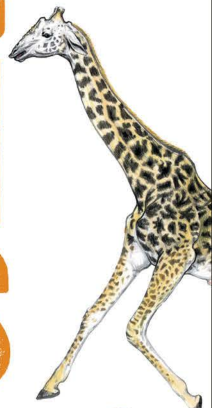
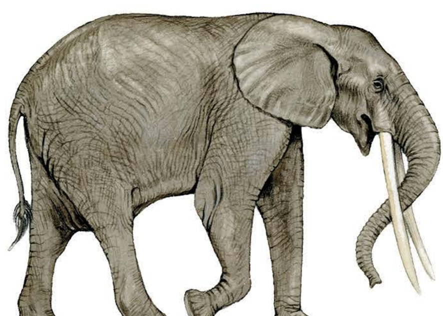
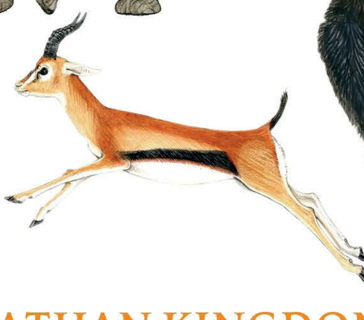
THE KINGDON FIELD GUIDE TO AFRICAN MAMMALS



SECOND EDITION





JONATHAN KINGDON

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SECOND EDITION

JONATHAN KINGDON

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About the author
Jonathan Kingdon was born in Tanganyika and has spent the better part of his life in Africa. He taught at Makerere University, Kampala, for many years and is now a Research Associate at the Department of Zoology, University of Oxford. He has been acclaimed as both a leading academic and a prominent artist, and awarded several prizes and medals. The millennium issue of *American Scientist* named his seven-volume *East African Mammals: an Atlas of Evolution in Africa* as one of the 'One Hundred Books that Shaped a Century of Science'. Richard Dawkins describes him as 'a world-class zoologist, ecologist and writer…a Living World Treasure…an artist with words and a poet with images'. First published in 1997, the *Kingdon Field Guide to African Mammals* was characterised as 'a work of almost heroic proportions…an extraordinary fusion between science, natural history and art' (Tim Flannery). The second edition of this guide greatly augments that work, incorporating much information accumulated over the intervening years. Kingdon was also founder and senior editor of the six-volume *Mammals of Africa*, which was awarded the prestigious Dartmouth Medal in 2014 by the American Library Association. Many of his 16 books (totalling 5,000 pages) have been translated into languages other than English and he has published numerous papers, articles and chapters. Exhibitions of his work have been shown in museums and galleries in Africa, Australia, Europe, Asia and the USA.

CONTENTS

PREFACE AND ACKNOWLEDGEMENTS

The motivation and impetus to prepare a guide to the African continent's greatest natural resource, its mammals, came from a mix of immediate and more distant influences. My parents, my ayah, Saidi Batale, and naturalists such as Bill Moore-Gilbert, Hamisi Sikana, Willoughby Lowe, Mtemi Senge Masembe, Hugh Elliot and Fairfax Bell illuminated a nomadic youth in Tanganyika. As a child I was subject to the vulnerabilities of existence during war-time, and a witness to famine, floods, locust swarms and grand dramas of life and death on the plains of Serengeti. I learned, early on, that all the glories of animal and plant life that surrounded me were no less than life's parade of triumph over all the vicissitudes that being and time could throw at them. My childhood awe for nature's dangerous beauty and wasteful fecundity soon led on to a more disciplined interest in natural history and an explicitly Darwinian outlook on life. Reg Moreau and Desmond Vesey-FitzGerald were early influences while L.S.B. Leakey, Sir Julian Huxley, Peter Miller, Leonard Beadle and Alan Walker were among those who helped, and provoked, my compiling *East African Mammals: An Atlas of Evolution in Africa* (Kingdon 1971-82). That work was an essential precursor to this book; indeed, since its publication there has been continuous pressure, from friends and publishers alike, to condense the text and enlarge the range of that work to embrace a continental scope. That, in turn, led on to the *Mammals of Africa* project, which was published in six volumes in 2013. I owe gratitude to all my fellow authors and editors on *Mammals of Africa*, most especially my brilliant co-editor, Mike Hoffmann.

A decisive influence on this field guide came from my family, especially my sons: Zachary, who read, processed, discussed and helped refine the entire text of the first edition, and Rungwe, who firmly pushed me into taking the first plunge. Elena selflessly supported a lifetime of research on mammals. This second edition owes its existence and completion to Laura.

I am indebted to many institutions for their support over the years, from Makerere University in Uganda, WildCRU at Oxford University in England, CSIRO in Australia, Skidmore College and Duke University in the United States to briefer or less formal associations with Kyoto University, Japan, various museums both within and outside Africa, Wildlife Departments, National Parks and numerous universities. I owe some independence of mind and movement to all those who have purchased my paintings, drawings, prints, sculptures and books.

The contents of this field guide are drawn from observations made in various parts of Africa, often in the company of friends and colleagues. They are also compiled from publications, correspondence and conversation with more people than can be acknowledged by name but some have had a more direct role. Tim Davenport, Morris Gosling, Colin Groves, David Pye, Simon Bearder, Alan Root, Joan Root, David Macdonald, Claudio Sillero, Patrick Duncan, Mark Stanley Price, Redmond O'Hanlon, Tom Butynski, Annie Gautier, Hilary Morland and John Fanshawe vetted structure, blocks of text or illustrations for the first edition. Annie and Jean-Pierre Gautier, Tom Butynski, Steve Gartlan and many others, including Tony Archer, John Skinner, Chris Hillman, Andrew Conroy, Gerard and Ahn Galat, Leslie Scott, Doug Shiel, Caroline Tutin, Tom Struhsaker, Lysa Leland, Robert Glen, Dick Estes, Keith Eltringham, Russel Friedman, Margaret Kinnaird, Tim O'Brien, Fritz Vollrath and Tim Davenport have hosted me in camps or homes in Africa. Their company, ideas and hospitality have contributed in more ways than can begin to be enumerated. Likewise wildlife and national park authorities in many African countries (notably Tanzania, Kenya, Uganda, Ethiopia, Côte d'Ivoire and Cameroon) have helped with permits, hospitality, transport and guidance, assistance that has been vital in building up a broad overview as well as detailed documentation of the mammals. The Wellcome Trust gave vital aid (1968–78).

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My association with Academic Press, which dated back to 1966, was always cordial and I thank Roger Farrand and Andy Richford for maintaining a long and fruitful collaboration, also Maggie O'Hanlon and Shammima Cowan for their editorial talents on the first edition. At Bloomsbury Publishing I've been more than fortunate in inheriting Nigel Redman as a dynamic commissioning editor, David and Namrita Price-Goodfellow as designers and Elaine Leek as copy-editor; I am deeply grateful for their very special talents. I am also grateful to Bloomsbury Publishing for allowing me to reproduce various maps, figures and illustrations from *Mammals of Africa*.

Perhaps this short list of today's enthusiasts will help give heart to tomorrow's warriors, who must carry on the fight to save Africa's fauna and flora and the deeper realities of which they are an expression.

CHECKLIST OF SPECIES

INTRODUCTION TO THE FIRST EDITION

A field guide, like any other artefact, has an individual history and behind that a much longer generic history, in this case of books about African mammals. Such books are products of their times as well as of authors, and over some 500 years they reflect a changing history of ideas as well as a growing list of species.

Acknowledging debts to previous authors is important both for the data and for the ideas they have bequeathed. They also provide juxtapositions to help define what is new about one's own time and about one's own work. A major peculiarity of this volume is its genesis within tropical Africa. Any home-grown author has frequent reminders that books on African subjects originated abroad and that visitors are still major interpreters. Field guides do not escape that legacy.

For the people who first printed books, African mammals were mostly distant fable. Thus, mythological Bestiaries were the first of four main phases in the development of books about African animals.

The second phase is linked with Europe's expansion and colonialism. Animals, as in Europe, were little more than playthings of the privileged – game. Guides for this period began as hunters' 'Records of Big Game'.

In the third phase there was a change in vocabulary, 'game' became 'wildlife' as vast urbanised audiences received animal images and natural history stories in their homes and schools via books and television. The life histories of some popular species became familiar through the work of talented film-makers, naturalists and scientists. This phase coincided with the growth of mass tourism and the declaration of many magnificent national parks. Most current field guides are oriented to this period of expanding tourism and the growth of natural history as a major form of recreation.

Now we have begun a fourth era, marked by our self-discovery as mammals that have created their own extraordinary niche. It is a niche in which consciousness and technological power have brought responsibility for the fate of our own and all other life on earth. Space travel and satellite photography have given us a new awareness of our cosmic fragility and biological limitations, while problems created by pollution and environmental degradation have led to a new concern for the health of the biosphere. As we are ever more frequently reminded of the finite nature of natural ecosystems and their fragile complexity, Africa's uniquely rich 'biodiversity' has become a by-word. That biodiversity happens to include us, so that the ecology that nurtured our ancestors and helped shape our intellect and character demand that conserving Africa's diversity of plants and animals receives global respect and support. Such contemporary perspectives have shaped this field guide as they have my other books.

We live in a time of unprecedented accumulation of knowledge. Each year we learn more about living and extinct animals, about pre-history, human origins and processes that govern our past, present and future. From this cascade of new discovery has come the awareness that the survival of other animals is not entirely detached from our own. At the same time human penetration into previously untouched habitats has led to the spread of African primate diseases, such as HIV and Ebola virus, to cities and communities around the world, heightening our sense of proximity to, yet ignorance of, the natural world from which we have emerged so very recently. This is no aesthetic or historical conceit. Detaching ourselves from our biological past renders us less likely to understand our true nature. Dangerous repercussions follow in medicine and human ecology.

There is everything to be said for the observation of African mammals as recreation. As more people gain the ability and leisure to see African wildlife their pleasure and awe may be heightened by an awareness that what they are seeing would have been a familiar aspect of the existence of their ancestors, from ancient hominids to recent hunter-gatherers.

We call individual types of organism 'species' but, in the texts that follow, I try to give an indication of the countless structured relationships that each animal has with other species of animal and plant, and with the African landscape, its climates and a pre-history that stretches back many tens of millions of years. For a naturalist there are few greater delights than that of discovering for oneself the extraordinary fitness of animals for the niches they occupy. As observation reveals why animals are formed the way they are and how they relate to their surroundings one's sense of wondering enquiry can only increase. Curiosity may be the underlying motivation for the study of natural history but knowledge of African mammals easily leads on to more involved interests. As we come to understand how human beings have evolved within African natural communities we can gain a perspective on ourselves as an inextricable part of mammalian life on earth. This, surely, adds a new incentive to the joys of learning about African mammals.

INTRODUCTION TO THE SECOND EDITION

In the nearly 20 years since the first edition of this guide was written, several revolutionary developments have taken place, suggesting that a new edition was due.

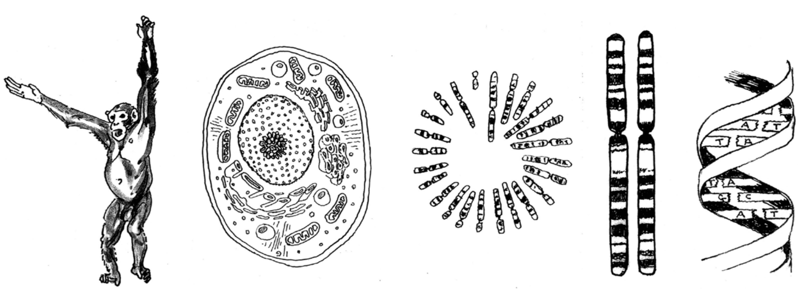
One important development has been a re-figuring of what our subjects mean in the context of human origins. It is now more fully realised that other mammals were dominant components of the community of plants and animals in which human ancestors, like any other mammal, struggled to survive over some millions of years. Our existence is proof of their success. We now know, with absolute certainty, that humans could *never* have evolved in the Americas or Australia. Only Africa (with some periods in and connection with Eurasia) could have generated a mammal with such a complex, convoluted evolutionary history. Only humans could have invented science and only a scientifically minded animal was equipped to enquire into its own origins!

Over the past 20 years scientists have posed just such questions and they have begun to develop tools for the task. Only in Africa have they a hope of finding answers and, step by step, discovering/recovering our *true* biological history. Many of the mammals portrayed here actually shaped aspects of human evolution (as competitors, predators, food, fur; as path-makers or sources of disease and epidemics). For 99% of history our ancestors had to fit in among them. Today mammals have to fit in among humans, but to fail to take our past into account for our future would be, and is, abject stupidity. This edition acknowledges the authority of that history; thus new information informs and extends this inventory of a continental fauna that is unlike any other. Among the more potent tools for this task is the science of molecular genetics.

During the past two decades the revolution in genetics has been gathering pace. Our knowledge of phylogenetic relationships has shifted from comparisons of external morphology and some inspired guesswork to much less subjective criteria. Thus a handful of very circumspect family trees in the first edition can be compared with this one, where more than a score of genetically based (sometimes dated), molecular phylogenies are on offer. These trees can be fallible and remain tentative, but our new-found ability to reconstruct genealogies continues to improve. It reflects a major advance in science (and, when applied to human origins, another step towards replacing poetic mythology with an inspiring, science-based re-telling of the story of how we came to be).

New genetic trees for all major mammal lineages have led to some significant re-ordering of the way organisms are classified and listed. It even led, in 1998, to recognition of an entirely new supercohort of mammals, the Afrotheria, with which this edition now begins. Indeed, the sequences and contexts in which mammal groups are now presented has been informed by the work of my many colleagues writing in *Mammals of Africa*, a handbook that I initiated in 1996 and led to completion in 2013. It is a measure of the pace of research and discovery that some of the most significant of all molecular phylogenies have only been published in the last year or so!

The genetic techniques and molecular clocks that have been developed over the past 20 years have greatly enhanced our understanding of biogeography and the evolution of species. This is because multiple genetic relationships, when plotted in space and time, help reveal pan-African dynamics of speciation. One pattern in particular recurs again and again, confirming that there are two major 'realms', effectively ecological and geographic 'islands', within this big, blobby continent.



Today, expressions of the 'science of shape' embrace internal organs, tissues, cells, enzymes and molecules. A living mammal contains multiple 'shapes', each of them expressions of self-regulating systems that range from gene to whole body. A chimp body contains about 100 trillion cells; each cell has a nucleus; each nucleus has 48 paired chromosomes; of every pair, one chromosome is from each parent; chromosomes consist of packed strands of DNA. Genes are DNA segments coded to make proteins.

Africa's 'up-ended L' shape has generated two axes, or biogeographic realms. One is an east–west axis that is dominated by latitudinal bands from forests to Sahelian steppes. The other is a north–south longitudinal axis running from Horn to Cape. (These realms are discussed further under the rubric of 'The Past' in the section on The African Environment.)

Yet another development has been discovery of many new species. A few are the outcome of modern penetration into remote regions or habitats (where local people were usually already familiar with animals only now proclaimed as new to science). However, other changes have resulted from new techniques, insights and theories leading to reassessment of earlier rankings. In many cases I pass on, and acknowledge these 'new' species (but, for caveats, see 'Naming Species'). Other scientific advances have enhanced our ability to comprehend the geology, topography and climatic past of Africa. Some of these are touched upon in my discussion of African environments.

Another very important development for Africa has been the grounding of national education programmes in science. This has made substantial advances in all progressive countries so that the educational role of this guide has also expanded. Affirmation of our commonality and of our recent biological origins in Africa is weakening some earlier, once-dominant, non-scientific cultures. Most notable among these were actual or would-be empires or theocracies, all of non-African origin, that trivialised, mythologised, commodified or infantilised animals. With the certainty that we, *Homo sapiens*, came out of Africa and evolved within its ecological communities, our cousin primates and other mammals have had to be taken more seriously, as has their conservation and the plight of Africa's natural environments. A reference book, such as this guide, serves to increase people's access to such essential and updated information. Even more important, it serves to reveal just how extraordinary Africa is – how unlike any other continent. In spite of this awareness, a new dilemma for Africa is the birth of a cosmopolitan generation that fails to appreciate this fact. It is a generation many of whom, unwittingly, collude in degrading Africa to the semblance of any other sorry continent.

A guide such as this one also has a role to play in Africa's current openness to the world. So I hope it will help ease access to some of the wonders of this unique continent. The past 20 years have seen a great expansion in tourism and the development of first-class national parks, reserves, lodges, conservancies and educational programmes. Botswana, once an environmental pariah, now has fine parks, conservation education in schools and a flourishing and much envied tourist industry that provides numerous forms of employment and a more environmentally oriented culture. Botswana's leading role in conservation is structurally linked to its rating (by Transparency International) among the top countries in the world for probity and sound governance.

By contrast, several African countries rank among the most corrupt in the world, namely Somalia, Sudan, Libya, Equatorial Guinea, Eritrea and Chad (Transparency International). As a result, all these countries have vestigial educational opportunities, are losing or have lost much of their large mammalian fauna and earn near-zero income from visitors. During the last two decades Ethiopia's globally important natural estate has suffered horribly under very poor leadership. Cameroon, biologically one of the richest regions on this planet, has become one of the most tragic of all African countries. Where I once walked in forests of unrivalled diversity and endemism, sterile rubber trees, oil palms or pineapples now grow in rows that stretch to the horizon. The last pathetic remnants of its forest fauna, like that of many other equatorial countries, hang, for all to see, on scaffolds beside main roads, their contorted, maimed and mistreated bodies a dying reproach to the cruelty and rapacity of humans.

National education and research programmes as well as the larger conservation community can all be faulted for neglecting to educate local people, such as those of south-western Cameroon, about the global significance of their own backyard. Some vision, better education and more local involvement in conservation could have opened new opportunities in research, teaching and in tourism infrastructure. Before it is too late, Cameroon and many other nations need to develop an awareness that Africa has more to offer the world than any outsider can offer Africa.

In conclusion, the first edition of this guide was written in a more leisurely era. Today, science has become the fastest-moving frontier in contemporary culture. Its commercial spin-offs are legion but, among them, we can already identify aspects of modern agribusiness that threaten the survival of many mammals and their habitats. The welfare of many rural people in Africa is no less at risk. In an ever-accelerating, ever more global and ever more predatory world we *must* identify and hold the main agents of destruction accountable. We must also invest in ecological research and environmental education – a more knowledgeable respect for nature in the mother-continent.

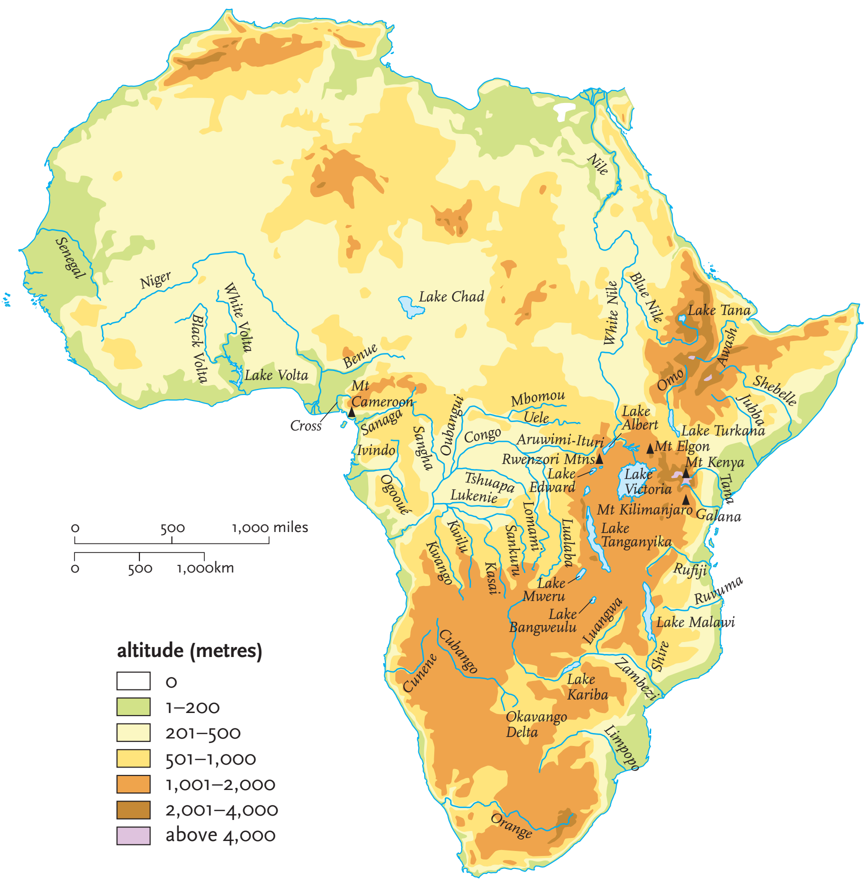
NAMING AND MAPPING SPECIES

This field guide lists more than 1,160 mammalian species from Africa and maps the majority. While it is certain that more species await discovery (especially among bats, shrews and rodents), the overall scale and composition of Africa's mammal fauna is now reasonably well known, even if names sometimes chop and change. As the checklist and guide to a continent's known mammalian fauna, the pages that follow have been brought up to date and some of the latest ideas about classifying and naming species have been incorporated. There are descriptions, illustrations and maps of all known species of primates, small groups, such as pangolins and hares, all large mammals, carnivores and squirrels. All genera of shrews, bats and rodents are described and illustrated but limitations of space have precluded species profiles in some genera with many species (for example, there are more than 100 species of *Crocidura,* the white-toothed shrews, and among some 100 species of gerbil are at least 36 species of *Gerbillus*). The written profiles of mammals are supported by a full-colour illustration (generally of an adult male), skull drawings of smaller mammals, and a map showing the animal's overall range. Bloomsbury Publishing has kindly authorised reproduction of the distribution maps used in this guide's sister publication, *Mammals of Africa*, with, where necessary, some additional, revised, enhanced or 'zoomed-in' maps. In some exceptional cases, past and present distributions are presented.

Political map of Africa.

Naming presents innumerable challenges for a work such as this. The classification and nomenclature first published by Linnaeus in 1758 provided a hierarchical system and a set of Latinised scientific names that could be applied to all organisms and be used by all nationalities. This has ensured that, no matter what language is used, all naturalists and scientists can be certain of referring to the same animal or plant so long as it has been correctly identified. Vernacular names are therefore much less important than scientific ones. The former often vary or have alternatives while the latter are arrived at by strict rules of priority and can only be changed when the rules are shown to have been broken by the application of a mistaken name. Many mammals have been given informal regional names and some of these are retained in this edition, but names used in the first edition have been augmented by ones published in *Mammals of Africa*. In addition to English and French, German and Swahili names have been given where possible.

Today new genetic techniques are refining the naming process, sometimes showing that long-recognised separate species should be amalgamated or, more frequently, subdivided. Molecular phylogeny also allows recognition of subgroups and species clusters. Where 'molecular clocks' can be attached to these trees the timing of branch internodes can be assessed. These, in turn, often suggest a re-ordering of the sequences in which species or groups are presented to the reader: more conservative taxa first, most recently evolved last. Changes in names and sequences can be confusing but, in the long run, naming and ancestral trees will, eventually, become more,



Altitudes and major rivers of Africa.

not less, stable. All changes in nomenclature still have to conform with well-tested Linnaean rules.

In the past two decades a dozen new species of primates have been discovered (or named/renamed on the basis of new information): a likely ur-mangabey on a Tanzanian mountain, some guenons in central Africa and still more galagos (their identities first signalled by sound recordings of their distinctive voices). Furthermore, genetics has led to re-groupings or revisions of species by specialists. New genetic evidence has created or abolished higher taxa, ranging from the genus to the family. These higher classifications help us to allocate individual species to their natural groupings. I have therefore included brief profiles of most tribes and families. To avoid unnecessary repetition, subgroups, infra-groups and super-groups are sometimes ignored or subsumed within larger categories.

Linnaean systematics were originally designed, like conscientious book-keeping, to bring order to the apparent chaos of diverse species. An almost incidental by-product of this hierarchical system has been the provision of a useful indication of relationships and hence a guide to how species have diversified and lineages branched out. As taxa move higher, a single species is joined by more cousins, each step embracing more and more ancestral categories. By way of illustration, the following represents the position of human beings within the Linnaean structure:

Class Mammalia
Subclass Eutheria
Order Primates
Suborder Haplorhini
Infraorder Catarrhini
Superfamily Hominoidea
Family Hominidae
Subfamily Homininae
Tribe Hominini
Genus *Homo*
Species *Homo sapiens*
Vernacular name Human Being

Reflecting on the family to which we all belong, Darwin, in 1837, wrote "animals, our fellow brethren in pain, diseases, death, suffering and famine – our slaves in the most laborious works, our companions in our amusements – they may partake of our origin in one common ancestor – we may be all netted together." Thus do deep truths lie bedded within the simplest outline of taxonomy.

Sometimes relationships between species are so close that the cluster is called a 'superspecies' or 'species-group'. Likewise, a genus is sometimes subdivided into subgenera. Similar clusters can be found at higher levels. For example, rodent diversity is so complex and layered that it requires numerous subfamilies. Likewise, a most useful taxon for antelopes is the tribe (a lower-level clustering that implies a more recent evolutionary radiation than that of the rodents).

Judging which taxonomic suggestions to embrace and which to reject has brought new perspectives to the old question 'What is a species?'. Mammals and primates are *our own*, parental branches on the vast tree of life and we, as global modern humans, represent that ultimate unit we call a species. Our unit emerged, as one among many, on a twiglet. This, in turn, belonged to a twig and so on, cluster by cluster, merger by merger, back to the mother tree – so asking 'What is a species?' is no trivial question. Trees and the dates for divergences are still tentative and subject to human error, but the reality of ancestry is incontestable.

Controversies over naming are still acute, especially when it comes to 'splitting' or 'lumping' species. This is most notable for ungulates, where a particularly severe application of the 'Phylogenetic Species Concept' (PSC) by Groves and Grubb (2013) has nearly doubled the suggested tally of species. One of the virtues of PSC has been to put a high value on distinctness at the population level. Over-zealous application of this concept, however, results in a huge proliferation of 'new' species because PSC explicitly ferrets out the *smallest* populations that show consistently identifiable differences. Thus small founder-effects can elevate tiny, labile populations to rank as species regardless of the ecology, behaviour or boom-and-bust dynamics that influenced their distinctness. More critically, 'PSC species' are mainly erected on the examination of museum specimens and distinctions between major and minor adaptive traits tend to get lost along the way. Thus naming gets immured in laboratories and museums and the most generally appreciated unit of taxonomy and nomenclature, a species, can get multiplied exponentially. Remembering to which, among a dozen PSC species, some local population might belong can acquire a spurious primacy. The confidence of non-scientists in their ability to identify an animal can be undermined by a plethora of species names. This contradicts a central purpose of this guide, which is to bring more clarity, not less, to the process of identifying mammals. A primary aim of this guide is to widen access to and share delight in the process that has given life to us and to all our fellow mammals. A guide such as this one invites confident participation, most particularly among my fellow Africans, in that finest of all recreations – natural history. In the pages that follow I have generally used the arrangement we followed in *Mammals of Africa* or, where appropriate, retained the format followed in the first edition of this guide. I comment on those subspecies that have recently come to be regarded as species by PSC taxonomists and I repudiate those most extreme among them that altogether reject subspecies as a category!

Much more interesting than squabbles over ranking are new links between name, lineage, distribution and evolutionary age. The best and most recent example of this concerns the Afrotheria. The very name (coined by Alan Walker) identifies a supercohort of mammals with its continent of origin. The genetic research that identified this lineage, when correlated with known-age fossils, has revealed that its origins go back well over 80 million years. Its six component orders began to differentiate early on, and one group, the sengis (Macroscelididae), is particularly ancient. Thus the supremely elegant giant sengi, has, with some justification, been called a 'living fossil' (I prefer the title 'ecological elder'). Its genus, *Rhynchocyon*, is already recognisable in 20-million-year-old fossils. Sengis are so distinctive that they differ more from any other living animal than, say, a pig does from a giraffe.

By contrast, the long-faced, short-necked Kongoni antelope, with its bizarre horns, is known to have appeared only within the last one million years. Fossils not only tell us that the Kongoni is a relative newcomer but they reveal that these large, oddly proportioned antelopes derive from much smaller, gazelle-like ancestors and were in an actively speciating phase when cattle and their owners arrived to displace them.

The recent evolution and graceful ancestry of Kongonis could never be inferred from the living animals alone, nor could superficial scanning reveal the unique conservatism and long ancestry of the giant sengis. These examples show that the process of identifying and naming a mammal not only invokes other sources of information, it is essentially the same process that names and classifies fossils and allows us to make sense of the great mammalian radiations in deep time. Yet a catalogue of ancient bones remains just that until each extinct animal's place has been found on the tree of mammalian evolution. Today, Kongonis are more numerous and have more impact on the landscape than giant sengis, yet, when it comes to evolutionary trees, their status is very different. Kongonis are represented by tiny, outermost twiglets while sengis derive from a long, thin branch that comes straight from the trunk. The tree on p.47 summarises current thinking about relationships between the major groups of mammals.

Mammal groups divide into those that were present in Africa before the first of a series of more recent immigrations from other continents (between about 23 million years ago (mya) and the present). Among the former are afrotheres and the ancestors of apes and monkeys. Among the colonists from Eurasia are hares, a succession of rodents, most carnivores and the odd- and even-toed ungulates. Among the immigrants, canids and Cheetahs originated in the Americas, as did zebras, which are among the most recent of all arrivals (via Asia, of course).

It is surprising to learn that the stock for many groups that now typify African fauna came from Eurasia or beyond, but other continents, too, owe their elephants, their primates and many other immigrants to Africa. Understanding all these ancient comings and goings depends on the interpretation, classification, naming and dating of both fossils and genes.

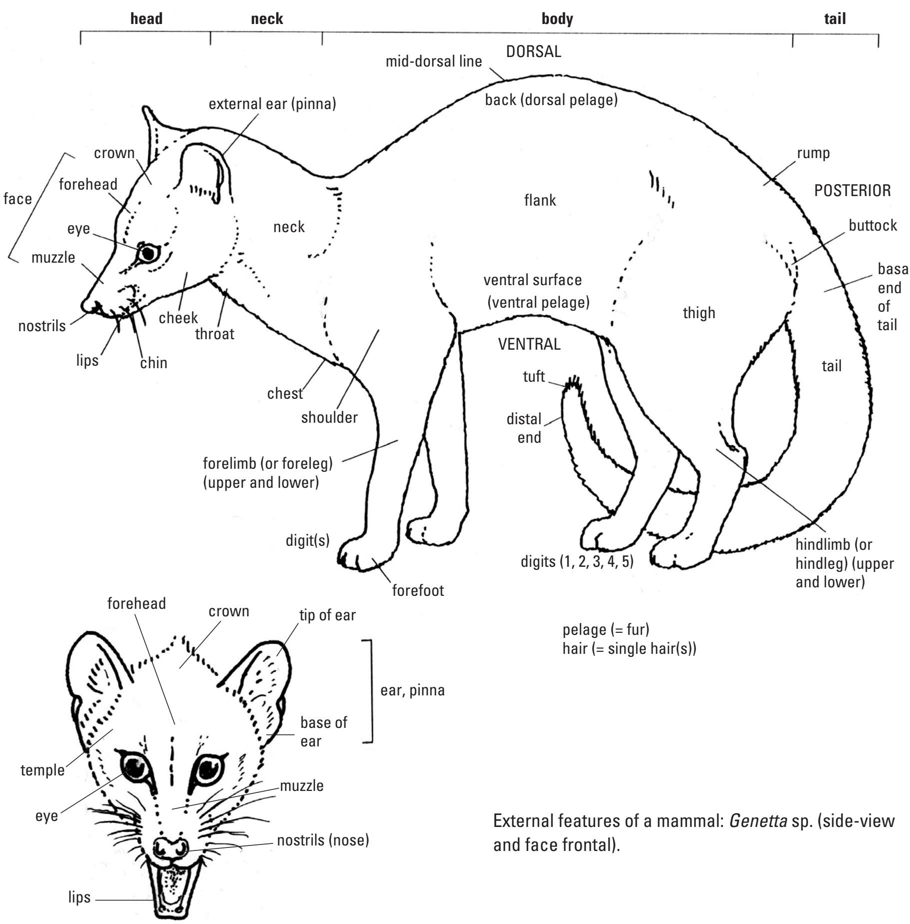
It is as well to remember that a great many living species, including so-called 'living fossils' that have survived the eons, are now, suddenly, heading for extinction at our hands. The pace of exterminations by humans now threatens to take on apocalyptic proportions unless we develop the will to create a more intelligent and humane culture that can take action on a global scale.

USING THIS GUIDE

Correct identification of an animal depends upon the nature of the encounter. In the field the great majority of clues are indirect but, in the guide to a fauna of well over 1,100 species, an inventory of tracks, outlines of burrows, forms of excreta etc., would be impractical. This guide is therefore limited to concise verbal descriptions and detailed full-colour illustrations (sometimes backed up by keys or diagnostic details in the skull, teeth or pattern).

Mammal books that emulate bird books with an item-by-item enumeration of colour patches, long or short crests etc, are not well suited to the more subtle variation and complexity of most mammals. Comparisons with familiar animals, such as dogs, cats, sheep etc., are rendered useless by the sheer diversity of African mammals. Therefore, the colour plates in this guide aim to assist identification by illustrating something of a species' 'jizz'. Jizz is the naturalist's word for the total sum of form, colour, stance, silhouette and movement that allows an accurate assessment of a species-specific shape. Ritualised displays often serve to emphasise a species' peculiarities. Some plates illustrate such postures.

While I hope the 'once-in-a-lifetime' visitor to Africa will find this guide useful, it is designed to help those with more sustained and involved interests in African mammals. It aims to outline the ecology and evolutionary history of mammals and is intended as a celebration of the great diversity of their forms. The guide includes summary descriptions of behaviour but readers seeking more



External features of a mammal: *Genetta* sp. (side-view and face frontal).

detail should refer to Richard Este's excellent *Behaviour Guide to African Mammals* and to this guide's sister publication, *Mammals of Africa*.

Species profiles present information under a set of standard headings. After scientific, English and other names are: Measurements, Recognition, Geographic variation, Distribution, Habitat, Food, Behaviour, Adaptations and, finally, Status. An abbreviated format is used for species or genera that are poorly known or have closely related species already described in greater detail. For profiles dealing with tribes, families or higher categories I have adopted a more flexible approach. A similar range and sequence of information is summarised, but formal headings are included only in longer profiles. These are: Recognition, Genealogy, Geography, Ecology, Natural History and Adaptations.

For the species profiles, the subheadings in sequence are:

MEASUREMENTS Head and body, HB; tail, T; total length, TL; standing height, SH (where appropriate); shoulder height, Sh. ht (where appropriate); ear length, E; forearm, FA (for bats); weight, W.

RECOGNITION This heading deals with what makes a species (or group of related animals) easy to recognise, with a focus on those characteristics that are unique to that species or group.

GEOGRAPHIC VARIATION (formerly Subspecies) When a species shows well-defined geographic differences these commonly receive recognition as subspecies. As more and better genetic evidence becomes available some former subspecies may be reclassified as full species. Some such revisions have found support in this edition. Others await further genetic evidence, yet others (notably *Damaliscus* populations) are unlikely to find general acceptance and are rejected. When a species varies clinally across its range this is noted wherever it is likely to affect recognition.

DISTRIBUTION Description of distribution is accompanied by a map, and special geographic features may be noted.

HABITAT Physical and climatic determinants of habitats are mentioned, with the central focus on vegetation and, for the smaller species, their micro-environment. All habitats can change, advance or contract under changing climates and, of course, under the impact of fire, grazing or agriculture. Such changes have not been taken into account in mapping the distribution of species, nor for the major vegetation zones, as shown on p.37.

FOOD Wherever known, dietary preferences are summarised by general characteristics (rather than long lists of species).

BEHAVIOUR Most profiles describe a 'nugget' of behaviour that is typical or diagnostic of the species. Where relevant, reference may be made to social structures, modes of communication, activity cycles, senses, gaits and breeding.

ADAPTATIONS Special adaptive characteristics that help to define the species, its niche or species-specific features of its anatomy or physiology.

STATUS Here an assessment of a species' conservation status may be given as published by the IUCN Species Survival Commission. The main categories used are 'extinct', 'extinct in the wild', 'critically endangered', 'endangered', 'vulnerable', 'near-threatened', 'least concern', 'data deficient' and 'not evaluated'. For some species the CITES listing is also given. As few African countries have been accurately evaluated for any but the commonest 'game' animals, most assessments need to be viewed with caution. The real situation may be much better or worse than recorded and the status of those species that are most vulnerable to the destruction of their habitat or to unregulated hunting is changing quite rapidly. Where IUCN assessments on status have yet to be made, a consensus of contemporary views from relevant authorities is offered.

FINDING AND RECORDING MAMMALS

The larger mammals, particularly non-forest species in well-protected national parks, are generally easy to view (sometimes on foot, but more usually from a vehicle or hide). Outside protected areas they can usually be seen only at some distance. The great majority of African mammals are small, very shy, mainly nocturnal species. Naturalists and scientists can now employ sophisticated methods to study such species, notably camera-traps, night-vision glasses, electronic sensors, radio- and spool-tracking, bat-detectors, hidden recorders and satellite tracking devices. However, for both the amateur naturalist and scientist alike, a good pair of eyes, a pencil and a notebook can be all that are required. To augment the naked senses and provide permanent records of momentary events, binoculars, a sound-recorder and hand-held digital camera are useful adjuncts. Camera-trapping has become a particularly exciting and informative technique for both amateur naturalists and professional biologists.

Anyone interested in mammals should keep notes and records. Every human–animal encounter has some significance, even apparent 'accidents', such as an otter-shrew in a fishing net, an African Wild Dog killed by a speeding lorry, or a tomb bat drowned in a school cistern. Indeed there are aspects of the biology of such animals that might never have been discovered but for such mishaps.

Most mammals are encountered indirectly, most commonly by their tracks, diggings, excreta and feeding sites. Bones and skulls are occasional finds but, sadly, some of the richest sites for animal remains, often of rare and little-known species, are on urban market stalls or beside main roads. This plunder is a growing menace in all those African countries that effectively permit the commercial exploitation of 'bushmeat' for urban markets. In the first edition I noted that a campaign against this highly damaging, and mostly illicit, trade was gathering momentum and deserved the widest possible support. Sadly, and disgracefully, this momentum has stalled in several major nations that are responsible for conserving or regulating precious biodiversity in Africa. It is to be hoped that Ethiopia, Cameroon, Bioko, France and China, among many others, will soon reform and stop turning a blind eye to the pillage of Africa's most precious resources.

We owe to amateur naturalists most of what we know about mammals in Africa, much of it recorded indirectly from keen African observers and hunters. From the earliest foreign explorers to contemporary civil servants, naturalists have recorded countless interesting details. The collators of this accumulated knowledge have, for the most part, been non-Africans writing for non-African audiences. Today this is changing. Fireside gossip is no longer the preferred medium for communicating indigenous knowledge about local animals. African naturalists and scientists now publish for international as well as for local audiences. This is the context for a new generation of field guides, including this one.

The authority for this book lies in an African childhood and a lifetime of research, travel, university teaching and writing on various aspects of evolution in Africa. My qualifications for the task lie with several previous works, most notably with *East African Mammals: An Atlas of Evolution in Africa*, *Island Africa*, *Self-made Man*, *Lowly Origin* and, most recently, as lead editor for *Mammals of Africa*. Most publishing projects rely on author, studio artist and graphic workshop to supply the texts, illustrations and maps for their cooperative enterprise. The dislocations are obvious to any careful analyst of the end result. This is particularly true for my own generation of scientists, whose literary and literal education was often at the cost of our visual intelligence. The earlier edition of this guide, *Island Africa* and *Mammals of Africa* have all broken new ground in that an author is also illustrator, cartographer and even designer. I trust that the results speak for themselves.

I hope this field guide will accompany solitary naturalists on their excursions through Africa's landscapes. I also hope it will reach new potential audiences in schools and cities. Most critically, I hope that new knowledge, such as is incorporated here, might reach and influence future policy-makers, even politicians. Contempt for their own natural environment and for nature (often combined with awe-struck obsession with novelties from abroad) characterise far too many of today's policy-makers. Yet there are encouraging trends, particularly in southern and eastern Africa, where there are new demands for a working knowledge of ecology. Rapid growth of economically vital tourist industries (mostly founded on wildlife and natural habitats) ensures that the new enthusiasts and wildlife experts are teachers in schools and universities, wardens, rangers, couriers and drivers, in school buses and minicabs or on park outings, sometimes students educating their parents! I hope that my work will help these new persuaders to convince both local people and visitors alike of the significance of African habitats and fauna. Here were the environmental settings within which our ancestors flourished; here our origins were tied into the mammal communities of which we were once a part; here were the settings within which our ancestors developed knowledge and experienced beauty and awe. In our uniquely rich natural heritage we can retrieve something like ancestral wisdom but also discover and develop new and unexpected sources of delight, wonder and understanding.

THE AFRICAN ENVIRONMENT

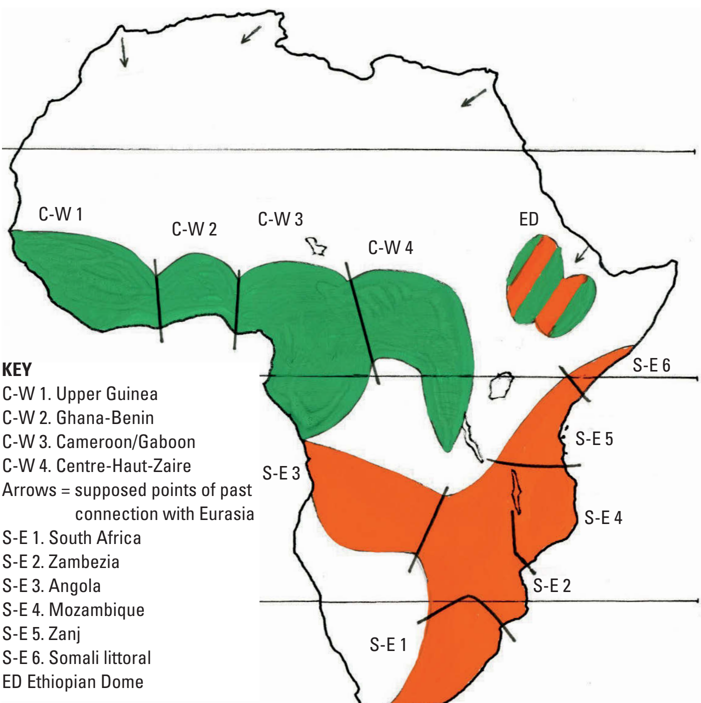
THE PAST

All life is built upon what went before and the lives of organisms differ greatly in duration. Trees being felled today were growing before the Pyramids of Egypt were built. A mouse born this year will be senile next. You and I come somewhere in between these extremes. Yet it is important to remember that the broadest outlines of modern habitats, deserts, forests and various intermediates, were already well developed some millions of years ago. However, the relative importance of, say, forest or desert has fluctuated widely, following huge swings in global climate that go back more than 15 million years but are best known for the last 1 million years.

Today's extensive rainforests and warm savannas are exceptional and we live in a period close to the wetter and warmer end of the scale. The last major spell of cold, dry weather peaked in Africa about 19,000 years ago, coinciding with the last global ice age. This was the most recent of more than 20 ice ages, each of which brought dry weather to most of Africa.

At such times lowland rainforests and all their associated biota would have retreated to especially favoured spots in Liberia, Cameroon, eastern Democratic Republic of Congo and Tanzania, all close to the Equator. (Of these countries, only Tanzania has made adequate efforts to live up to its responsibilities as custodian of global treasures.) The communities of animals and plants that are now restricted to cool, relatively dry belts on African mountains would then have spread over very extensive areas. Mammals that are now restricted to temperate or cool areas (like the Springbuck in southern Africa or the Gelada in Ethiopia) are known from fossils to have once been abundant in today's tropical areas.

The gross pattern of climatic change is a simple one. Dry habitats have tended to expand or contract from north to south and vice versa, sometimes creating dry corridors that crossed the



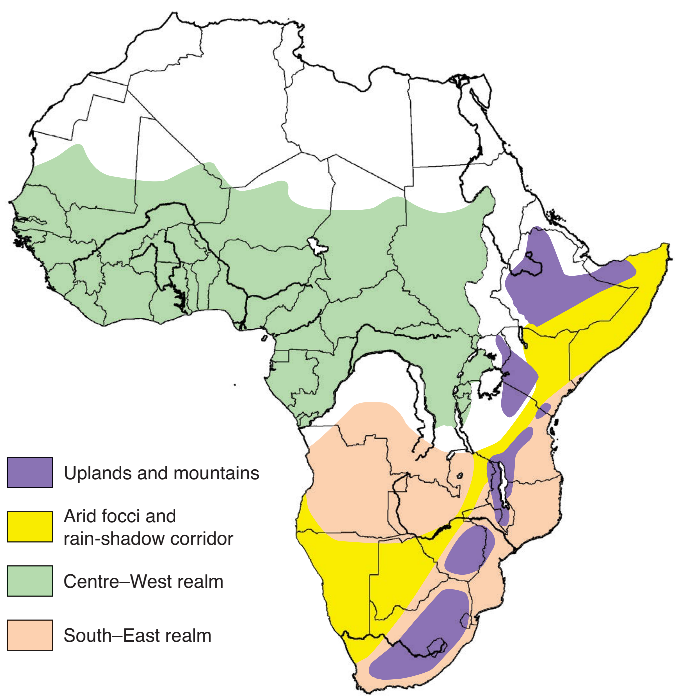
Division of sub-Saharan Africa into two major evolutionary realms. 1. Humid, latitudinal 'Centre–West' (C–W). 2. Drier longitudinal 'South–East' (S–E). It is postulated that populations originally confined within either realm may extend into intervening areas (most notably to the Ethiopian Dome) or may eventually spread more widely as new species. Past changes in climate, augmented by geographic barriers, have subjected each realm to further (and changing) subdivisions or conjunctions.

entire continent. Warm, wet periods on the other hand cause forests to pulse on an equatorial east–west axis. The result has been repeated fragmentation of both wet and dry habitats and, with that fragmentation, populations of animals and plants have suffered repeated bouts of isolation. While relatively stable species have simply pulsed with their habitats, many others have made local adaptations and speciated or subspeciated.

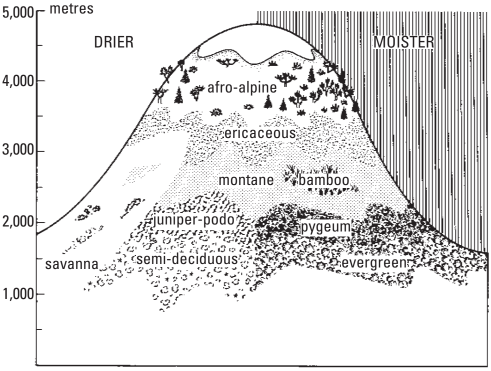
Many animals and plants have diverged into two distinct/discrete populations, one in each of these biogeographic realms (see map opposite and refer to maps for baboons, Giraffes, porcupines and wild pigs for examples). Furthermore, each of these realms fragments still further and the distribution of subspecies or distinct populations often corresponds with some, or all, of these subdivisions (see key to subdivisions opposite).

The natural barriers separating such sibling populations vary but the clearest and most frequent boundaries are the lower Congo R., Lake Tanganyika and a long arid corridor that links the dry Horn of Africa with Namib/Kalahari drylands in the south-west. This corridor is essentially a rain-shadow behind a long (and once very high) chain of uplands stretching from the Taita hills in Kenya through the 'Eastern Arc' and Malawi Rift mountains to the Kalahari and Namib drylands. These uplands intercept moisture blown in off the Indian Ocean, causing the land lying in their western lee, their 'shadow', to suffer desiccation. The barrier effect of this rain-shadow has been most decisive for moisture-dependent biota at tropical latitudes and during glacial periods. In spite of its porosity for some species, the arid corridor that skirts Mt Kilimanjaro and runs on to the south end of Lake Tanganyika is now recognised as a convenient marker for a boundary of great biogeographic significance.

Subdivision of sub-Saharan Africa into two realms or 'islands' helps to explain the extraordinary diversity of species and subspecies, especially among equatorial mammals. Correlating the distribution patterns of many primates, squirrels and small carnivores with their phylogenetic trees suggests how climatic changes drove speciation. Many now isolated populations belong to earlier branches of their lineage: they now live in corners of their previous range. These localities are often identifiable as refuges, sometimes high on cool uplands, sometimes in enclaves within much more extensive, but newly grown forests.



Arid corridor between NE and SW Africa. A long succession of highlands intercepting humidity off the Indian Ocean have generated this corridor of rain-shadows.

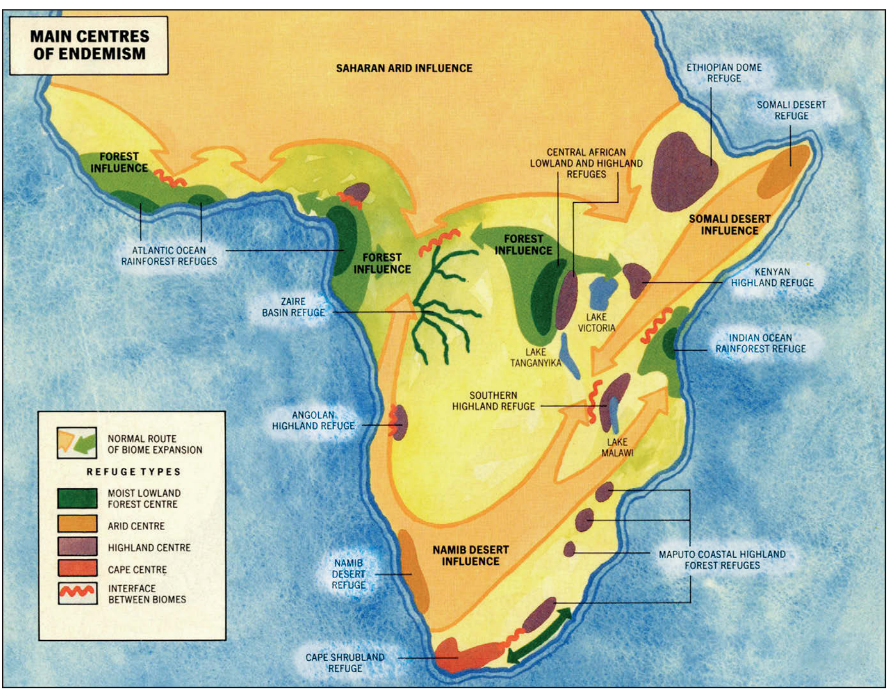


Montane and forest vegetation in relation to altitude and moisture.

Amid all the changes there have been identifiable areas of stable climates. Somalia has always been a hot, dry spot, Namibia a cool one, Cameroon consistently warm and wet, Ethiopia high and dry, and Rwenzori high and wet. The coast and mountains of equatorial East Africa have always caught rain from the Indian Ocean while Liberia and Cameroon have caught it from the Atlantic. At the centre, the Rwenzori Mountains are moistened all year from both east and west.

Where major variables meet along consistent boundaries many biological niches become possible. Wet meets dry, high meets low, cold meets warm. Faces of hills, mountains or escarpments tilt towards rain or rain-shadow, towards moist or desiccating winds. Many localised species survive in these narrow zones, which are found on mountain slopes in southern and south-west, north-east, eastern and central Africa.

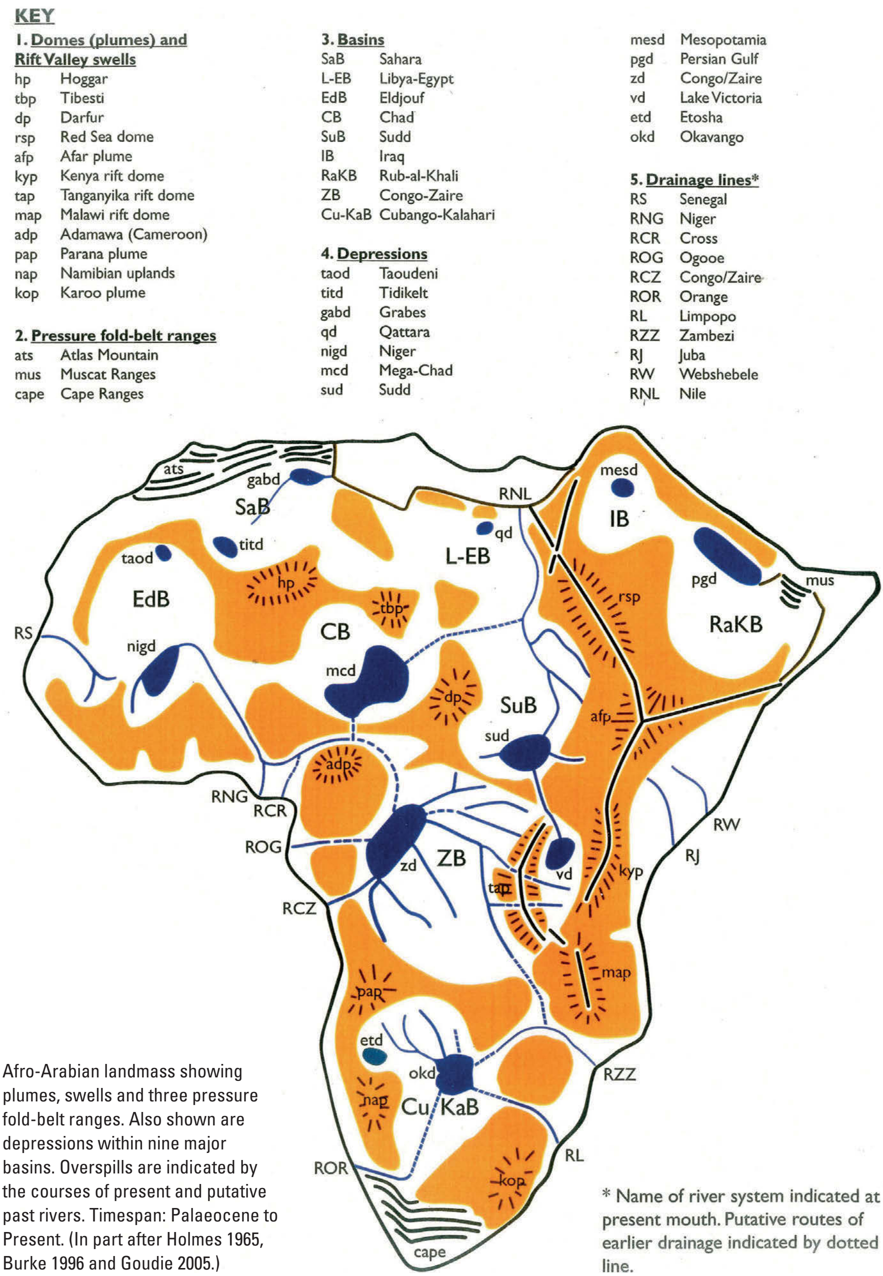
These narrow corridors and the stable foci, both wet and dry, are 'centres of endemism' and they give a special interest to areas such as the Cape, the equatorial coasts and mountains, Ethiopia and Somalia as natural 'reserves' or refuges for rare and conservative species. The details of their morphology or physiology, even their localised presence and survival, are only comprehensible in terms of their past, their 'natural history'.



Main centres of endemism in sub-Saharan Africa. Showing N–S, S–N expansion and contraction of arid foci and E–W, W–E expansion and contraction of humid foci. Intermediate ecotypes (often narrow) are typically located along interfaces between these biomes and on piedmonts of upland massifs. A more extensive exploration of the dynamics of fauna and flora is available in *Island Africa* (Kingdon 1990).

PHYSICAL LANDSCAPE

All continents are plates of once molten material that have become crusts, which swing and slither over the Earth's surface. Africa is the largest and, in terms of its global position, the least mobile fragment left over from the break-up, between 180 and 110 mya, of the super-continent Gondwanaland. Its other fragments, South-East Asia, Antarctica, Australia, India, South America



Afro-Arabian landmass showing plumes, swells and three pressure fold-belt ranges. Also shown are depressions within nine major basins. Overspills are indicated by the courses of present and putative past rivers. Timespan: Palaeocene to Present. (In part after Holmes 1965, Burke 1996 and Goudie 2005.)

and Arabia, peeled away, piece-by-piece, and now are mostly scattered across the southern hemisphere. India broke away about 120 mya, South America had separated by 110 mya, while Arabia began to break away about 35 mya. The residue of those serial fractures still exists in the form of raised land along Africa's eastern and western margins. Those marginal mountains, especially the Red Sea hills (paired with the escarpments of western Arabia), not only hint at the mechanism underlying Gondwana's fragmentation, they illustrate the dynamics that have created a geology and geomorphology that is unlike that of any other continent. The overall continental pattern is one of swells around a scatter of basins. The swells are thought to be the product of relatively stable plumes, or 'hot spots', down in the mantle, which have thrust up the land surface above them.

Because they drift in a particular direction (northwards for Africa), tectonic plates acquire linear scars wherever a mantle plume beneath punches upwards. Thrust up into a ridge, some such elongated domes split open to form the celebrated Rift Valleys of Africa. Rift valleys are the beginnings of seas and, eventually, oceans.

Domes and swells vary greatly in height and extent, and only sometimes fracture to release volcanism. One plume, beneath the Rwenzori Mountains, has pushed ancient bedrock up to over 5,000m and pock-marked the neighbourhood with volcanoes and craters of all sizes, but most swells, such as those that surround the Okavango, Congo, Sudd, Chad and Eldjouf basins, have raised rafts of crystalline basement rocks over very extensive areas with little or no volcanics. Erosion has exposed bedrock over much of these shallow swells, so they have very low fertility and, in the near-absence of nitrogen in the soil, selection has favoured the evolution and dominance of leguminous plants that can fix atmospheric nitrogen. These nutrient-deficient landscapes, typified by the Miombo woodlands (made up of leguminous trees), support fewer mammal species, which generally live at relatively low densities. As a result, large predators are scarce and the main large antelope in Miombo, the Sable Antelope, *Hippotragus niger*, survives on a grazing strategy that probably resembles that of the low-density desert antelopes from which it likely descended. During the rains Sable crop thin, short grasses and herbs growing under the woodland canopy. Then, as the wooded slopes dry out, they seek out termitary/hardpan fringes where precious nutrients leach out (or are dredged up by termite action) and there is sufficient moisture to stimulate green growth (an equivalent ecotone in western Australia is known as 'pindan'). Before the rains return, the herds (averaging 15–20 animals) are sustained by green flushes that follow burns in the cotton soil '*mbugas*' (wide, flat, grassy valley bottoms). The search for graze takes Sable over ranges of up to 118km^2 but this antelope's survival is predicated on the rarity of Lions, hyaenas and hunters in Miombo. While Lions and scarce green grazing are immediate factors in Sable biology, it has been the underlying geology of Africa's ancient Precambrian 'shield' that ultimately governed the evolution of this splendid antelope.

Map of Precambrian surfaces in Africa.

The great Rift Valley system has derived from several phases of uplift down the eastern side of Africa. The most recent major upheavals have been dated to 22 million, 6 million and 2.5 million years ago. The largest dome, 400km wide, embraces Ethiopia and Yemen. South of the Ethiopian dome, stretching thousands of kilometres and in a jagged course from north to south, uplifted land has split along axes to form rift valleys that average about 40km in width. Associated volcanics have spewed out lava over extensive areas and thrown up volcanoes such as Kilimanjaro, which is 5,895m high. Earlier volcanoes have eroded away and deposited deep sediments. Cycles of erosion and deposition have created dramatic landscapes of mountains, deep valleys and gorges. Recent volcanics and the tipping of extensive land surfaces have changed the direction of rivers and diverted waters from one basin to another; the River Nile, finding every exit to the Indian Ocean blocked by uplift, has had no alternative but to flow north, in the process becoming the longest river on earth. Among many dramatic and consequential developments of uplift are rift valley lakes and periodic ponding in other basins. Some of these have been ephemeral. L. Chad in the Sahara has expanded and contracted more than once, the Qattara, Tidikelt and Makgadikgadi depressions, once lakes, are now salt pans.

Distribution of rivers and lakes in Africa.

L. Victoria began as a result of the blockage of two large tributaries of the Congo R. Due to uplift in what is now Rwanda and Burundi the waters of these rivers ponded back, creating the present very shallow lake. All these lakes have been important as barriers to the spread or mixture of mammal populations. In the Congo basin a very large lake persisted for several million years until the mid Pliocene. Then, cut-back by a small Atlantic river created a new drainage line, emptying the Congo basin of its huge lake. This relatively recent event has left a pattern of distribution that makes the Congo R. one of the most consistent and major biogeographic boundaries in Africa (in spite of the vegetation north and south of the river being superficially indistinguishable). Overspills from the long-lived and always very wet Congo basin may have cut exits in several directions (even, perhaps, to the south-east, into today's lower Zambezi). Other possible exits were northwards into today's Benue valley and, later, down the Ogooué valley, which is disproportionately deep and wide for its contemporary catchment area.

Another major biogeographic boundary, along the Cross R. in east Nigeria, may also find its explanation in the re-routing of a once major river emptying down the valley of the Cross R.

Other geological events have shaped recent distributions. In the Virunga Mts area, major eruptions about 22,000 years ago blocked and deepened L. Kivu. Subsequent eruptions, one as recent as 9,000 years ago, are thought to have depleted fish and reptile fauna and it is possible that release of vast accumulations of methane gas in L. Kivu combined with tremors and eruptions to send a poisoned fireball down over the slopes west of L. Kivu. In any event, this area has many unusual anomalies of mammalian distribution which require research and explanation.

In contrast to these dynamic and recent events are the eroded, geologically ancient landscapes of the Karoo, the Cape and the Drakensberg, reaching over 3,480m. Here ancient or conservative mammals, such as golden-moles, blesmols and the Cape Grysbok, occupy the vestiges of a temperate region that has slowly shrunk as Africa migrated north.

Africa's links with Eurasia have pivoted on relatively brief periods of connection. Sometimes the land masses touched at the south end of the Red Sea, but mostly it has been in the north, at Suez. The land bridges between Morocco and Spain, across the Straits of Gibraltar, and between Tunisia and Italy over the Straits of Sicily, appear to have been less influential for mammals, but the Gibraltar connection is known to have been narrow but solid at about 5.5 mya.

At least five periods of connection, during which significant exchanges of fauna and flora took place, occurred between 23 mya and the present. The better-known emigrants were African apes, monkeys and elephants, while early ungulates, hares, a succession of Eurasian rodents and carnivores were immigrants. Altitude, latitude, natural barriers and soils all influence mammals in ways that are touched upon in the profiles of species.

CLIMATE

Africa is a relatively dry continent and its rain derives from evaporation off seas that warm and cool with the seasons and with ocean currents. Wind and rain cycles are set in motion by temperature differences over land and sea, so northern and southern hemispheres have single seasons while the equatorial belt enjoys two wet seasons.

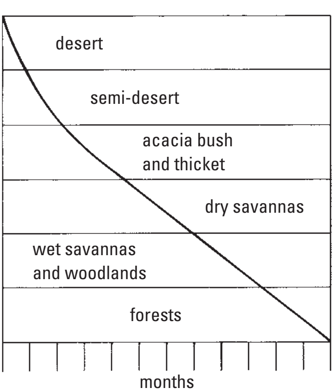
Because cooler conditions bring less evaporation, Africa is dry north of the Equator during the northern winter and dry to the south in the southern winter. In the subtropics, conditions are hotter than in temperate latitudes and drier than in equatorial ones. The mountains have their own climatic pattern, with marked temperature extremes between day and night, heavy rainfall, especially in the equatorial and tropical belts, and generally cooler temperatures overall. The Cape and Mediterranean littorals have different patterns of dry summers and wet winters.

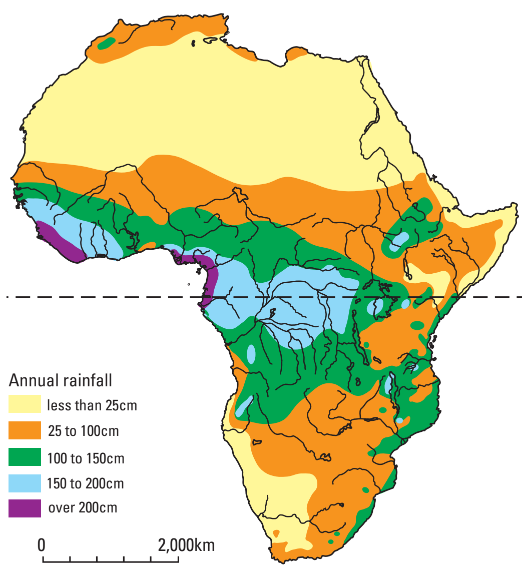
Excluding the Equator, coastal strips and mountains are the main beneficiaries of rain coming in off the Atlantic and Indian Oceans, and heavy rains in all tropical uplands create long river systems that often flow across otherwise arid lands. The archetypal river of this sort is the Nile, but many less well-known rivers show a similar pattern. A worrying trend of hijacking source-waters of rivers, great and small, to irrigate agribusiness schemes leaves people and animals downstream finding their pastures and water drying out.

Seasons are irregular, especially in the subtropics and in the dry corridor that runs from NE to SW Africa. Droughts are often followed by floods – in shallow basins, such as the Rukwa depression and L. Chad, massive evaporation and empty feeder-streams cause periodic drying up of these lakes with attendant die-offs of large antelope and hippopotamus populations. Very arid hinterlands may have narrow coastal strips where nocturnal fogs are sufficient to support some vegetation. On the Namibian foreshore, the Somali coast, up the Red Sea, and along the Mediterranean and Atlantic coasts, these dew thickets or fog-fed grasses support uniquely adapted plant and animal communities that survive on narrow 'island strips' bounded by sea on one side and true desert on the other (mammal examples comprise several gerbil species tied to north and south Atlantic, and Mediterranean, coastal dunes, a vole on the eastern Libyan littoral, the Silver Dikdik in Somalia and Grant's Golden-mole in Namibia).

The Sahara and Horn of Africa desert areas are part of a much larger zone, stretching to the Himalayas, where dry air subsides and clouds rarely form. Throughout Africa it is drought that inhibits plant growth, not absence of light, nor low temperatures. Snow and frost are regular features only on the very highest mountains and at the temperate extremities of Africa. Surface drinking-water

Rainfall and vegetation: the diagram below correlates the duration of humidity (in months) with vegetation zones. Rainfall exceeding 5cm indicates a humid month.



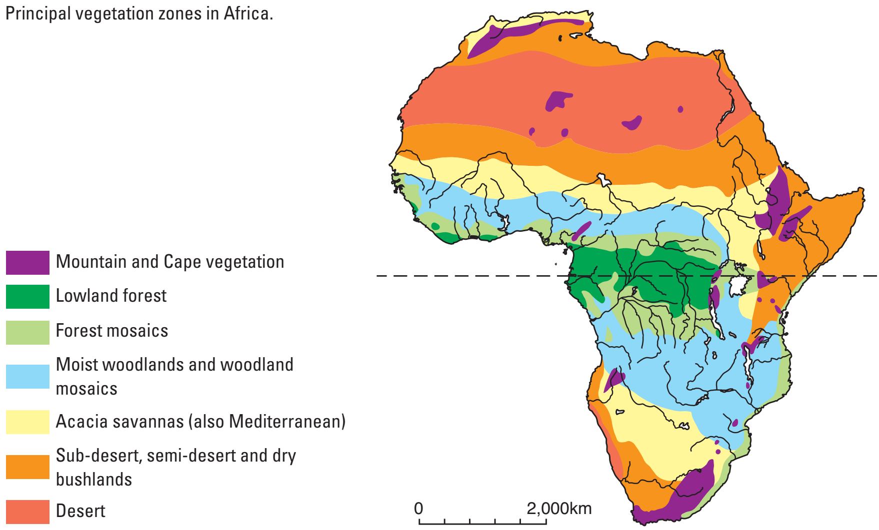


is the single most limiting climatic influence for the majority of mammals, and pastoralists denying wild animals access to waterholes continue to precipitate die-offs over extensive areas. Those species that can extract sufficient moisture from their food alone are the classic desert rodents, some antelopes and some carnivores. It is symptomatic of the short-sightedness and indiscipline of human cultures that all the larger animals best adapted to survive in the Sahara desert have been exterminated. It was said it could not be done, but in less than a century an area larger than the USA has indeed been stripped of all its larger mammals by several generations of ignorant boys playing with guns, fences and vehicles.

VEGETATION

African vegetation is dominated by an equatorial belt of rain-fed forest and three principal desert areas: the Sahara, the Horn (Somalia) and south-west Africa (Namibia). Between these extremes are moist forest–savanna mosaics, woodlands (dominated by leguminous trees, called Miombo in the south-east and Doka in the north-west), various wooded grasslands or savannas, often dominated by *Acacia* bush or scrub, and verging on sub-desert or semi-desert in places. The desert graduates from bare sand dunes (erg) and rocky pavements or screes (hammada) through various conditions in which ephemeral grasses or herbs, scattered shrubs and small trees modify the desert sufficiently to permit various mammals to survive.

Principal vegetation zones in Africa.



Montane areas also range from nearly bare screes on the top of Mt Kilimanjaro through various afroalpine habitats to montane grasslands, moorlands and forests. In the Cape and Karoo there are unique shrublands, moors, grasslands and semi-deserts subject to frequent summer fires and sustained by winter rains. There are few places where these vegetation communities have not been affected by human settlement, felling, frequent fires and large herds of livestock. Nonetheless, Africa's fabled national parks have often succeeded in maintaining relatively healthy and representative communities of indigenous animals and plants.

The gross vegetation zones listed above break down into subtypes that often define the habitats of particular mammal species. Some major types and categories are:

A. FOREST

1. Lowland rainforests (wetter and drier types)
2. Dry evergreen forests
3. Swamp forests (palms, mangroves etc.)
4. Montane forests (afromontane, Mediterranean etc.)
5. Mediterranean oak and conifer forests
6. Various mosaics and transitions

Partially cleared forest, Yekepa District, Liberia. PHOTO: M. COE

Afro-montane rainforest, Parinari mist forest, Mount Nimba, Liberia. PHOTO: M. COE

Forest–savanna transition Pare Mountains, Tanzania. PHOTO: J. KINGDON

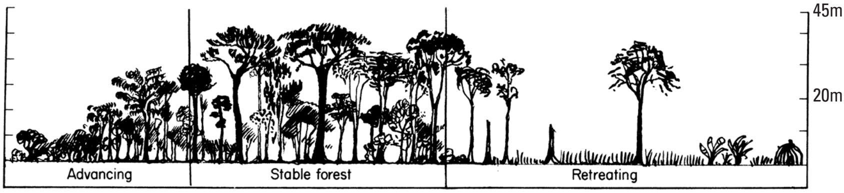


Diagram of forest profile, showing changes in ground cover.

Swamp forest, *Phoenix*, *Marantocioa*, *Pseudospondias*, *Elaeis*, *Mitragyna*, *Calamus.*

Montane forest, *Podocarpus*, *Cyathea*, *Ocotea*, *Aningeria.*

B. WOODLANDS

1. Miombo (*Brachystegia*/*Julbernardia* dominant)
2. Sudanian doka (*Isoberlinia* dominant)
3. Mopane (*Colophospermum* dominant)
4. Various mosaics

Mopane woodland, Zimbabwe. PHOTO: M. COE

Woodland, *Brachystegia*, *Terminalia* spp.

C. SAVANNAS, BUSHLANDS AND THICKETS

1. Various *Acacia* dominant (evergreen to very dry)
2. Bushlands and thickets (often *Commiphora* dominant)
3. Mosaics (from moist to very dry)

Open *Acacia* savanna, Nyambeni, Kenya. PHOTO: M. COE

Acacia savanna, *Acacia* spp.

Thicket, *Commiphora*, *Combretum*, *Acacia*, *Teclea*, *Maba*.

Acacia/*Commiphora*/*Combretum* thicket, Mkomazi, Tanzania. PHOTO: J. KINGDON

D. GRASSLANDS AND MARSHES

1. Fire-induced grasslands (*Themeda* etc.)
2. Valley bottom grasslands (some semi-aquatic)
3. Montane grasslands
4. Various mosaics and secondary types

Fire-induced grassland, Samburu, Kenya. PHOTO: B. WHITE

Swamp, *Pistia*, *Nymphaea*, *Phragmites*, *Papyrus*, *Miscanthidium*, *Phoenix.*

Swamp vegetation, Okavango, Botswana. PHOTO: M. COE

Giant groundsel, Afro-alpine zone, Mount Kenya. PHOTO: M. COE

E. MONTANE AND AFROALPINE

1. High-altitude alpine types
2. Bamboo (plus forest/grassland mosaics)
3. Undifferentiated (from arid to humid)

Juniper–hagenia forest/grassland mosaic, Bale Mountains, Ethiopia. PHOTO: J. KINGDON

Alpine zone, *Lobelia*, *Carex*, *Senecio.*

Subalpine or ericaceous zone, *Erica arborea.*

Bamboo, *Arundinaria.*

F. SHRUB, SCRUB, MOOR AND SEMI-DESERT
1. Semi-arid shrublands
2. Succulent Karoo types
3. Cape fynbos
4. Desert margins scrub and mosaics

Cape fynbos. PHOTO: J. KINGDON

G. DESERTIC
1. Absolute desert
2. Sand deserts (ergs)
3. Stone deserts (hammada, reg)
4. Sub-deserts (graded or mosaic)
5. Semi-deserts (graded or mosaic)

Subdesert, Namaqualand, South Africa. PHOTO: M. COE

Semi-desert, *Aloe*, *Calotropis*, *Sansevieria*, *Commiphora*, *Balanites*, *Euphorbia.*

MAMMALIA MAMMALS

ORDER 1: Hyraxes
ORDER 2: Proboscids
ORDER 3: Sea-cows (Sirenians)
ORDER 4: Afrosoricids
ORDER 5: Sengis (Elephant-shrews)
ORDER 6: Aardvark
ORDER 7: Primates
ORDER 8: Rodents
ORDER 9: Hares
ORDER 10: Hedgehogs
ORDER 11: Shrews
ORDER 12: Bats
ORDER 13: Carnivores
ORDER 14: Pangolins
ORDER 15: Odd-toed Ungulates
ORDER 16: Cetartiodactyls

Every user of this book is a mammal and, as doctors, physiologists and other scientists have always known, the study of human kinship with other mammals offers us many fundamental truths about ourselves. Take warm blood for example. Internally stable temperatures are central to what mammals are. A naked human freezes to death within hours in a northern winter and, likewise, quickly dies of heatstroke if exposed to a desert midsummer. This is because *biologically* we are still fragile equatorial primates. While we have developed technical solutions to both these extremes of climate (i.e. clothes or air conditioners), other mammals have biological techniques that enable them to survive both extremes, relying on fur for insulation against extremes of temperature, and sweating or panting in order to cool down.

It is glands similar to sweat glands, mammae, which have been modified to produce milk, that give mammals both their common and their scientific name – mammals are animals whose mothers have mammary glands.

Mammal mothers are unique not only in nursing their offspring on milk but in nurturing them *before* birth through a placenta that grows into the wall of the uterus. The placenta allows the foetus to plug into its mother's circulation and so share in her respiratory and excretory systems and in the nutrients carried in her blood. It also stops the mother rejecting the foetus as an alien body.

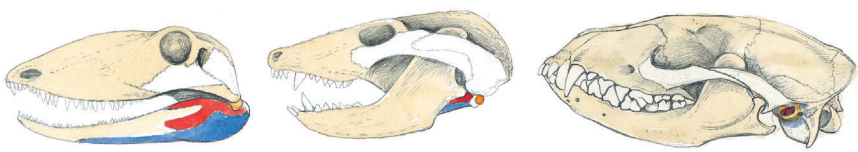
A mammal is not only sheltered as a foetus in the womb, maternal care also shelters it after birth. Whereas emergence from an egg exposes a newly hatched invertebrate, fish or reptile to predators, competitors, changes in climate and the need to find food, newborn mammals escape these rigours through maternal care. Mammals are also relatively independent of the environment for the duration of their infancy and adolescence. This trait is unique to mammals and is most prolonged in primates, especially hominid apes. Among hominids, humans have extended this central mammalian characteristic furthest. Not only has our childhood been extended biologically, contemporary humans continue to extend its environmental dimension – detachment from ecological systems. Because much of our technology plays a role analogous to maternal protection we have, in a limited sense, become permanent youngsters, the most mammalian of mammals.

Mothering is also the key to social life in mammals. The physical costs of bearing and suckling offspring are so great for the females that they go to elaborate lengths to fit the timing of reproduction to the best time of year and to ensure access to the best resources both for themselves and for their offspring. To achieve this some species share or enter the territories of prime male land-holders. Others seek out the protection of dominant males at the top of a strict hierarchy while still others choose males that will help raise offspring.

Different patterns of male competition and female choice have dramatic consequences for the external appearance and anatomy of males. Weaponry, in the form of horns, tusks or antlers, has been developed to defend territories or rank. Age-graded gigantism has evolved in the males of hierarchical species, such as gorillas, elands and Giraffes. Long-term pair-bonding is usually matched by the sexes being of similar size (typified by African Wild Dogs).

Diversity of size and form is built on those most fundamental of faculties: finding and processing food. Major groupings within the mammals are often named and defined by the shape and form of their teeth (such as rodents, scandents, tubulidents). Furthermore, mammals as a whole have uniquely modifiable teeth and lower jaws. Although these derive from structures similar to those in other vertebrates, the jaw consists of a single mandibular bone anchored in and powerfully hinged onto the skull. Reptiles, by contrast, have jaws that are a weaker assemblage of bones.

Long series of fossils of the now-extinct 'mammal-like reptiles', or synapsids, have revealed that the tooth-bearing bone (the reptilian 'dentary') first developed a hinge with the squamosal, or cheekbone, about 200 million years ago. As a consequence, three of the original reptilian jaw bones (themselves derived from fish gill-arches) declined in size and became detached from the lower jaw. However, these diminutive bones did not become redundant but attached themselves to the skull base, where they became the inner components of the mammal ear capsule. Partly because of the fine tuning of these minute bones mammals have developed a much more discriminating sense of hearing than reptiles and have elaborated numerous forms of sonic communication, sonar orientation and detection systems. Thus mammals owe their good ear for the nuances of sound to their peculiar legacy from a reptile-like anatomy.



Transformations through time. Synapsid (mammal-like reptile) skulls: *left*, *Ophiacodon* (an early form); *centre*, *Probainognathus* (a later form) compared with a modern mammal, the civet, *right*.

The senses play a very precise role in the life of all mammals. Sight, hearing, scent and touch are balanced in permutations that are unique to each species, and that balance finds a gross expression in the shape of animal heads. For example, a Serval's huge ears, a fishing genet's moustache of face whiskers, a galago's bulging eyes and an Aardvark's nose tube each manifest unique techniques for finding food. All possess a full set of faculties but the Serval must pick up sound waves from mice in dense grass, the genet senses waves from small fish in water, the galago

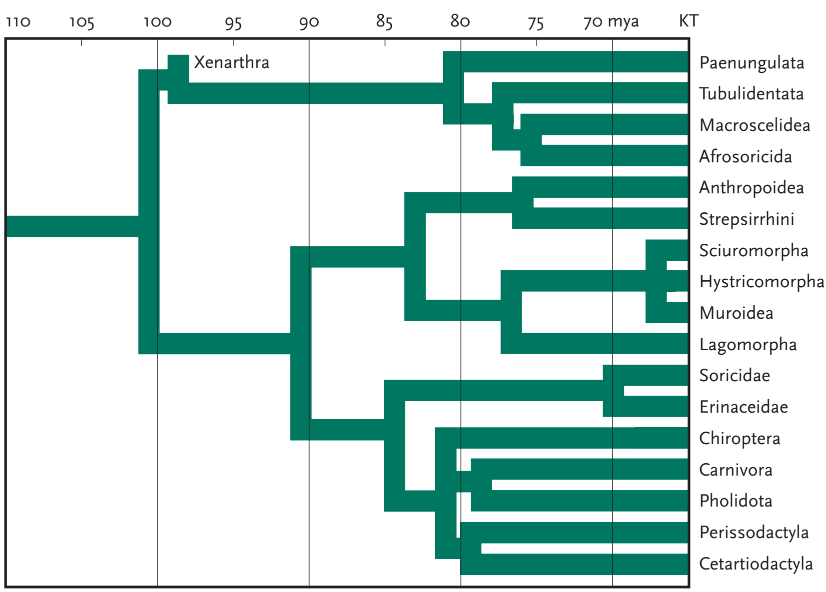
Mammal heads and senses: (a) Serval (hearing); (b) Fishing genet (touch); (c) Galago (vision); (d) Aardvark (hearing).

receives optical wavelengths in near total darkness and the Aardvark locks onto molecular traces of scent emanating from termites hidden deep in the soil. All these faculties had to be developed by stages from the less specialised conditions that preceded them.

The overall shape and proportions of a mammal are therefore the end-products of its lineage and its progressive adaptation to an exact and exacting ecological niche. Much of the fascination of observing animals lies in matching such expressions of form to function. Form is not only anatomical; mammals act, behave, occupy habitats and have habits that are all expressions of their total adaptation. Every species manifests a unique way of making a living.

Much of that life is accessible to quiet observation but any serious contemplation of mammals can only be a humbling experience. In their world we are like deaf-mutes. We can neither register nor interpret the most important dimension of their existence: scent. For a few species (mostly primates like us) scent may be subordinate to vision but for the majority scent is a central regulator of their social life, a major mechanism for orienting themselves and a source of what we would call 'exquisite sensations'.

If mammals have been shaped by the way they make a living, they also shape the lives of their prey and of the plants they eat. An example is my own discovery of a unique relationship between bark-eating anomalures and the awoura (*Julbernardia*) trees on which they feed (see p.250). This interdependence between gigantic, slow-growing forest trees and small, short-lived, gliding rodents is so specific that it must go back millions of years. In keeping their flight paths to the tree trunks clear, the anomalures prune (and eventually kill) the tree's competitors, thereby compensating them for wounding their bark. Mutually beneficial relationships are known among bats and the flowering plants that they pollinate, and among primates and the tree seeds that they disperse, but many, much subtler relationships await discovery and study. The inter-relatedness of mammals and all other organisms in natural communities is a compelling reason why we should strive to conserve ecosystems intact, as well as the entire range of mammal species, not just the ones we find attractive or agreeable.



Tentatively dated molecular tree for mammalian radiation before the KT event (65.5 mya) (after Meredith *et al.* 2011).

AFROTHERES AFROTHERIA

During the nearly 20 years since the first edition of this guide was written and published, an entirely new supercohort of mammals has been recognised. We owe this recognition to the science of molecular phylogeny, which has clarified relationships within and among virtually all mammal groups through detailed comparison of their genetic profiles. About 80 species of extant afrotheres are currently recognised, these include three elephants (two of which are African species), four sea-cows (two African), nine hyraxes, one aardvark, 18 sengis (elephant-shrews) and 21 golden-moles (all African) and three otter-shrews, which have some still poorly understood affinity with Madagascan tenrecs.

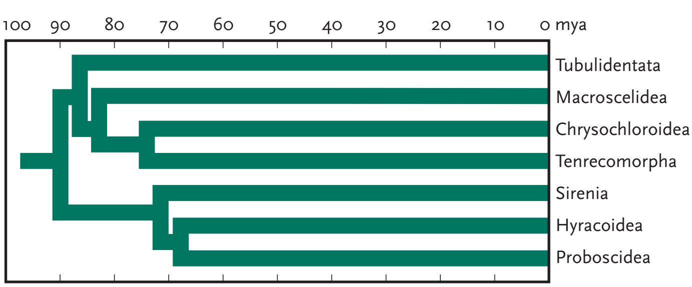
The afrothere radiation in Africa is tied in to the central question of just where modern placental mammals arose. Are these animals modern derivatives of the very earliest placental mammals or are they a later product of a chance over-sea rafting during the continental isolation of Afro-Arabia? If the Afro-Arabian continent was as decisively isolated as is currently thought, its placental afrotherian colonist must have had some tolerance for exposure at sea. Whether this implies semi-aquatic habits remains a conjecture. Both placental mammal and afrotherian origins continue to be matters of ongoing debate. Nonetheless, the reality of Afrotheria is but part of a global effort to construct genealogical trees for all biota – ultimately the single Tree of Life. Several mammal lineages from outside Africa and members of the Afrotheria share many similar or convergent adaptations, such as ant-eaters with sengis, large-scale aquatic whale and hippo-like mammals resembling afrotherian sea-cows and, on a miniature scale, true shrew-like moles converging with afrotherian golden-moles.

The oldest, undisputed members of afrotherian orders appear as fossils in north-west Africa. No other group of placental mammals is known to have existed in Africa before the Afrotheria and they represent a continuous presence for at least 65 million years and perhaps as much as 90 million years. Outrageously, but also sadly, environmental and biological ignorance among contemporary policy-makers, economists and 'developers' renders them indifferent to the survival of Africa's fauna, including Afrotheria, our most ancient indigenous mammals.

PAENUNGULATA

The six orders of Afrotheria have been divided, quite recently, into two cohorts: elephants, sea-cows and hyraxes comprise Paenungulata, while the new cohort, Afroinsectiphillia, embraces the Aardvark, sengis, otter-shrews and golden-moles. Vast differences among its members would make their common grouping scarcely credible until we learn how long ago the lineages are thought to have diverged – paenungulates and afroinsectiphillians between 90 and 80 mya while ancestral elephants and sea-cows, now superspecialised, diverged from the more typically mammalian hyraxes some 75–65 mya.

Compared with other placental radiations, paenungulate species are very few. Extant species are also highly specialised, which reflects a long head-start in adapting to difficult niches. The low diversity of surviving species, notably elephants and sea-cows, has been influenced by human predation. There is evidence for prehistoric and historic humans exterminating at least 10 species. This guide begins with hyraxes, as the least derived of all afrotheres.



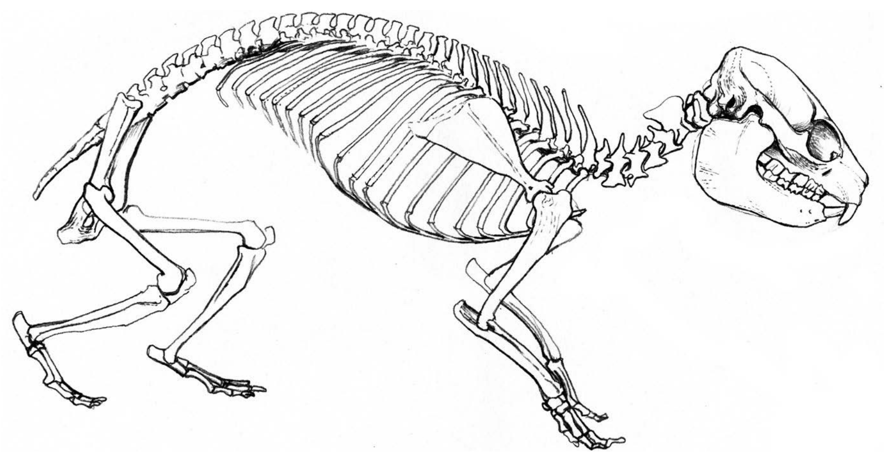
Tentative phylogenetic relationships of afrotherian mammals based on analysis of genomic data (after Meredith *et al.* 2011).

HYRAXES HYRACOIDEA

Hyraxes are small, woolly animals with no visible tail and blunt digits. Vernacular names such as 'rock rabbit', 'coney' and 'dassie' ('little badger') illustrate traditional uncertainties about what sort of animal they are, and they still tend to be likened to guinea-pigs or groundhogs! It was that exceptionally perceptive anatomist Thomas H. Huxley who first put them into an order of their own and this has been followed up to the present. At least 20 genera of hyracoids are known from Africa, many from the Oligocene, some 30–25 mya, at which time some were dominant herbivore species. They have been almost totally replaced by modern ruminants but the reasons for the hyraxes' decline probably has less to do with their digestion (which, judging from modern hyraxes, was probably hardly less efficient than that of ungulates) than in a poor ability to regulate body temperature, a lack of stamina, short legs and a primitive brain that still shows resemblances to those of 50-million-year-old 'near ungulates'. Other limitations could be slow reproduction and their cumbersome, though fast, way of cropping vegetation. The tusk-like incisors of hyraxes are given over to defence and grooming, which has forced the molars and rear of the mouth to combine the functions of food-gathering and chewing.

Hyraxes were first classified with elephants because early fossils of both lineages were similar. That several ancestors had much larger body sizes might be relevant to understanding their 7-month gestation and the very advanced state of development of the newborn. More immediate ancestors of modern hyraxes are likely to have escaped competition from bovids of Eurasian origin by adapting to the rocky thickets that are scattered over a large part of Africa. If rock-dwelling was the initial innovation of the ancestors of all living hyraxes, the two specialisations that have developed since are arboreal skills at one extreme and grass-eating at the other. The Bush Hyrax has the most generalised dentition.

All three genera are successful and they flourish in two environments that hoofed ungulates cannot cope with: trees and rock piles.



Skeleton of *Procavia capensis*.

HYRAXES PROCAVIIDAE

Rock hyraxes	*Procavia* (5 species)
Bush Hyrax	*Heterohyrax brucei*
Tree hyraxes	*Dendrohyrax* (3 species)

The three genera of hyraxes show few easily observable external differences: all are rabbit-sized, woolly and brown, with a large-mouthed, deep-jawed head and rubbery, blunt-fingered hands and feet. Their loud voices are highly distinctive and their calls are currently the subject of systematic analysis.

Although skulls and teeth remain the most reliable guides to genera, each occupies a different niche with a distinct diet. Rock hyraxes are mainly diurnal, arid-adapted grazers, living in colonies among rocks. Tree hyraxes are mainly nocturnal browsers, scattered singly or in small groups among moist forest trees. Bush Hyraxes are diurnal browsers that feed in trees but live in colonies among rocks.

All species have very long bodies that are concealed by a hunched posture and long fur. All have long, tactile hairs, especially on the muzzle, throat, brows, cheeks, rump and limb joints. All species have skin glands that run down the spine and most have differently coloured hair patches that can be erected or fanned open as scent-dispensers. Both identity and status are signalled by scent. Disproportionately large jaws and an ability to draw the lips right back allow them to bite off and chew large mouthfuls of vegetation at a time. This means that two or more short feeding bouts are sufficient to fill the stomach.

Long periods of inactivity (in carefully chosen sites and sometimes lasting several days) both conserve energy and also help digestion. Hyraxes can weather extended droughts in the absence of water and on diets of very low nutritive value. Both gut and kidneys are highly efficient at extracting nutrients and saving water. Urine is copious and dilute in the wet season but very concentrated and syrupy in the dry season. Several species urinate at communal ‘latrines’ that may be centuries (or millennia) old. All species drop their dung at specific spots. Dung, urine and very loud calls (amplified by guttural pouches) are used to define territories. These may be effectively group territories but are primarily defended by single adult males. The male’s home range is shared by one or more females and their offspring. The age at which young males are expelled varies. They disperse into peripheral ranges, there to develop or await tenancy of their own territories in a very vulnerable situation.

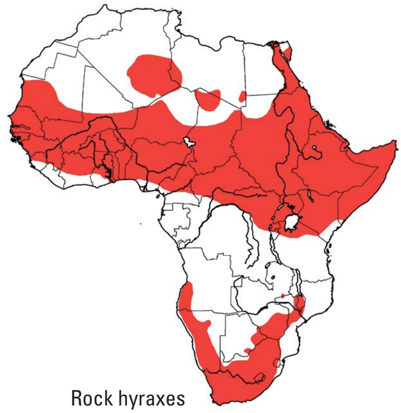
Low-level aggression underpins much of the hyrax’s social life. Dominance is indicated by bristling fur, an exposed dorsal gland, tooth-grinding, snapping and growling. Upper incisors are very sharp and can inflict deep and damaging bites. Appeasement gestures are therefore pervasive, especially ‘presenting’ of the rump with fur and body as flat as possible. This may help explain why hyraxes typically enter holes, huddle in groups, and even brawl, facing backwards.

The genera differ substantially in their mating calls and genital structures. Most species are seasonal breeders. In males the weight of the testes increases by up to 20 times, with corresponding surges in testosterone and male aggression. A gestation of 7 or 8 months is almost without precedent in such a small animal but the infant is born fully developed and takes its first nibble of plants within 4 days. Young are weaned by 3 months and are sexually mature by 16 months. They are known to live for up to 12 years.

In addition to persecution from humans, hyraxes suffer predation from numerous carnivores and raptors, especially cats, jackals, eagles (most notably a hyrax-eating specialist, Verreaux’s Eagle) and eagle-owls.

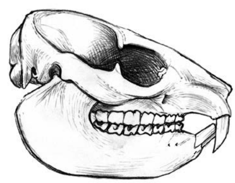
Rock hyraxes (*Procavia*): Tooth-row tapered and bowed, with broad and deep teeth. Row of four front teeth shorter than that of the three back teeth. Attachments for temporal chewing muscles converge on midline of domed braincase. Advertising call is a long series of ascending yelps descending to grunts.
Bush Hyrax (*Heterohyrax*): Cheek-teeth intermediate but sharply cusped. Row of four front teeth about equal to that of the three back teeth. Attachments for temporal muscles meet or nearly meet on top of curved braincase. Advertising call is a penetrating series of whining mews.
Tree hyraxes (*Dendrohyrax*): Cheek-teeth narrow, relatively shallow, sharply cusped. Row of four front teeth longer than that of the three back teeth. Attachments for temporal muscles widely separate on sides of flat braincase. Advertising calls are very variable but all have ascending cries and very loud crescendo.

Ethiopian Rock Hyrax



Rock hyraxes

Black-necked Rock Hyrax



Black-necked Rock Hyrax

ROCK HYRAXES *Procavia*

Five forms, treated here as full species (see below)

OTHER NAMES Klipdassie. Fr. *Daman de rocher*. Ger. *Klippschliefer*. Swah. *Pimbe mawe.*

MEASUREMENTS HB 380–600mm. W 1.8–5.5kg.

RECOGNITION Blunt-faced hyraxes that vary in colour both regionally and individually but generally brown with a paler underside.

GEOGRAPHIC VARIATION Sometimes treated as a single species, *Procavia* has also been divided into five species, some still further subdivided into subspecies. Dorsal patches can be yellow, black or piebald in the two most central populations but outlying species are more consistent in the colour of their patches.

Cape Rock Hyrax, *P. capensis* (S and SW Africa): black dorsal patch; **Ethiopian Rock Hyrax**, *P. habessinica* (NE Africa and Arabia): variable dorsal patch; **Black-necked Rock Hyrax**, *P. johnstoni* (central and E Africa): variable dorsal patch; **Kaokoveld Rock Hyrax**, *P. welwitchii* (Kaokoveld): pale cream dorsal patch; **Red-headed Rock Hyrax**, *P. ruficeps* (S Sahara): orange dorsal patch.

DISTRIBUTION Drier rocky areas of Africa and Arabia.

HABITAT Mainly rock outcroppings, often in areas where the rocks themselves assist the growth of vegetation by trapping moisture or nutrients. Rocks also create micro-climates that can be cooler, warmer, drier, moister, more shady, sunnier or less windy than the surroundings. Hyraxes can therefore counteract climatic extremes to some extent by finding surfaces or crevices that suit their physiological needs at any particular time. Crevices also provide shelter from predators.

FOOD Mainly grasses and herbs grazed within easy reach of shelter. Common grasses taken are species of *Aristida*, *Chrysopogon*, *Tetrapogon* and *Latipes*. In the alpine region of Mt Kenya *Festuca* is a staple. Shrubs and trees are also climbed and browsed, sometimes only seasonally. Feeding is limited to about 1 hour in the early morning and a longer session in late afternoon. Animals may feed at night during desert summers.

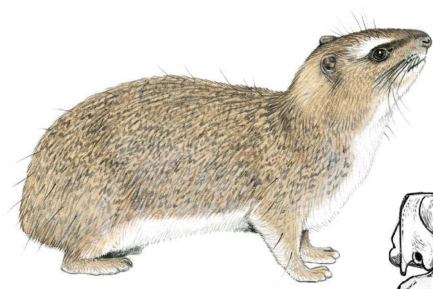
BEHAVIOUR Territorial, with single male territories containing various numbers of females and their offspring, up to a total of about 25 animals. In an outcrop the number of territories depends partly on their individual defendability but mainly on their year-round resources of food and shelter. Females are generally closely related and frequently come into close physical contact with other females and young within their unit. However, adult females have their own exclusive core areas, albeit ones that are very close to their fellows. There is no very marked hierarchy other than the territorial male's position of dominance. His intolerance of maturing male offspring leads to an emigration and selective exposure of young males, which leads to an imbalance of the sexes, especially among adults.

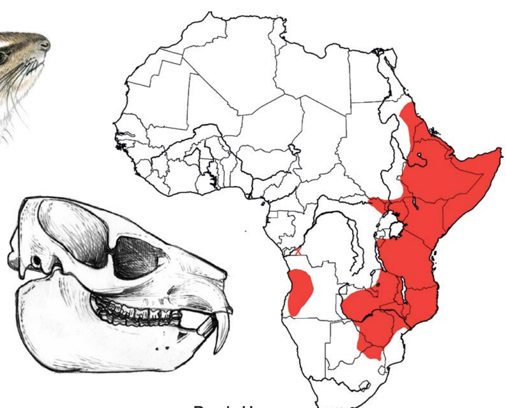
All members of a single territorial group or colony share a number of latrines. These appear to be of two types. Urine is dribbled down very exposed, outward-facing rocks where calcium carbonates dissolve and are deposited as very conspicuous white or light-coloured streaks. These may serve as external olfactory and visual markers for specific colonies. The second type of latrine is situated in more shaded, protected sites. Both dung and urine are dropped in the same place, preferably on a flat or nearly flat surface. Here liquids and solids congeal slowly, there is less evaporation and the smell can be very strong indeed. These latrines appear to function as scenting parlours where all members of the group come to share a common smell that scents their feet and fur.

Breeding seasons are often very local and can differ from the top to the bottom of an escarpment. The male is very vocal during the mating season and shakes his head while approaching the female, his dorsal gland open and actively exuding scent. Up to six young are born after a gestation of 214–240 days. Almost immediately active, and soon eating plants, young frequently climb onto their mother's back where they may become scented by her dorsal gland and warmed by her body.

ADAPTATIONS Main speciality is ability to live off coarse desert grasses. Both teeth and digestion differ substantially from arboreal, folivorous species. Conservative in being weaker and less agile climbers.

STATUS Although subject to periodic epidemics, heavy natural predation and very localised depletion or extermination, all major populations of *Procavia* are still numerous.





Bush Hyrax

BUSH HYRAX *Heterohyrax brucei*

OTHER NAMES Yellow-spotted Hyrax. Fr. *Daman de steppe*. Ger. *Buschschliefer*. Swah. *Perere mawe*.

MEASUREMENTS HB 320–570mm. W 2.0–3.5kg.

RECOGNITION A relatively small hyrax with conspicuous pale 'eyebrows', a white or off-white underside and a greyish, pepper-and-salt agouti body colour on some but not all regional variants, with a yellow dorsal spot. Snout more pointed than that of the rock hyraxes; altogether more lightly built.

GEOGRAPHIC VARIATION More than 20 subspecies described, based on variation in coat colour, but many may not hold up to taxonomic scrutiny. Genus formerly thought to include two further species: *H. antinae*, which is a form of *Procavia*, and '*H. chapini*', from the mouth of the Congo R., which probably represents a variant of the dark, thickly-furred Angolan race, *H. b. bocagei*.

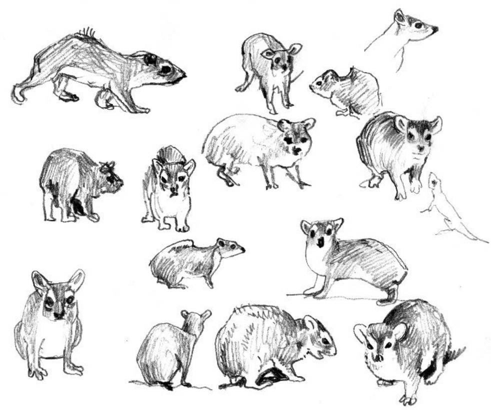
DISTRIBUTION Eastern half of Africa and Sinai with extensive outlier in Angola. Includes higher altitudes (notably around north end of L. Malawi/L. Nyasa).

HABITAT Wooded localities on river banks, escarpments and rock outcrops. Normally shelters in rocks but may resort to trees, termitaries or old burrows. Often found in joint colonies with rock hyraxes.

FOOD Leaves, fruits, stems, twigs and bark. On Serengeti outcrops virtually the entire diet comes from two trees, *Acacia tortilis* and *Allophylus*. Acacias are a major food over most of the species' range.

BEHAVIOUR Single colonies can number up to 34 individuals with females mixing very readily with each other and also, where present, with female rock hyraxes. They utter sustained 5-minute bouts

Sketches of Bush Hyrax. Note the erectile fur tract above the dorsal gland.



of loud calls, a whining croak that is much less resonant and deep than that of other hyraxes. Their very bird-like alarm whistle alerts other species, including rock hyraxes and Klipspringers. They flag their heads with a pronounced shiver.

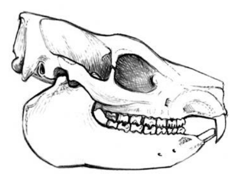
ADAPTATIONS The Bush Hyrax appears to illustrate the earliest steps in the colonisation of trees by an animal apparently ill-equipped to do so. Their primary asset in this niche is probably their exceptionally efficient gut, capable of digesting difficult plant foods.

STATUS Widespread and extremely abundant in many localities.

TREE HYRAXES *Dendrohyrax*

Eastern Tree Hyrax	*Dendrohyrax validus*
Southern Tree Hyrax	*Dendrohyrax arboreus*
Western Tree Hyrax	*Dendrohyrax dorsalis*

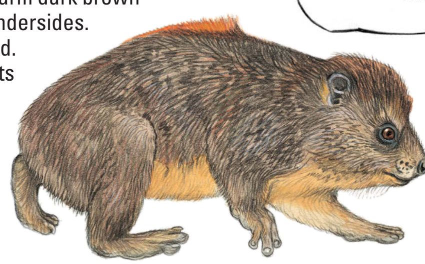
EASTERN TREE HYRAX *Dendrohyrax validus*



OTHER NAMES Fr. *Daman d'arbre*. Ger. *Ostlicher Waldschliefer*. Swah. *M'ha*, *Perere ya miti*.

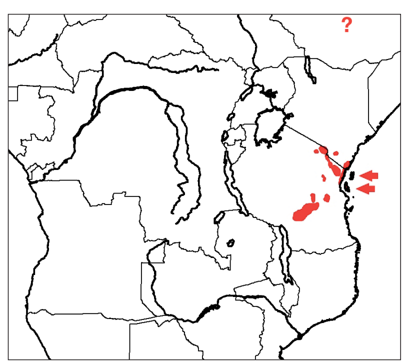
MEASUREMENTS HB 470–580mm. W 2.5–3.0kg.

RECOGNITION Variable colouring, mostly warm dark brown to greyish with off-white to cinnamon undersides. Dorsal spot 20–40mm long, russet-coloured.



GEOGRAPHIC VARIATION Possibly represents more than one species. *D. v. validus* (Mt Meru and Mt Kilimanjaro), *D. v. terricola* (Taita Hills, Usambara and Pare Mts), *D. v. schusteri* (Uluguru and Udzungwa Mts – latter may be a distinct form), *D. v. neumanni* (Zanzibar, Pemba and Tumbatu Islands), *D. v.* sp./ssp. nov.? (Ethiopian highlands).

DISTRIBUTION Eastern Arc Mts also Zanzibar and Pemba Is. Ranges from sea level to 3,000m. Sharing the same mainland region, the Eastern Tree Hyrax is restricted to mountains while the Southern Tree Hyrax dominates the lowlands. This suggests a relict distribution partly determined by competition arising from the spread of a more recently evolved species.



Eastern Tree Hyrax

HABITAT Montane forests on the mainland 1,700–3,070m (Kilimanjaro) and lowland forests on the islands. This species used to be particularly common in the higher reaches of montane forest where an impoverished flora grows on leached substrates.

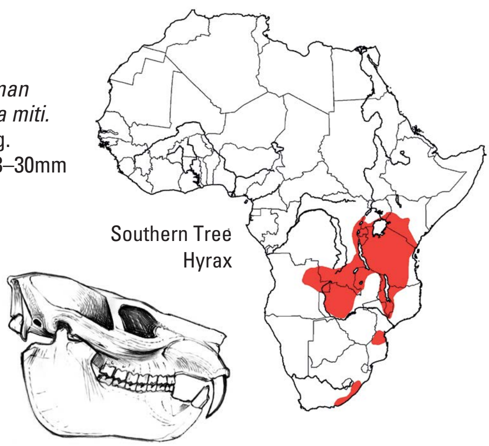
FOOD Predominantly an arboreal leaf-eater but also eats herbs and climbers. Feeding peaks at dusk and dawn. At the top of its altitudinal range in the Udzungwa Mts, this species lives at very high densities in low canopy mist forest where a very rare and localised species of African violet, *Saintpaulia grotei*, grows abundantly, often rooted in decayed hyrax faeces. These violets seem to escape the heavy browsing of hyraxes in this habitat, suggesting that the herb is distasteful to them. *S. grotei* seems to derive competitive, as well as nutritional advantages from its association with the hyraxes, suggesting that herb and herbivore might have co-evolved.

BEHAVIOUR Generally solitary but densities in the upper Udzungwa Mts (notably on the Gologolo crest) appeared to be very high in 2001, with at least 17 per ha estimated (from frequency and distribution of calls). Calling peaks just after dusk and before dawn and the frequency of calls has been reported to show little change over a period of 8 months. A common pattern consists of bursts of short hacks, sometimes building up to a crescendo of what have been called 'ping-pong' sequences for their resemblance to the sharp crack of a bouncing ping-pong ball. Very loud screams are common in areas of higher density. In the Pare Mts local Eastern Tree Hyraxes make what appears to be a contact call in the timbre of a man's voice asking 'whatsit?' In the Udzungwa Mts middens of faeces and urine can spread over several square metres and cover trunks and the surrounding ground with a very strong-smelling, thick, tarmac-like coat. Animals contributing to this olfactory beacon or 'scenting parlour' clearly acquire a group scent. It is likely that such sites serve to identify local 'clans' and that social behaviour may turn out to be complex and mediated by both sound, scent and physical contact. Gestation is about 7.5 months and births peak on Kilimanjaro in August.

STATUS Eastern Tree Hyraxes are at risk from felling and firing forests on Pemba and Zanzibar Is. In the mountains, hunting and logging are the most immediate threat. Lack of research into the basic biology and ecological needs of this species is regrettable because their uneven abundance and patchy distribution will need to be understood before practical conservation plans can be attempted. The state of local and distinctive populations of the Eastern species need attention and a yet-to-be described form of tree hyrax from forest relicts in Ethiopia is a particular cause for concern.

SOUTHERN TREE HYRAX

Dendrohyrax arboreus



OTHER NAMES Southern Tree Dassie. Fr. *Daman d'arbre*. Ger. *Waldschliefer*. Swah. *Perere ya miti.*

MEASUREMENTS HB 440–560mm. W 1.2–2.6kg.

RECOGNITION Soft-furred, dorsal patch 23–30mm long and cream-coloured.

GEOGRAPHIC VARIATION *D. a. arboreus* (Eastern Cape, KwaZulu-Natal and central Mozambique), *D. a. braueri* (Eastern Angola to L. Tanganyika and Zambezi R.), *D. a. mimus* (vicinity of L. Malawi/Nyasa), *D. a. stuhlmanni* (Tanzania and vicinity of L. Victoria), *D. a bettoni* and *D. a. crawshayi* (Kenya), *D. a. adolfi-frederici* and *D. a. ruwenzorii* (high mountains of central Africa).

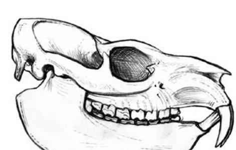
DISTRIBUTION Eastern, southern and south-central Africa in a somewhat scattered range as far as the eastern Cape.

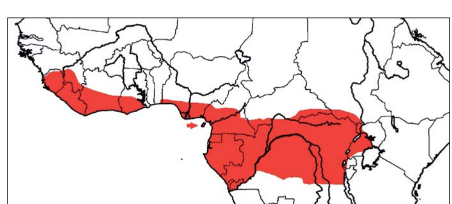
HABITAT Forests, moist savannas, evergreen thickets and mosaics (derived from forest) and montane habitats. *D. arboreus ruwenzorii* and related forms are (or were) abundant throughout the afroalpine and forest zones of W Uganda and E DR Congo. On the higher reaches of these cold, wet mountains the hyraxes live among rocks, are partly diurnal and have colonial habits. In montane forest they are arboreal, nocturnal and tend to be more solitary.

FOOD Leaves, fruits and twigs in the canopy, grasses and sedges on screes. Giant groundsel and numerous aromatic leaves and herbs are regularly eaten. Rapid feeders, these animals can eat a third of their own body-weight of food in a day.
BEHAVIOUR In the Rwenzori and other high mountains of central Africa these hyraxes can live at very high densities. Elsewhere they tend to be more scattered. They are territorial and very aggressive during the mating season. Both males and females exude secretion from their dorsal glands at this time. Male courtship involves following the female, calling and gland-fanning with penile erection. Gestation is about 8 months, with the precocious 400g newborn able to climb on its first day.
ADAPTATIONS As with all tree hyraxes, the most obvious speciality is contortionist mobility in their relatively long limbs and body. Mainly nocturnal habits may have stimulated the extraordinary volume, variety and frequency of their calls. Loud advertising or territorial calls are particularly variable, even within one species and from one side of a big river to another. All loud calls involve long series of cries that gradually grow louder, climaxing in barks, shrieks or choking screams. Extreme volubility in tree hyraxes is sometimes seasonal and can begin well before dark and continue all night during peak periods and in areas of high density.
STATUS Southern Tree Hyraxes could be at risk from clear-felling in some localities, from snaring in others. Snaring for meat and skins is also severe in many central African mountains.

WESTERN TREE HYRAX *Dendrohyrax dorsalis*

OTHER NAMES Fr. *Daman d'arbre*. Ger. *Waldschliefer*. Swah. *Maparaka*, *Perere miti*.
MEASUREMENTS HB 440–570mm. W 1.8–4.5kg.
RECOGNITION Very coarsely furred, dark brown to black (although pale, cream-coloured morphs are also known). Tends to be softer-furred in the lowland forests of Uganda, probably a consequence of long-term hybridisation with the Southern species, *D. arboreus*.
GEOGRAPHIC VARIATION Fifteen supposed subspecies have been named. So far there is no basis for assessing the validity of any of them.
DISTRIBUTION An equatorial species from both sides of the Congo R. Known from the Scarcies R. in Upper Guinea to the Nile R. in Uganda. The Western Tree Hyrax is a lowland forest species that has reached the Nile leaving populations of the Southern species isolated in the higher reaches of central African mountains.
HABITAT Lowland rainforest but also in degraded patches within cultivated savanna mosaics.
FOOD Nocturnal browser of leaves, shoots, twigs and fruits in the canopy but occasionally forages on the forest floor.
BEHAVIOUR Little known but generally thought to be solitary and territorial. Gestation is about 8 months and young can reach adult size between 120 and 200 days.
ADAPTATIONS Possibly the most adept climber among all tree hyraxes, possessing an exceptionally strong, firm grip with all four feet. Both sexes utter very loud, long cries that gradually grow louder, repeated 22–42 times and climaxing in an eerie shrieking crescendo. Calling frequency varies seasonally and with peaks between 20.00 and 22.00 and 04.00 and 05.00 hours. They have been heard to stutter, snap their teeth and salivate when excited.
STATUS Widespread and not endangered overall but a sudden increase of hyraxes on market stalls on Bioko Is. suggested hunters had discovered new techniques for catching them.



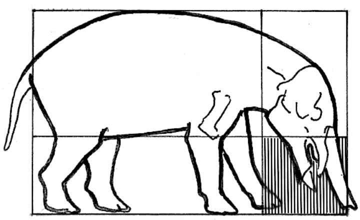


Western Tree Hyrax

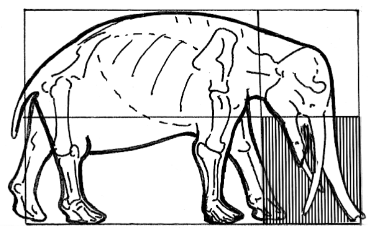
PROBOSCIDS PROBOSCIDEA

The proboscis or trunk is thought to have been the primary structure that made possible the evolution of elephants' great size, height and long tusks. Trunks are capable of powerful twisting and coiling while gathering food or wrestling with other elephants but can also perform delicate movements, such as picking berries, rubbing eyes or exploring orifices. Trunks can draw up columns of water or dust, and their great length can reach up to 7m or burrow down into sand, soil or crevices to reach deeply hidden water. While the development of a trunk relieved the incisor teeth of most of their feeding functions, the incisors' potential as weapons developed rapidly as the elephants' ancestors increased in size. As they evolved bigger and bigger bodies, elephants lost versatility in their limbs, which, first and foremost, had to bear great weight. Physical contacts with fellow elephants and with the environment became focused on the head: the trunk handled food and gentler forms of social contact; tusks became both tools and weapons of defence used in ritualised fighting with their own species.

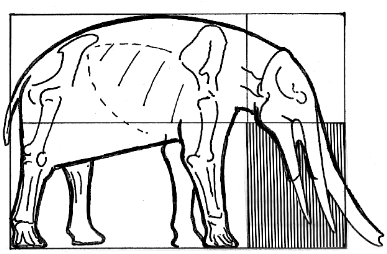
Elephants fossilise well, so an ever-more detailed picture of later elephant evolution continues to unfold from a wealth of fossils (the earlier stages are less well documented). Before 65 mya elephants had shared a common ancestry with hyraxes. Early elephants and early sea-cows began as wallowing herbivorous cousins but one remained terrestrial while the other became wholly aquatic.



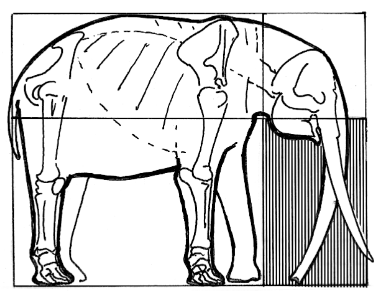
Phiomia



Gomphotherium



Stegotetrabelodon



Loxodonta

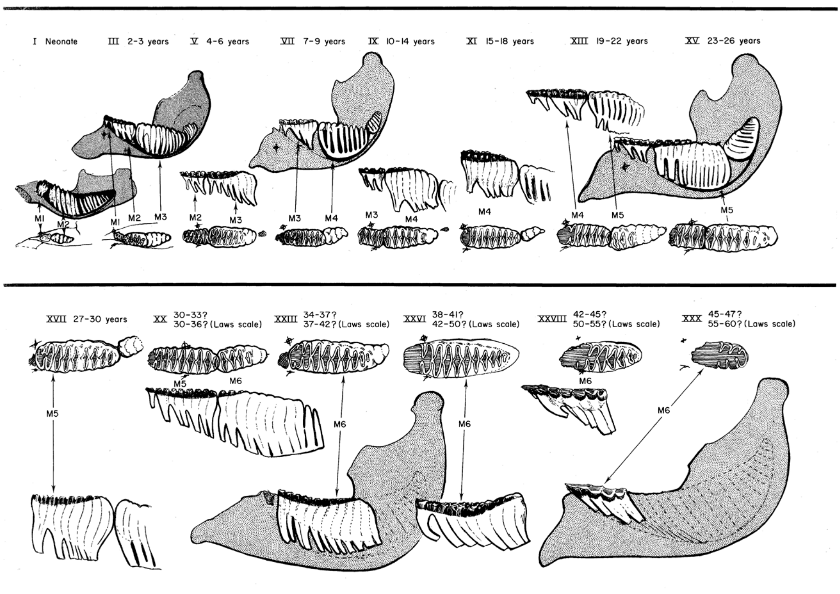
Elevation of proboscid feeding zones through time.

The earliest fossil, *Phiomia*, dates from about 35 mya and appears to have been a swamp-dwelling equivalent of the modern tapir. *Gomphotherium* (25 mya) shows that, as size and weight increased, limbs had to become more like columns. Both tusks and trunk became progressively elongated. By 7 mya *Stegotetrabelodon* had become tall, heavy and long-trunked but retained tusks in both upper and lower jaws. Improvement in the mechanics of chewing led to a rapid decline and elimination of the lower tusks but vestiges of their bony sleeves can still be traced in the lower jaws of living elephants (particularly in the Forest Elephant, *Loxodonta cyclotis*).

The direct ancestors of the African and Asian elephants and the mammoths split into three lines about 5 mya but reached their greatest diversity (at least 10 species) by less than 1 mya. Just as elephants were reaching the peak of their evolutionary and ecological success they became prey to a new predator – humans. Directly or indirectly, as a result of human activity eight species of elephant have become extinct within less than half a million years.

ELEPHANTS ELEPHANTIDAE

Modern elephants evolved in Africa with startling rapidity and seem to owe their later success to an adaptive shift out of very wet, marshy environments into drier, more open and difficult habitats where they became the prime specialist in bulk-feeding on coarse vegetation. To cope with rougher diets their teeth became heavy-duty 'rasp-grinders': single molars set in very short jaws. In the course of a lifetime six cheek-teeth succeed one another, travelling very slowly along the jaw at an angle that wears them away from front to back. Each in turn drops out once its grinding surface is used up. After the sixth tooth the sequence has run its course and the toothless elephant dies. Elephants are thought to live longest where wear of the teeth is slowest and their life-spans may range from about 50 to no longer than 65 years.

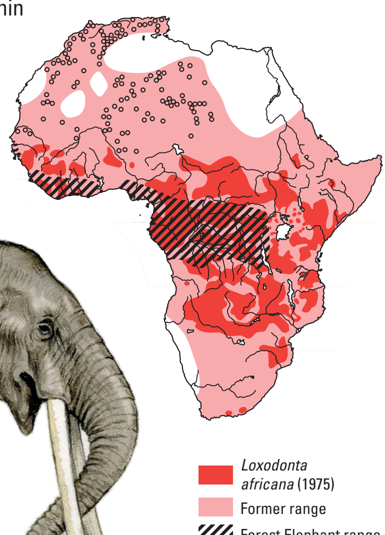


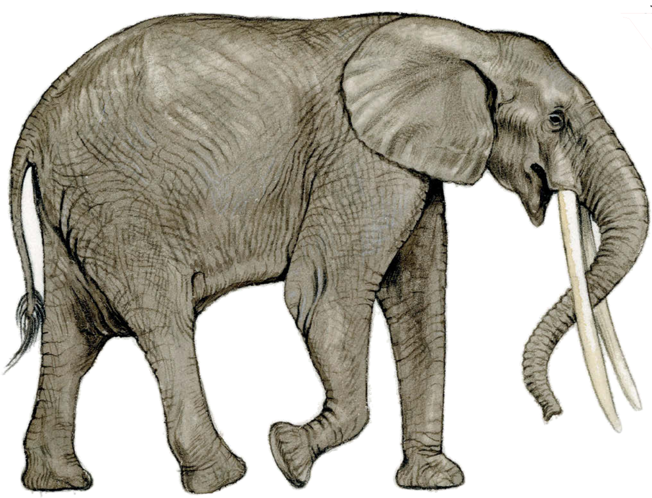
Toothwear and succession in the Bush Elephant. Roman numerals are 'Laws' age scale'. Molariform teeth are numbered 1 to 6. M1 to M3 are equivalent to milk molars in non-proboscids.

Linked with long life and very large size are slow growth and many years of slow maturation. This in turn demands tightly knit social groups that are both durable and reliable, not least because of the dangers to youngsters from large predators. Adult elephants are invulnerable to all living predators, except humans, but young calves are not. Maintaining complex social bonds with dozens of 'clan' members and many hundreds of regular acquaintances demands memory and intelligence of a high order. Because of a long learning period within a stable (and often very mobile) social group, elephants build up a highly flexible, multifaceted relationship with the environment, its changing resources and the other animals that inhabit it. Learnt skills help them to weather substantial fluctuations in climate and vegetation. Similar advantages were clearly shared by mammoths, *Mammuthus*, in Ice Age Eurasia and North America and by the Indian Elephant, *Elephas indicus*, in S Asia. Throughout some 4 million years of climatic instability *Elephas* was a highly successful species in Africa as well, becoming extinct there as late as about 20,000 years ago. By contrast, today's African elephants, *Loxodonta*, are absent or rare as fossils. The most likely explanation for this is that their ancestors became specialised for life in the moist forests (where bones seldom fossilise). Here the very distinctive Forest Elephant, *Loxodonta cyclotis*, still exists. It is now well known that mammal populations can change their body size over very short periods of time, so the Forest Elephant's emergence has probably been followed by just such a secondary enlargement. In the first edition of this guide African elephants were treated as a single species. In the intervening years convincing genetic evidence for two species has been published. Nonetheless, Forest and Bush Elephants are very closely related and retain much in common. Much less intensively studied, the Forest Elephant profile must necessarily be briefer and focuses on identifiable differences. African *Loxodonta* species were probably beneficiaries of the *Elephas* extinction. However, the human hunting skills that probably helped to destroy *Elephas* in Africa have now been honed on *Loxodonta* and may well bring about their extinction as well. Only a collective human will to preserve elephants and their habitats can save them now.

FOREST ELEPHANT *Loxodonta cyclotis*

OTHER NAMES Fr. *Eléphant de Foret*. Ger. *Waldelefant.*
MEASUREMENTS Sh.ht 1.6–2.4m (♀), 1.7–2.8m (♂). T 0.5–1.2m. W 900–3,000kg (♀),1,200–3,500kg (♂).
RECOGNITION Tall, long-legged, large-eared, short-necked grey animal with trunk and tusks. Forest Elephants differ from Bush Elephants in overall size, in more rounded ears and more slender tusks (of harder ivory). Feet tend to differ in retention of more nails in Forest Elephants (five nails on forefeet, four on hindfeet).
GEOGRAPHIC VARIATION A tendency for precocious growth of the tusks in young males and their early separation from their maternal groups misled early observers into supposing that such small animals were a distinct ‘pygmy’ or ‘dwarf’ species or subspecies. No other evidence for variation has been observed.
DISTRIBUTION Originally throughout western and central African forest zone. Now vestigial populations are being eliminated completely as sophisticated firearms fall into the hands of unsophisticated poachers. African governments within the rainforest zone seldom have the power or the inclination to discipline or disarm the practitioners of highly profitable poaching networks. On current projections Forest Elephant range will continue to shrink and no mapping of its range is likely to be accurate for very long.
FOOD Forest Elephants were originally able to subsist on fruit for much of the wet season. Up to 70 species of fruits have been recorded. Distribution and periodicity of fruiting largely determined elephant movements within the forest during the rains. Foliage and bark are mainly eaten in the dry season. Grasses are only grazed at marginal times and in marginal habitats. Mineralised earths are commonly excavated and may be consumed in substantial quantities.





BEHAVIOUR Forest Elephants seldom aggregate into large groups. Ranging from 2–20 individuals, family groups average out at about three individuals. Groups centre on a female and her offspring, with males leaving the maternal group earlier and more consistently than female offspring. Females mature at 12–14 years and may stay with their mother after parturition or form their own nuclear family. Gestation is about 660 days. Males come into musth for up to two months at a time and mainly during the dry season. Females only exhibit activity of the temporal glands during extreme stress. Lactating females have been observed suckling baby elephants that were not their own offspring.

There is a strong preference for diurnal activity. Individuals are highly 'talkative' with both audible and ultrasound signalling frequent and varied. Forest Elephants maintain conspicuous paths in the forest, a habit that facilitates their killing by poachers.

ADAPTATIONS Recent studies of the genetics of Forest Elephants in central West Africa have corroborated my suggestion (1976) that these could be dwarfed ecological isolates descended from the extinct *Loxodonta adaurora* (last fossils 2 million years old). If so, Forest Elephant populations could represent a particularly ancient lineage at the centre of their distribution. Less conservative populations may traverse the same region (between Cameroon and the Congo R.) and certainly occur in other parts of the *L. cyclotis* range. If Bush Elephants have derived from these small forest animals their enormous size must be a very recent and secondary development. Contrasts in size and habitat could inhibit mixing but there are undoubted periods and areas where 'hybridisation' takes place between Bush Elephants and Forest Elephants. There are also places where they co-exist as separate entities without genetic mixing.

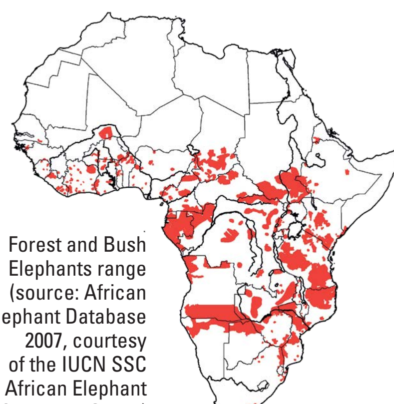
STATUS Although all trade in Forest Elephant ivory is prohibited by international treaties, bushmeat and ivory poaching remains relatively open and without regulation over much of its range. Eliminated from most of its former range, further depletion is now exceptionally rapid through widespread use and trade in automatic firearms. Logging concessions now operate over the greater part of this species' range and logging companies generally collude in the killing and transport of meat and ivory. Elephant family members are reluctant to abandon one another or disperse, and a single armed poacher can therefore dispatch or wound all members of a family group. In this way it is common for up to 10 elephants to be killed at the same time. Illicit bushmeat hunting and steel-wire snaring inflict cruel and ever-more pervasive suffering upon remaining populations.

BUSH ELEPHANT *Loxodonta africana*

OTHER NAMES Savanna Elephant. Fr. *Eléphant d'Afrique*. Ger. *Afrikanischer Elefant*. Swah. *Ndovu*, *Tembo*.

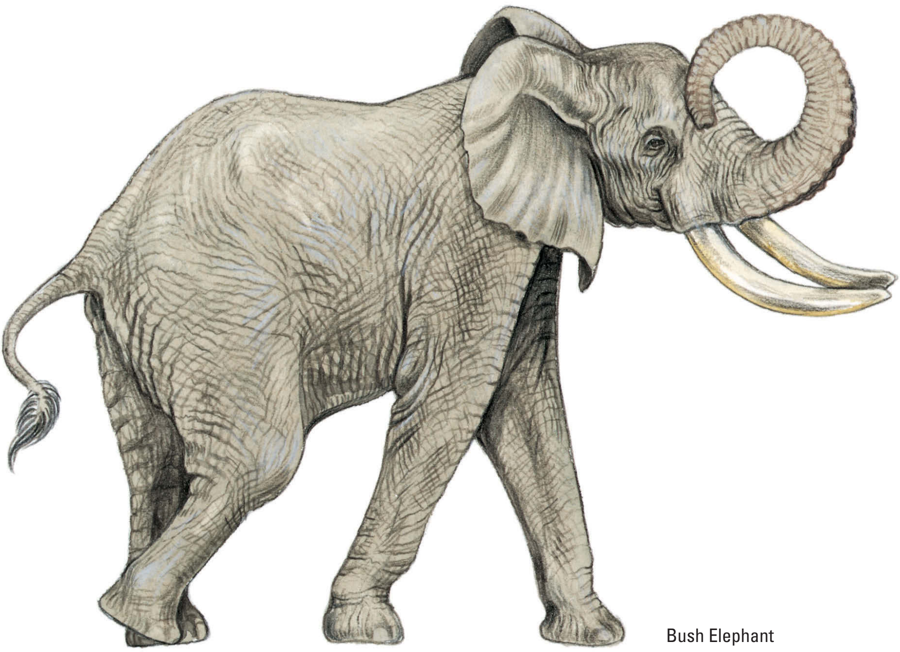
MEASUREMENTS Sh.ht 2.4–3.4m (♀), 3.0–4.0m (♂). T 1.0–1.5m. W 2,200–3,500kg (♀), 4,000–6,300kg (♂).

RECOGNITION The largest land animals, Bush Elephants are easily identifiable in having a trunk, tusks, large ears and pillar-like legs (see also Forest Elephant). Their thick skin is only superficially pigmented and the intensity of the melanin layer varies from a dense black to pale grey, brown or, in rare instances, depigmented pink (in patches or overall). Newborns are often very hairy and adults retain coarse, short bristles on the trunk, chin and, as abraded remnants, in the crevices over much of the rest of the body. The large, round ears are not only sound-catching dishes and flagging devices but also a cooling mechanism. The backs of the ears are laced with blood vessels that help to reduce overall body temperature when the ears are fanned. The tusks are modified incisors composed of layered dentine and their presence or absence, size, shape, orientation and microstructure are subject to much variation.



Forest and Bush Elephants range (source: African Elephant Database 2007, courtesy of the IUCN SSC African Elephant Specialist Group)

The feet are columnar, with the original five toes bound into a hoop of tissue, skin and nail above a cushion of elastic tissue. Nails vary from five on both fore- and hindfeet to four on the forefeet and three on the hindfeet, the latter being the norm in Bush Elephants. The smooth but cracked foot



Bush Elephant

pads leave individually recognisable tracks, circular for the forefeet, smaller and more elongated for the hindfeet. Tracks, frequent boluses, occasional urine puddles and extensive harvesting of plants are the most commonly seen signs of elephants. Elephants of both sexes and all ages have temporal glands behind the eye which secrete a liquid called temporin. The flow of this secretion becomes visible (and presumably smellable) when the elephant is excited, or during periodic male 'musth', as does the plasma flowing from the penis of males in musth.

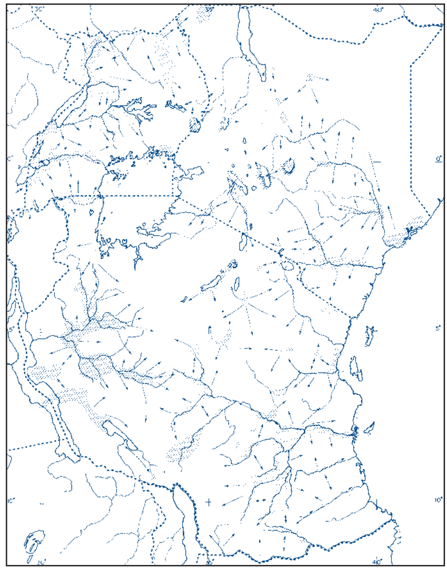
GEOGRAPHIC VARIATION Because successful adaptation to peculiar ecological conditions depends upon long-maintained family traditions, elephants readily evolve subpopulations. These can show consistent characteristics in size, ear shape, limb or pad proportions, skull and tusk shape, number of nails, skin texture and colour. As a result, 25 subspecies have been proposed, but see Adaptations below.

DISTRIBUTION Formerly most of Africa except the driest regions of the Sahara. Even so, their ability to forage as far as 80km from water greatly augmented their overall range in otherwise marginal areas. Conflict with farmers increases as the latter continue to expand into the elephants' remaining pockets of range. However, most attrition is due to the illicit ivory trade for mainly Asian markets.

HABITAT All major vegetation types, usually more than one being included within the annual cycle. The Bush Elephant's dependence on shade and water is well illustrated by the pattern of dry-season retreat into forests and swamps (shown for East Africa). This could be influenced by the short time (about 10,000–20,000 years ago) since they expanded into drier regimes. Although elephants mainly eat the plants that are available they have preferences and dislikes, which results in the local disappearance, selective survival and dispersal of particular plants and plant communities. In this way elephants have been a major influence on most vegetation communities for many millennia. The physical impact of elephants is also evident in browse lines, broad pathways, sunken waterholes, 'ploughed' soil and caves excavated for salt.

FOOD Grass and browse are taken in different and changing proportions by season (see above). Elephants consume about 5% of their body-weight (i.e. up to 300kg) in 24 hours and vegetation takes about 12 hours to pass through the animal. The bush-bashing that is typical of many male ungulates has a nutritional byproduct for the elephants. Trees are most frequently felled by young

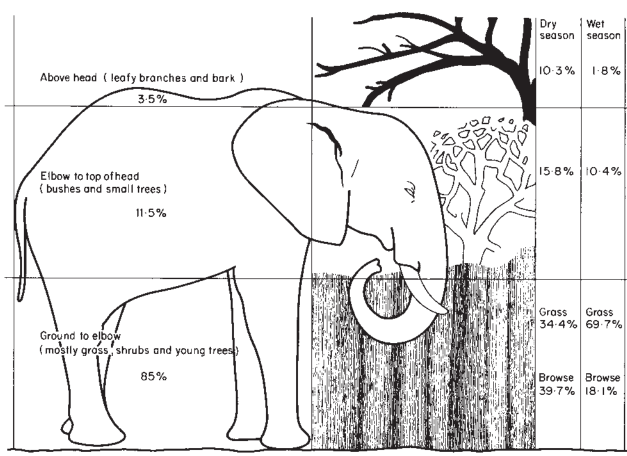
Season	Ecological Conditions	Elephants
DRY	Fires and destruction of grass	Move towards refuge areas Avoid fires and human activities
	Flood plains dry but grass still growing	Move on to flood plains Temporary concentrations in borassus groves
	Surface water finished	Move to hills, forests or rivers for permanent shade Less feeding, more resting Barking trees
Early rain		
WET	Flushes of green growth	Major movement initially by males Concentration on localised pastures, followed by dispersal
	Rapid growth everywhere	Longer feeding, more active
	Some valley soils gluey	Avoid slippery, sticky soils
	Grass long	Well dispersed in grasslands and savanna
End of rain		



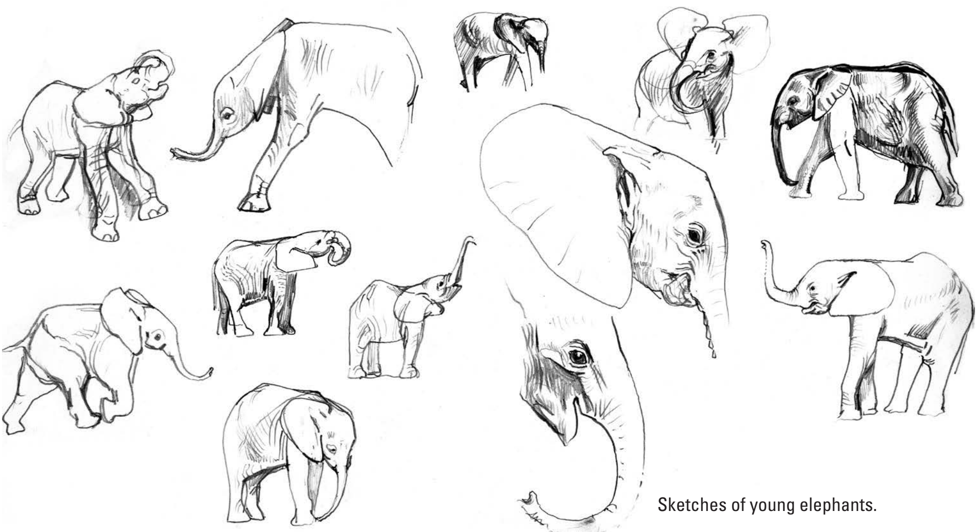
Dry season refuge areas with wet season dispersals suggested by arrows. The map summarises knowledge of seasonal movements. Elephants have now been eliminated in a number of areas shown here. (Data from Brooks and Buss, 1962a; Lamprey, 1963; Cobb, 1976; Uganda, Kenya and Tanzania Game Dept. records; and personal research.)

or solitary males, so obtaining out-of-reach fruits, leaves, pith or branches may not be the only reason for such behaviour. The crash of a felled tree sometimes attracts families or other solitary males and the arrival of the latter may precipitate chases and contests.

BEHAVIOUR The central social unit is the mother and her offspring. Female elephants are not able to conceive until 8 years of age (20 at latest), but once they become mothers they soon become unit leaders, or 'matriarchs'. Bush Elephants find it easier to forage, find one another and travel in larger groups but even here the nuclear family tends to split by the time there are 10 daughters and grandparents. Nonetheless, closely related 'matriarchal' groups in the same vicinity maintain frequent and friendly meetings for many years. These and larger associations have been variously labelled 'bond-groups' or 'clans'. Males are driven out of these associations at about 10–14 years of age. They may join with other males but tend to choose partners that are either substantially



Elephant feeding levels.



Sketches of young elephants.

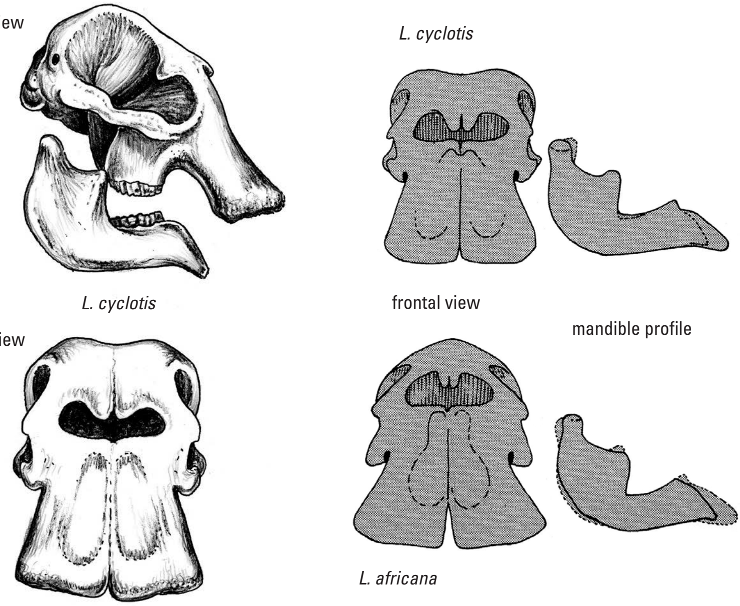
younger or older than themselves in an informal, linear hierarchy. Dominance is less a feature of female groups but age, size and health determine the 'matriarch' in large family groups. Very aged or permanently disabled females are forced to drop out of their groups.

Female elephants are frequent 'talkers', using rumbles, growls, roars, snorts, squeals and trumpets to convey a variety of signals, conditions and emotions. The most remarkable part of their repertoire, infrasound, was first described by scientists only in 1987.

Females come into oestrus for 2–6 days after an interval of anything between 3 and 9 years. Their advertisement of this rare and vital condition depends on a unique sequence of sounds emitted at below the threshold of human hearing but perceptible at least 4km away and, depending on the weather and topography, sometimes much further. Females routinely use infrasound to keep in touch with and monitor other groups in their clan or regional population. Males are more silent but passively eavesdrop until the unmistakable mating song is heard, whereupon all males within range immediately hasten towards the singer, the fastest and most urgent suitors being those that are in 'musth', periodic rutting behaviour marked by a continuous flow of temporin lasting 1–103 days. Rutting males also develop a swollen, semi-erect penis that dribbles urine and a greenish fluid. Tests have shown that the aggressiveness of musth bulls is linked with high levels of testosterone. Males in this condition appear to intimidate all other classes of elephant but are the preferred partners for oestrous females, who benefit from their close (but not continuous) attention because they discourage the attentions of numerous other males.

Gestation lasts 650–660 days and one, very rarely two, young are born, with a slight peak of births in the rains. Although they rise to their feet within hours, newborns are visibly unsteady for several weeks (a feebleness that attracts Lions and hyaenas). Mothers are alert to all their infant's needs, helping it over all manner of obstacles with trunk and feet. They are particularly sensitive to any signs of dehydration and, in the absence of other sources, will regurgitate water from their own stomachs. Mothers will pump water directly into their infants' mouth and will squirt and massage it while playing in shallow water. Although calves can survive on solid food before they are 2 years old, mothers tend to remain in milk for about 4 years (some lactate continuously throughout their reproductive life). Offspring become independent at varying rates; some scarcely leave their mother's side until they are nearly 10 years old (an age at which some will already have calves of their own). Body size and the development of tusks are also very variable, making overall estimates of age by height or tusk length difficult. In the case of dead elephants, jaws provide a reliable measure of age (see p.57).

ADAPTATIONS Before widespread and recent extinctions, species of elephants were diverse, abundant, highly successful and actively evolving new forms in special habitats and on many



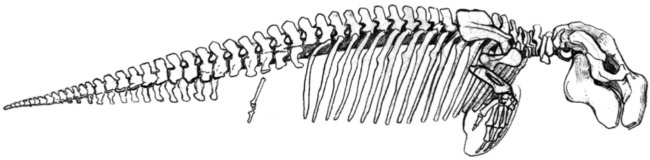
Skulls of *Loxodonta* spp. compared.

offshore islands. On a much smaller and shorter scale, modern African elephants had begun to diverge along similar lines: e.g. desert specialists in Namibia, dwarfs in the Atlas Mts. In the swamps of the R. Rufiji delta a trend towards particularly large ears, a smooth skin and tuskless jaws shows that families and subpopulations can maintain peculiar, possibly adaptive, traits even in the absence of complete isolation. Numerous features of the Bush Elephant's biology, especially its sensitivity to dehydration and heat, suggest that adaptation to arid environments is a recent and ongoing process. The surviving populations of elephants, small and scattered as they are, still exemplify great diversity and continuous adaptation to climate and the new challenges posed by human control of their environment.

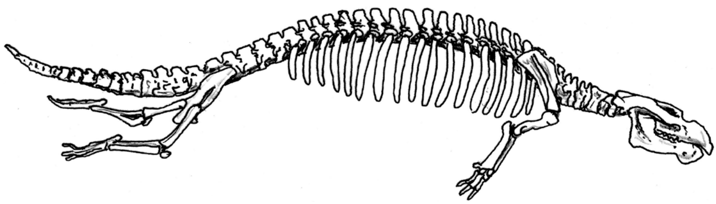
STATUS Recent surges in elephant killing across Africa have provoked calls for international conservation action. Declines, fluctuations and elimination of elephants in Africa is not new. They were first eliminated from North Africa by about the 4th century AD through a combination of ivory-hunting and increasing aridity. Then they were exterminated by the settlement of South Africa during the 18th and 19th centuries and over much of West Africa in the 20th century. Low ivory prices and legal protection between 1920 and 1970 allowed an extensive recovery in much of tropical Africa, only to be followed by massive declines in the 1980s as new business interests, as well as corrupt politicians and soldiers, organised the wholesale killing of elephants for ivory. From between 5 million and 10 million in the 1930s and 1940s, African elephants have declined to between half a million and three-quarters of a million at the present time. Numerous bodies exist to protect elephants, both nationally and internationally. The ultimate success of all these initiatives depends upon long-term, sound education and sustained, honest management at the most local level.

SEA-COWS SIRENIA

The name Sirenia derives from the legendary 'sirens', so-called 'mermaids'. Fossil forms are known to have grown up to 10m in length. They share terrestrial origins with elephants and, unlike most other aquatic mammals, they subsist almost entirely upon flowering plants growing in rivers, estuaries and the sea. The evolution of sea-cows seems to be associated with the Tethys Sea (precursor to the Mediterranean). There are two extant families of sirenians: Dugongidae, along Indo-Pacific shores, and Trichechidae, in waters surrounding the tropical Atlantic.



Fossil skeleton of an extinct quadrupedal sirenian, *Pezosiren* (*below*) compared with the skeleton of the extant Dugong *Dugong dugon*.



DUGONG DUGONGIDAE

This family has just a single representative.

DUGONG *Dugong dugon*

OTHER NAMES Fr. *Le Dugong.* Ger. *Dugong.* Swah. *Nguva.*
MEASUREMENTS HB 2.4m (2.2–3.31m) (♂). Flippers 300–420mm. W 250–420kg.
RECOGNITION The entirely aquatic Dugong is a large, grey torpedo-shaped animal with horizontal, whale-like tail-flukes. Externally there is no suggestion of neck or upper arm, both being contained within the regular, cylindrical form of the body. The forearm and hand form simple paddles which have a stabilising function and are occasionally used to free food plants in sand. The main propulsive force is provided by undulating movements of the tail-flukes and body. Small lidless eyes

adult male

Dugong