

CONTENTS

	List of Illustrations	vii
	Preface	ix
	FRANÇOIS SIMON	
	Acknowledgements	xiii
	WILLIAM H. SCHNEIDER	
ONE	The Histories of HIVs <i>The Multiple Viruses That Caused the AIDS Epidemic</i>	I
	WILLIAM H. SCHNEIDER	
TWO	Explaining the Emergence of HIVs	26
	PRESTON A. MARX	
THREE	The Origins of HIVs and the Epidemiology of AIDS	58
	ERNEST M. DRUCKER	
FOUR	From Chimps to Humans <i>A Historical Epidemiology of HIV Beginnings</i>	86
	TAMARA GILES-VERNICK AND STEPHANIE RUPP	
FIVE	A Social Virus <i>The Emergence of HIV-1 in Colonial Kinshasa, 1900–1960</i>	127
	DIDIER GONDOLA AND AMANDINE LAURO	
SIX	The Cameroonian Puzzle <i>Historical and Virological Aspects of the Emergence of HIV-1 Groups O, N, and P</i>	172
	GUILLAUME LACHENAL	
SEVEN	The Emergence and Spread of HIV-2 in Ivory Coast and Guinea-Bissau	195
	JORGE VARANDA	
EIGHT	Histories of HIVs in Broader Perspective	244
	WILLIAM H. SCHNEIDER	

About the Contributors	253
Index	257

ILLUSTRATIONS

Figures

1.1.	Timeline of HIV and SIV discoveries	2
1.2.	Number of new HIV infections and AIDS-related deaths, global, 1990–2018	8
1.3.	Timeline of HIV in context of African history	15
2.1.	Areas where SIVs of forty-six simian species have spread	31
2.2.	Bioko Island: Geological history	32
2.3.	Subspecies of mainland monkeys isolated on Bioko Island at end of Ice Age	33
2.4.	Sources in Africa of the slave trade and SIV hosts	35
2.5.	Exposure to SIV: Processing monkey bush meat for market in Sierra Leone: a family business	41
2.6.	How serial passage increases potency of SIV in humans and becomes HIV	44
4.1.	Historical range of sooty mangabey monkeys, from Senegal to Côte d’Ivoire	91
4.2.	The Sangha-Congo River network of equatorial Africa	99
5.1.	Spatial and chronological dynamics of HIV-1 group M spread	130
5.2.	Leopoldville’s African population sex ratio, 1926–55	134
5.3.	Leopoldville’s population, 1923–49	136
5.4.	Leopoldville birth and death differential, 1929–47	139
6.1.	The two-phase emergence of nonpandemic HIV-1 group O in Cameroon	179
6.2.	Health expenditures (francs per inhabitant) in French Africa, 1922–29	183
6.3.	Main accidents during mass campaigns (esp. Pentamidine/Lomidine) in Cameroon and adjacent countries, 1930–65	185
7.1.	Location and sightings of sooty mangabeys in Guinea-Bissau	200
7.2.	Major towns/cities and national parks in the range of the sooty mangabey in the Ivory Coast	203

7.3. Smallpox and yellow fever vaccinations in Ivory Coast, 1939–57	206
7.4. Map of Guinea-Bissau	209
7.5. Map of main governmental health facilities, 1972	219
7.6. Map of overlapping of war-controlled areas and tours of mass injection and vaccinations, 1964–67	226
7.7. Map of overlapping of war-controlled areas and tours of mass injection and vaccinations, 1969–70	227

Tables

1.1. Known HIV groups, geographical origins, dates, and number of cases	3
2.1. Predominant HIV origin theories	37
2.2. Extent of HIV adaptation	47
3.1. Estimated per-act probability of acquiring HIV from an infected source, by exposure act	59
3.2. First indications of HIV-1 prevalence in Central Africa, 1959–89	68
3.3. Populations studied: Blood sent to Seattle	69
3.4. First indications of HIV-1 group O prevalence in Central Africa, 1994–97	72
3.5. First indications of HIV-2 prevalence in West Africa, 1965–80	74
3.6. First indications of HIV-2 prevalence in West Africa, 1985–87	75
7.1. Population of major towns/cities of Ivory Coast	202
7.2. Urban and rural population of Guinea-Bissau, 1928–70	211
7.3. Prevalence of sexually transmitted diseases in Guinea-Bissau, 1909–74	217
7.4. Injections and vaccinations in Guinea-Bissau, 1935–60	221
7.5. Injections and vaccinations in Guinea-Bissau, 1960–70	222
7.6. Procedures using blood transfusion in PAIGC-controlled hospitals	225

PREFACE

It has been over a century since the human immunodeficiency viruses (HIVs) have infected the human population as the result of their emergence through several interspecies transmissions from nonhuman primates naturally infected by simian immunodeficiency viruses (SIVs). So far, more than forty species of African monkeys and great apes have been found to be naturally infected by SIVs, but there is little or no disease in the simian hosts. In recent decades, at least thirteen cross-species passages have been discovered from simians to humans. These viral passages to the human population have produced quite different results, ranging from several tens of millions infected to a few rare cases of a single patient. The polymorphisms of the two types of HIV and their epidemiological differences are good indicators of the difficulties encountered by the simian viruses in adapting to our species, in spite of the genetic similitudes between humans and great apes. The adaptation of a virus to a new host cannot be achieved only by overcoming the immune defenses of the host. They must also persist, depending on the epidemiological conditions, especially demographic ones, which must also be favorable for the adapted virus to become widespread.

At present, two types of HIVs have been reported with different origins and numerous subgroups classified for each. The HIV-1 types were the result of transmissions between great apes and humans; the HIV-2s are the product of transmissions from West African monkeys to humans. There are four HIV-1 groups, very unequal in the number of infections they have produced, but very useful for comparison by researchers studying them. Both their origins and clinical presentations are different. Group M (for *main* and responsible for the pandemic) and group N (for *non-M non-O*) are the result of chance transmissions from chimpanzees of Central Africa. Group O (*outlier*) and the latest group P (*putative*) come from SIV-infected gorillas. For HIV-2, there have been nine groups reported so far, all originating from sooty mangabey monkeys. These HIV-2s appear to be less adapted for infecting humans, inasmuch as although they inevitably lead to immunosuppression, the time is usually longer than is the case with HIV-1 infections.

In the past centuries, there have probably been multiple other viral interspecies transmissions between simian viruses and the human populations in Africa. But none produced an epidemic widespread enough even to be reported by the local populations and colonial doctors who watched closely for such developments. The recent emergence of so many HIV strains in such a short time therefore strongly suggests a common explanation. It cannot be the case of an isolated passage of the virus to a single case index, but, rather, recent and ongoing new conditions affecting the two species participating in the cross-species transmission, thus resulting in a successful infection of humans. It was thus only in the twentieth century that a favorable set of circumstances existed for the epidemic explosion of these viruses that changed not only the history of medicine but also our society.

Since the recognition of AIDS and the discovery of HIV, numerous questions have been raised by specialists and the general public. Most of them can be summarized as follows: Why did these HIVs emerge in human populations in the twentieth century in an extremely short time, given how long the simian viruses have existed in primates? How and why have some HIVs infected so many people worldwide while other strains have remained isolated in Africa? What can be learned from the differences between viruses and their epidemiology? Why are some HIVs less pathogenic than others?

Several studies have attempted to respond to some of these fundamental questions raised by this world-changing pandemic. This volume offers the most complete overview of the origins of the HIV viruses and their relationship to ancestral simian viruses. But the great value of the current volume is to combine African history, including colonial medicine and anthropology, with the basic sciences of virology and immunology to examine these questions. Among the findings of this novel approach are the unintended consequences of new medical interventions that became available in Africa after the First World War, such as injections and blood transfusions. Although greatly beneficial to the health of Africans, these medical procedures also favored the adaptation of the simian viruses to humans. These viruses probably emerged first in populations living in rural areas before expanding secondarily to cities like Leopoldville and others thanks to successive mutations and recombination between different strains. Then the

adaptation to humans of these cross-species transmitted viruses was generally favored by direct passage via unsterile syringes and transfusion. The human-adapted viruses further took advantage of the troubles and disturbances in the rapid urbanization of the 1960s to create one of the worst pandemics in human history.

In addition to describing the biology and epidemiology of HIV-1 and HIV-2, including their adaptation to humans, this work also demonstrates the need for close study of social behavior and the serious disruptions of traditional rural societies by colonization and urbanization that laid the groundwork for the epidemics. To that end, this volume includes an anthropological study of southeastern Cameroon that delineates the potential early path of the virus in Central Africa. Meanwhile, the chapter on the urbanization of colonial Kinshasa is a model for understanding the setting of HIV's spread there. The chapters on the history and biology of major HIV variants like HIV-1 group O and HIV-2 present the clinical and epidemiological history that underlines the heterogeneous character of these viruses and the need to examine contextual influences to explain their adaptation to humans. Even though less widespread than the major HIV strain, these variants demonstrate the need to consider all influences—whether biological, environmental, or social—to understand how an epidemic becomes pandemic.

What lessons will be learned about the zoonotic risk detailed in this work? The primary interest is to recognize the importance of medical and social interventions for triggering the HIV epidemics and to show that the origin and causes of the epidemics are different from the origin of the viruses. Ultimately, human activities are responsible, both historically and presently, for this humanitarian catastrophe. And in the recent decades, HIVs have not been the only viruses involving invasive procedures such as drug injections and vaccinations in this part of the world. At the same time and in the same regions, the hepatitis C virus has been responsible for an epidemiological disaster also linked to questionable medical interventions in mass campaigns, with major health consequences.

This history of AIDS and HIVs shows that virology is not only a natural science but also a human and social science. Unfortunately, despite what we have learned with HIVs and their origins in nonhuman

primates, inattention to wildlife and basic sanitary measures has resulted in the spread of a new coronavirus that has killed millions of people around the world in slightly over a year. Interspecies jumps like the coronavirus are probably very frequent but thankfully occur more often without epidemic consequences. The emergence of SARS-CoV-2 infections has probably followed a similar exotic interspecies path from benign animal virus to pathogenic or highly pathogenic virus in humans. SARS-CoV-2 looks particularly well adapted to human species and the current pandemic will probably be out of control for many years before natural or vaccine immunizations will help us to greatly reduce its worldwide spread.

The history of HIVs is a key to understanding the future of the COVID-19 epidemic. At a time of the emergence of a new pathogen in human populations, with up to now well over a hundred million infected and the world economy and health systems shaken, we have much to learn from the lessons of the HIVs. Here virology teaches us that history does repeat itself and that a heavy price is paid by the world community for the neglect of necessary monitoring of animal species. Like the earlier HIV pandemic, the SARS-CoV-2 pandemic has revealed the weakness of our global health systems and social organizations; it also emphasizes that political management of health does not make effective health policy.

This work successfully combines the natural and social sciences to provide the most complete and up-to-date view of the mechanisms responsible for the HIV pandemic, and it also provides a valuable new perspective on what is happening today to our world. Independently of the future success of vaccines and treatment for both the AIDS and COVID-19 pandemics, all those involved in virology and epidemiology are aware that these viruses are following a path for a long stay in the history of humanity and that major changes are badly needed to protect not only wildlife but also human life.

François Simon, MD, PhD
Faculty of Medicine—University of Paris
Head of Medical Laboratories, Hôpital Saint Louis

ACKNOWLEDGEMENTS

It is impossible to acknowledge all who helped make possible a book this long and involving so many collaborators. Nonetheless, we must first recognize and thank the major financial supporters, including the Brocher Foundation, which provided crucial support at the beginning of the project, and a major Collaborative Research Grant from the National Endowment for the Humanities that made possible the completion of the project. Research was also supported in part by Public Health Service grant RO1 AI076067 and grant P51 OD011104 to the Tulane National Primate Research Center.

I am also very grateful to the contributors for their exceptional willingness and ability to work together with colleagues from very different fields, and for their patience in seeing the project through to completion. Each of them has numerous people and institutions to acknowledge for their help, including but not limited to Indiana University, the University of Coimbra, Hôpital Saint-Louis (Paris), the Nantes Institute for Advanced Study, and the American Museum of Natural History, which kindly provided space and logistics for our meetings and conferences.

Finally, both I and my collaborators thank the editors and production staff at Ohio University Press for their dedication and perseverance under very trying conditions in order to publish this book. We hope the actual contents of the volume will help us to understand and prevent such extraordinary circumstances occurring again.

William H. Schneider
Indianapolis