

## Alan Walker and Pat Shipman, *The Ape in the Tree. An Intellectual and Natural History of Proconsul*

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Since the early 1930s, when the first fossil catarrhines from the early Miocene of East Africa were introduced to the scientific community, these primates have figured prominently in interpretations of the phylogeny of apes and humans. Indisputably, the best known of these fossil catarrhines is *Proconsul*, which is represented by hundreds of teeth, jaw fragments, and isolated postcranial elements, as well as a number of partial skeletons, from sites in Kenya and Uganda. In fact, we know more about the skeletal anatomy of *Proconsul* than any other Miocene catarrhine. Although there has been considerable debate about the phylogenetic placement of *Proconsul* (opinions range from it being a stem catarrhine, a stem hominoid, and a stem great ape), there is, nevertheless, universal agreement that *Proconsul* is profoundly important for understanding the divergence, evolutionary history, and paleobiology of the earliest hominoids.

The *Ape in the Tree*, written by a husband and wife team, explores what we know about the evolutionary relationships and biology of *Proconsul*. Alan Walker is the narrator; Pat Shipman is the principal writer. Fortunately, Walker is a wonderful storyteller and raconteur, while Shipman is a gifted writer, with the ability to present complex concepts and ideas with superb clarity, elegant style, and above all a faithfulness to reporting popular science without compromising its accuracy or rigor. The authors have worked together previously on other successful publishing ventures, and this book is a similar triumph. I was initially concerned that *Proconsul*, which lacks the immediate appeal of Shipman's previous subjects (such as *Archaeopteryx*, *Homo erectus*, Neanderthals, and racism), may be a hard sell for a book topic aimed at a general audience. However, where this book wins out is that Walker has been directly involved, as one of the major players, in research on *Proconsul* for the past two decades, and he has contributed so much to what we know today about its natural history and evolutionary relationships. This book is a personal reflection of Walker's involvement with *Proconsul*, and it is chock-full of fascinating anecdotes and insights.

However, the story of *Proconsul* begins about a decade before Walker was born. The first finds were made in the late 1920s and early 1930s by a handful of intrepid paleontologist and colonial

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officers. Walker and Shipman relate the stories of these early expeditions to East Africa, beginning in 1909, and culminating in the first discoveries of *Proconsul* by Dr. H. L. Gordon at the site of Koru in Kenya in 1927. Gordon's finds were forwarded to A. T. Hopwood at the British Museum of Natural History in London, who immediately realized their importance, and set off (with a young Louis Leakey) in 1931 to collect additional fossils. On his return, Hopwood described several new species of fossil primates, including *Proconsul africanus*. As someone who directs paleontological research in East Africa today, I share Walker's admiration for the resilience and fortitude of these pioneering figures. I suppose there is nothing quite like unconditional belief in the virtuous enterprise of Empire-building or missionary zeal to motivate young men and women to excel and persevere under the most arduous of circumstances. As Walker and Shipman recount, D. B. Pigott, one of the first colonial officers to survey paleontological sites in Kenya, had his boat capsized by a wounded hippo and was then eaten by a crocodile (and I think that I've been on some tough expeditions!). In an act of whimsy, Pigott's legacy in African prehistory lives on because an extinct species was later named in his honor – of course, you guessed it – a fossil crocodile.

The most influential and productive phase of research on *Proconsul* was initiated by the fieldwork of Louis and Mary Leakey and their colleagues from the early 1930s until the 1950s. The Leakeys collected at a number of key Miocene localities in Kenya during this period, but the most productive sites were those at Songhor and on Rusinga Island. The key contributions at this time were the remarkable discoveries of a skull and a partial skeleton of *Proconsul* in 1948 and 1951, respectively, followed by the landmark monographs written by Le Gros Clark and Leakey and Napier and Davis describing the wealth of new material. This is where Walker first crossed paths with *Proconsul*, as a doctoral student of John Napier's in London in the early 1960s. Interspersed in the narrative of the early history of *Proconsul* are tales of the remarkably preserved fossil insects from Rusinga Island, and how Le Gros Clark mistakenly described crocodile femora as *Proconsul* clavicles. As a graduate student I was always reassured and heartened by the latter story because if an anatomist of the stature of Le Gros Clark could make such an error, then surely a neophyte such as myself would be excused similar transgressions during my career. However, I have since learned that this is not the case, and fossil clavicles and marine mammal ribs should be avoided at all cost.

In the early chapters of the book, Walker and Shipman also tackle the thorny problem of interpreting the phylogenetic relationships of *Proconsul*. They explain that *Proconsul* is a stem hominoid (a somewhat different view from that presented in Walker's earlier writings, where he favored its great ape status), a deceptively difficult concept to appreciate for the general reader, but the authors do an exceptional job in explaining it. Unfortunately, Walker and Shipman also perpetuate the historically-rooted preconception that the phylogenetic placement of *Proconsul* must be an either/or dichotomy. In other words, is it an ape or a monkey? Since there is no question that *Proconsul* is not an Old World monkey, then logically it must be a hominoid. However, having introduced the concept of stem group, a third option remains a possibility, that *Proconsul* is a stem catarrhine (i.e., the sister group to hominoids and cercopithecoids). This latter view is briefly mentioned by the authors (as the viewpoint subscribed to by this reviewer), but dismissed with little discussion. This is fair enough, since the prevailing view is that *Proconsul* is a stem hominoid, and it avoids cluttering the narrative with too many contrary opinions. Besides, it would take a very discerning consumer to buy a book entitled "The Stem Catarrhine in the Tree."

The story then leaps forward in time to 1980, where Alan Walker becomes directly involved with research on *Proconsul*. As a result, more than a decade of history is overlooked, and important fieldwork and intellectual contributions by David Pilbeam, Peter Andrews, and Martin Pickford, among others, are only fleetingly cited. Given that this book is intended to be Walker's

personal reflections, such an oversight is perhaps forgivable, and besides, these colleagues can always write their own books and fill in the missing chapters.

The centerpiece of the book (Chapters 4–6) describes Walker's role in the discovery of important new pieces of the famous *Proconsul* skeleton, and the spectacular discovery on Rusinga Island in 1984 of nine partial skeletons of *Proconsul*, ranging in age from infant to adult. The subsequent analyses of these finds by Walker, and his colleagues and students, have provided major advances in our understanding and appreciation of *Proconsul*. It is a wonderful story of paleontological discovery at its best. Subsequent chapters (7–8) review what we now know about the anatomy, alpha-taxonomy, and evolutionary relationships of *Proconsul*. This is fascinating stuff, and shows how much can be deduced about the paleobiology of an extinct primate by skilled and creative anatomists and paleontologists. The last few chapters (9–12) of the book detour into Walker's work on other Miocene catarrhines, life history and dental development, molecular clocks, the "In and Out of Africa Hypothesis," and his latest research on the relationship between the bony labyrinth of the inner ear and locomotor behavior. Although *Proconsul* remains a tangential thread throughout this discussion, I have to confess that the book loses its narrative coherence at this point. I think that the general reader will find it difficult to relate these diverse research projects to the simple theme of finding out more about *Proconsul*. The earlier chapters on the history, discovery, and analysis of *Proconsul* were more enjoyable and more enlightening, and the material available so rich, that it could have been expanded to fill the entire book.

In sum, *The Ape in the Tree* is an enjoyable and worthwhile read for anyone interested in vertebrate paleontology and primate evolution. I recommend it highly. It informs us about what can be inferred about the life-ways of an extinct form from the tattered fragments of biology that are revealed to us from the fossil record. More than that, it provides a reflection of Alan Walker's passion to know and understand *Proconsul*. Most would view *Proconsul* as a collection of fossil teeth and bones laid out in museum drawers, but for Walker it is an opportunity to explore the natural history of a unique and fascinating primate, one that just so happens to have been extinct for the past 14 million years.