that evolutionary history is not only reticulate, but also divergent and diversifying. When discussing barriers to genetic exchange, I follow the conceptualization championed by Dobzhansky in *Genetics and the Origin of Species*; I discuss various barriers in the context of their being either pre- or post-zygotic (i.e. pre- or post-mating according to Dobzhansky 1937).

One of the paradigm shifts that I feel our group has contributed to in a substantial way is that relating to an appreciation of hybrid fitness. Scott Hodges and I argued for the concept of environment-dependent fitness in a 1995 *TREE* paper. Members of our research team subsequently demonstrated the relative fitness of plant hybrids under a number of natural and artificial environmental settings. Noland Martin and I recently (i.e. 2010, *TREE*) revisited the concepts and hypotheses suggested by Arnold and Hodges concerning hybrid fitness, finding support for many of the proposals made 15 years earlier. However, the idea of varying hybrid fitness predated our own work by at least 136 years. Thus, Darwin reported varying fitness among hybrids and parental forms of plants and animals. So, though Chapter 5 in this text reports novel means by which the fitness of hybrids can be estimated, we should keep in mind that many before us predicted these results. However, it is now accurate to state that estimates are available for the fitness effects of specific genomic regions (and in some cases, even specific genes) on the fitness of hybrids under varying environmental conditions. This is an enormous advance in our understanding of the role of genotype × environment interaction in catalyzing the outcome of reticulate evolutionary events.

In Chapter 6, I return to the topic of the outcomes of genetic exchange in terms of the evolutionary and ecological trajectories of individual lineages and entire clades. Though I restrict the examples to animals and plants, I discuss topics as diverse as adaptive radiations and molecular evolution. Examples of both homoploid and allopolyploid hybrid speciation that resulted in sexual or asexual animal taxa are highlighted; animal assemblages characterized by homoploid sexual, parthenogenetic, hybridogenetic, or gynogenetic derivatives are discussed. In addition, studies of allopolyploid sexual and parthenogenetic animal lineages are also presented. Finally, I discuss evidence for an array of genomic changes caused by the whole genome duplications in the animal allopolyploid species. Likewise, I review the overarching role of whole genome duplication (i.e. polyploidy) in plants. In the context of allopolyploidy, I discuss the role of reticulate evolution in adaptive radiations in entire plant clades. Similar conclusions regarding a primary role for hybridization in adaptive radiations of animal assemblages is also discussed in the context of the "hybrid swarm" model of Seehausen.

Introgressive hybridization involving endangered plants and animals continues to be perceived as having mostly negative impacts. Thus, concepts of species "integrity" etc. are often raised. Indeed, the potential loss of biodiversity through genetic assimilation of rare forms by more numerous/prolific congeners is real. However, it is also accurate that more and more instances of intentional introgression into rare forms, to increase genetic variation, have been instigated. In Chapter 7, these and other issues surrounding the conservation of plants and animals involved in divergence-with-gene-flow are discussed. While trying to recognize the real potential for extinction via genetic exchange, I also warn against a simplification of what we now understand concerning evolutionary pattern and process. In particular, I stress that conservation biologists should guard against hiding, from contributors and policy makers, the widespread evidence for non-allopatric divergence. Obfuscation might lead to a loss of credibility for the conservation biologists and thus a diminution of critical conservation priorities.

Debates concerning the evolutionary history of *Homo sapiens* have included many arguments over whether or not lineages related to anatomically modern humans crossed with related species. This includes hybridization within pre-*Homo* clades such as *Australopithecus*, as well as between the proto-*Homo* lineage and proto-*Pan* and proto-*Gorilla*. However, most of the disputes concerning reticulate evolutionary processes have centered on tests of whether or not, as the species migrated out of Africa, *H. sapiens* mated with now-extinct congeners. In Chapter 8, I review both fossil and genomic evidence that falsifies the hypothesis that humans spread into their current geographic range without introgressing with other members of *Homo*. Instead, overwhelming evidence points to a complex evolutionary history involving many genetic exchange events with multiple taxa. I point to the fact that this resembles all other examples in which related primates overlap spatially and temporally. I end the discussion in Chapter 8 with examples of how organisms making up the ecological setting for *H. sapiens* also reflect web-of-life processes. To emphasize the widespread nature of reticulate evolution and the human environment, I discuss examples of plants and animals that provide food, companionship, and drugs.

Chapter 9 is very brief, but summarizes the conceptual framework around which this book was built. Specifically, I draw attention to the underlying pattern of a web of life leading to evolutionary diversification in contrast to the tree of life envisioned by Darwin and others. In particular, I again argue that divergence accompanied by genetic exchange occurred across all domains of life and thus that it has been inaccurate to assign a major role for allopatric diversification. I end this text by suggesting that the "laws" alluded to by Darwin at the end of his *Origin of Species* now must include genetic exchange.

A glossary of definitions can be found after Chapter 9. All terms listed in the Glossary are italicized in the text where they are first used.

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