

Introduction: The Convenient Tooth

A book about fossil teeth would have been unthinkable before 1669. Three years earlier, a group of Tuscan fishermen caught a colossal white shark. As Brian Switek tells the story in his engaging book, *Written in Stone: The Hidden Secrets of Fossils and the Story of Life on Earth*, that shark excited the imagination of Medici Grand Duke Ferdinando II, a great patron of the sciences (1).

The shark's body was too large to transport and had begun to decompose anyway, so its head was cut off and sent to the Grand Duke, who chose his most talented resident anatomist for the privileged job of dissecting it (Figure 1). Danish-born Nicolaus Steno (aka Niels Steensen) turned out to be the man for the job (1). As he poured over his dissection, Steno was struck by the uncanny similarity of the shark's teeth to what were then popular triangle-shaped stones called *glossopetrae* or "tongue stones" (2, 3) (Figure 1).

At the time, *glossopetrae* were used for all sorts of purposes: as antidotes to snake venom, treatments for epilepsy, amulets, and when ground into a fine powder, as toothpastes (2, 3). Roman philosopher Pliny the Elder thought *glossopetrae* dropped from the sky on moonless nights (4). Inspired by his shark dissection, Steno published his own explanation in 1669. He suggested that the corpuscular theory, which held that matter was made of tiny corpuscles, could explain how shark teeth turned to stone (5). When the teeth were buried in sediments, the corpuscles of minerals gradually replaced the corpuscles that made up teeth, transforming them into stone. This explanation is not so far from our modern understanding of how fossils form. In the case of fossil teeth though, most of the original mineral remains while mineral from surrounding sediments fills in tiny pore spaces within them in the process of permineralization.

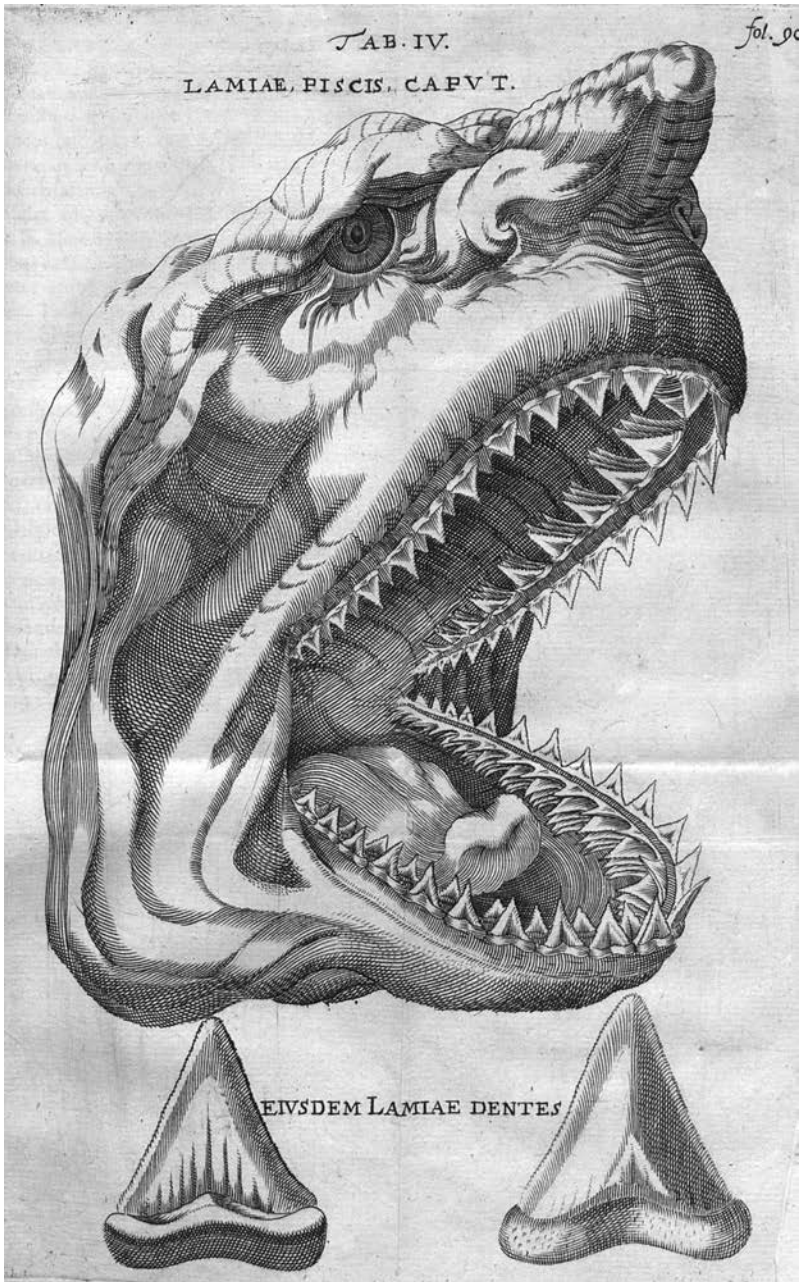


FIGURE 1: Shark head dissected by Niels Steensen (Steno). Image from *Elementorum myologiae specimen*, 1669.

That fossil teeth played such a starring role at the dawn of paleontology is no coincidence. To be sure, sharks lose a lot of teeth. But it is the fact that teeth are hard, compact, and composed of mineralized tissue that makes them prime candidates for preservation and fossilization. Indeed, most of the fossil record consists of teeth and that is also true of the human fossil record. This book is about what fossil teeth tell us about human evolution. Though they probably can't cure snake bites (I am not sure anyone has tried), the fossil teeth of our ancestors are surprisingly versatile in their uses for telling us about our past.

Teeth are the only parts of our skeleton that interact directly with our environments. Their direct interactions with food place them squarely in the path of evolutionary change. Thus, in large part, teeth tell us so much because they have evolved *directly* in response to our diets and changing ways of life. Our ancient ancestors had big teeth for processing hard and in some cases tough foods. Yet, over our evolutionary history, as we became increasingly dependent on cultural solutions such as tools and fire to break down food, our teeth dramatically reduced in size. The types of foods our ancient ancestors ate and how they ate them also left behind traces in their teeth during their lifetimes. These traces include distinctive microscopic marks on teeth produced by chewing different kinds of foods and tiny plant parts preserved in calcified plaque (dental calculus).

A less well-appreciated fact is that, as parts of our anatomy, teeth are affected *indirectly* by changes occurring elsewhere in our bodies, whether these changes occurred over evolutionary time scales or during the lifetime of an individual. Thus, evolutionary changes in a species' teeth tell us about evolutionary changes in the species as a whole. For example, like the rings of trees, growth lines in enamel (the outer covering of teeth) form at known intervals. But, instead of representing years of growth like tree rings, enamel growth lines represent *days* of growth and are preserved in enamel that is millions of years old. Because the growth of different parts of our body is generally integrated, the pace at which teeth grow, to a large

extent, reflects the pace at which our bodies grow. We can track the evolution of extended juvenile growth periods, a hallmark of humanity, by tracing changes in tooth growth in our ancestors through time. Over individual lifetimes, tooth growth during childhood can be disrupted by malnutrition and disease, telling us about episodes of physiological stress our ancestors experienced as they grew.

Evolutionary changes in teeth took place in the broader context of human environments that included social relationships and culture. The direct and indirect responses of teeth to our physical, social, and cultural environments make teeth a model system for tracing the origins and evolution of our dietary diversity, extended childhoods, long lifespans, and other key features of our unique biology. These insights are made possible because over the millions of years of the fossil record, teeth preserve a high-fidelity record of their own growth, wear, chemistry, and pathology.

On top of this, the morphology of teeth – their shapes, cusps, and grooves – is highly heritable. This means that a great deal of variation in dental morphology is caused by variation in genes, rather than by the environment (6). For this reason, dental morphology can be used as a marker of species identities and relationships. It's no wonder that the eighteenth-to-nineteenth century French naturalist Baron George Cuvier is reported to have said "Show me your teeth and I will tell you who you are." Cuvier was referring to the distinctive features of vertebrate species' fossil teeth. He could just as well have made the same claim on a smaller scale for hominins, the taxonomic group of related species that branched off from our common ancestor with chimpanzees. (Figures ii and iii illustrate the morphology and names of the principal cusps of modern human molars. These principal cusp names will be used throughout the book.)

I have studied many of the teeth of fossil hominins, from *Australopithecus* to Neanderthals, and have conducted research on or related to several of the topics covered in this book. In doing so, I have grown to appreciate the importance of teeth in our evolutionary

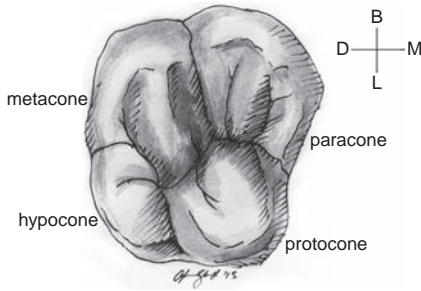


FIGURE II: Occlusal (chewing surface) view of upper right first molar with names of principal cusps. In the upper right of image is a direction key. "B" stands for "buccal," the side of the tooth facing the cheek; "L" for "lingual," the side of the tooth facing the tongue; M for "mesial," the side of the tooth facing the midline (and in the case of molars toward the front of the mouth); and D for "distal," the side of the tooth facing toward the back of the mouth. Drawn by Alyssa Starrett.

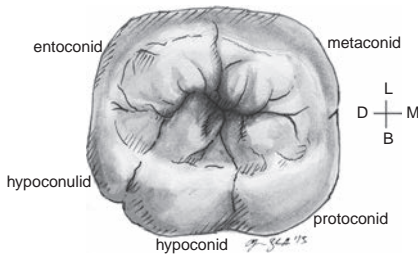


FIGURE III: Occlusal (chewing surface) view of lower right first molar with names of principal cusps. At the right of image is a direction key. "B" stands for "buccal," the side of the tooth facing the cheek; "L" for "lingual," the side of the tooth facing the tongue; M for "mesial," the side of the tooth facing the midline (and in the case of molars toward the front of the mouth); and D for "distal," the side of the tooth facing toward the back of the mouth.

history and the many clues about our past that fossil teeth hold. What prompted me to write this book was a desire to synthesize dental insights into human evolution. Here, I emphasize how evolutionary changes in human teeth are linked to key evolutionary trends in human evolution: the broadening of our diets, our increasing reliance

on culture, our expanding brains, and the lengthening of our childhoods and lifespans. Because of these links, and because of the detailed information fossil teeth preserve, insights into human evolution are possible that are difficult, if not impossible, to achieve through other sources of fossil or archaeological data. Here, I further highlight how the evolution of teeth reflects human evolutionary dynamics, in which cultural adaptations shape and are also shaped by biological adaptations.

This book is meant to be an accessible account of many of the major insights into human evolution that can be gleaned from the study of teeth. In some instances these insights are about our teeth themselves, but more often these insights relate to larger evolutionary trends. The book is not about the detailed morphology of teeth but about the hard-earned insights into human evolution that dedicated researchers have extracted (excuse the pun) from fossil teeth. I intend the book for those who have a passion for human evolution in general and/or a particular curiosity about how human teeth inform us about our evolutionary history.

Intended readership also includes undergraduates in human evolution or dental anthropology courses. But the book is not meant to be a textbook for these courses. The book integrates dental findings with debates and issues in paleoanthropology, and in this respect, I hope that the book will be used to generate discussion in undergraduate classes. Most of the chapters (i.e., the nonintroductory ones, Chapters 1 and 5) would also work as starting points for discussion in graduate-level classes.

The book is divided into two parts: the first concentrates on the earlier time period of human evolution (primarily on Australopiths) and the second on the later time period (focusing on the genus *Homo*). (See Figure iv for a timeline of human evolution.) Most chapters emphasize particular species or lineages that are subjects of debate and/or extensive research activity. Part I covers the broad outline of early human evolution with special attention to teeth (Chapter 1), explores what various lines of dental evidence tell us about diet in our

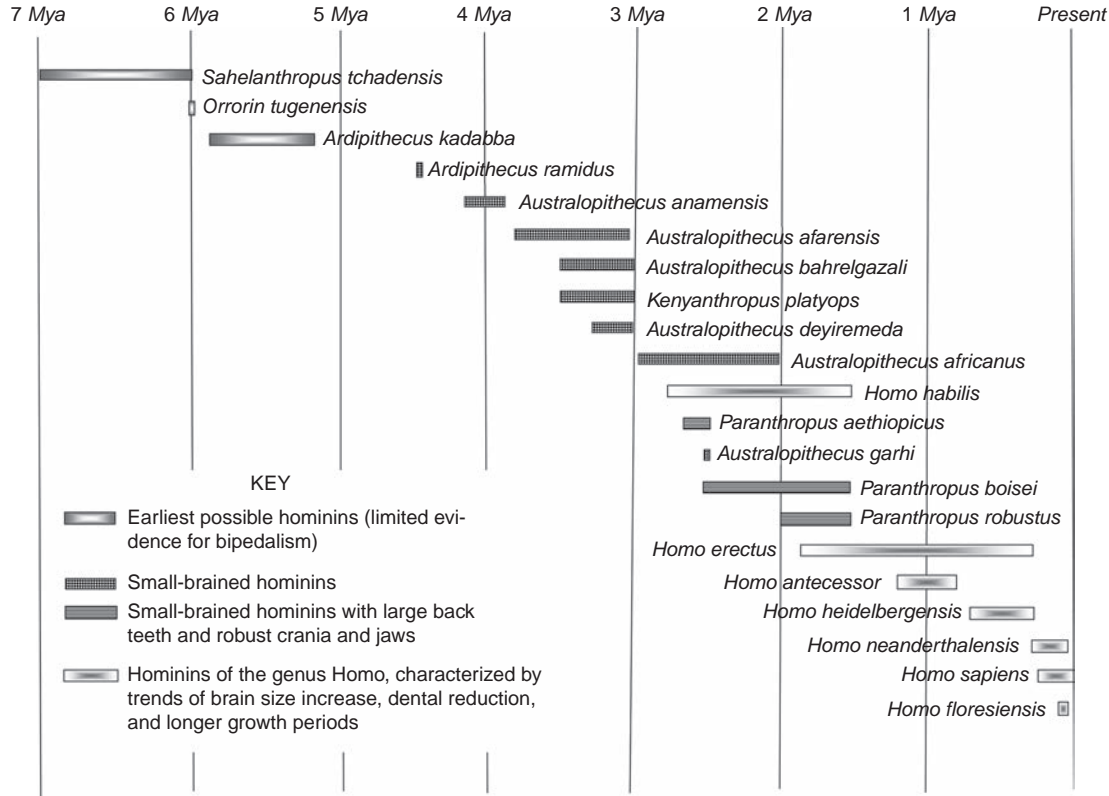


FIGURE IV: Time-line for human evolution. Species are ordered chronologically by their approximate first appearance dates. Drawn by author.

early (pre-*Homo*) ancestors (Chapter 2), considers whether sexual dimorphism in hominin canine teeth is related to levels of competition among males (Chapter 3), and synthesizes our understanding of what incremental growth lines in fossil teeth reveal about the length of juvenile growth periods in our earliest ancestors (Chapter 4).

Part II focuses on the genus *Homo*. Chapter 5 sketches the broad outline of evolution within the genus *Homo*, again with special attention to teeth. Chapter 6 explores interrelationships among changes in tooth size, culture, and diet in the genus *Homo* prior to Neanderthals and modern humans. Chapter 7 evaluates dental evidence for the evolution of childhood and longevity in the genus *Homo* before Neanderthals and modern humans. Chapter 8 highlights dental insights into Neanderthal phylogeny, behavior, diet, and life history. Chapter 9 emphasizes the contribution of teeth to understanding the origin of anatomically modern *Homo sapiens* and our dental diseases. Concluding, Chapter 10 recapitulates the book's main points and explores how an appreciation of our dental past can help us understand how we view and treat teeth today.

To pursue the insights that fossil teeth offer, we first need to discuss how evolutionary relationships among fossil species are assessed and to sketch the broad outlines of early human evolution.