

The
RISE
and
REIGN
of the
MAMMALS

*A New History,
from the Shadow of the Dinosaurs to Us*

STEVE BRUSATTE
WITH ILLUSTRATIONS BY
TODD MARSHALL AND SARAH SHELLEY



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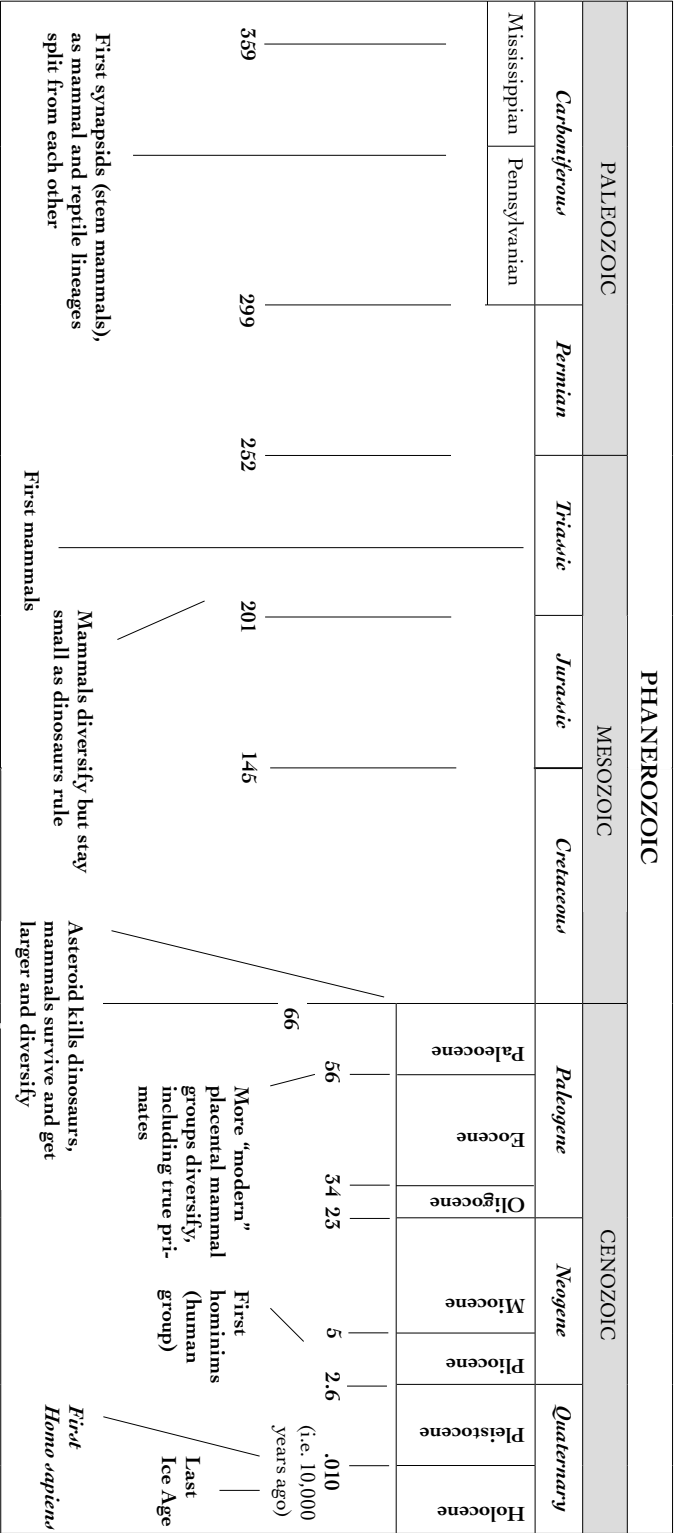
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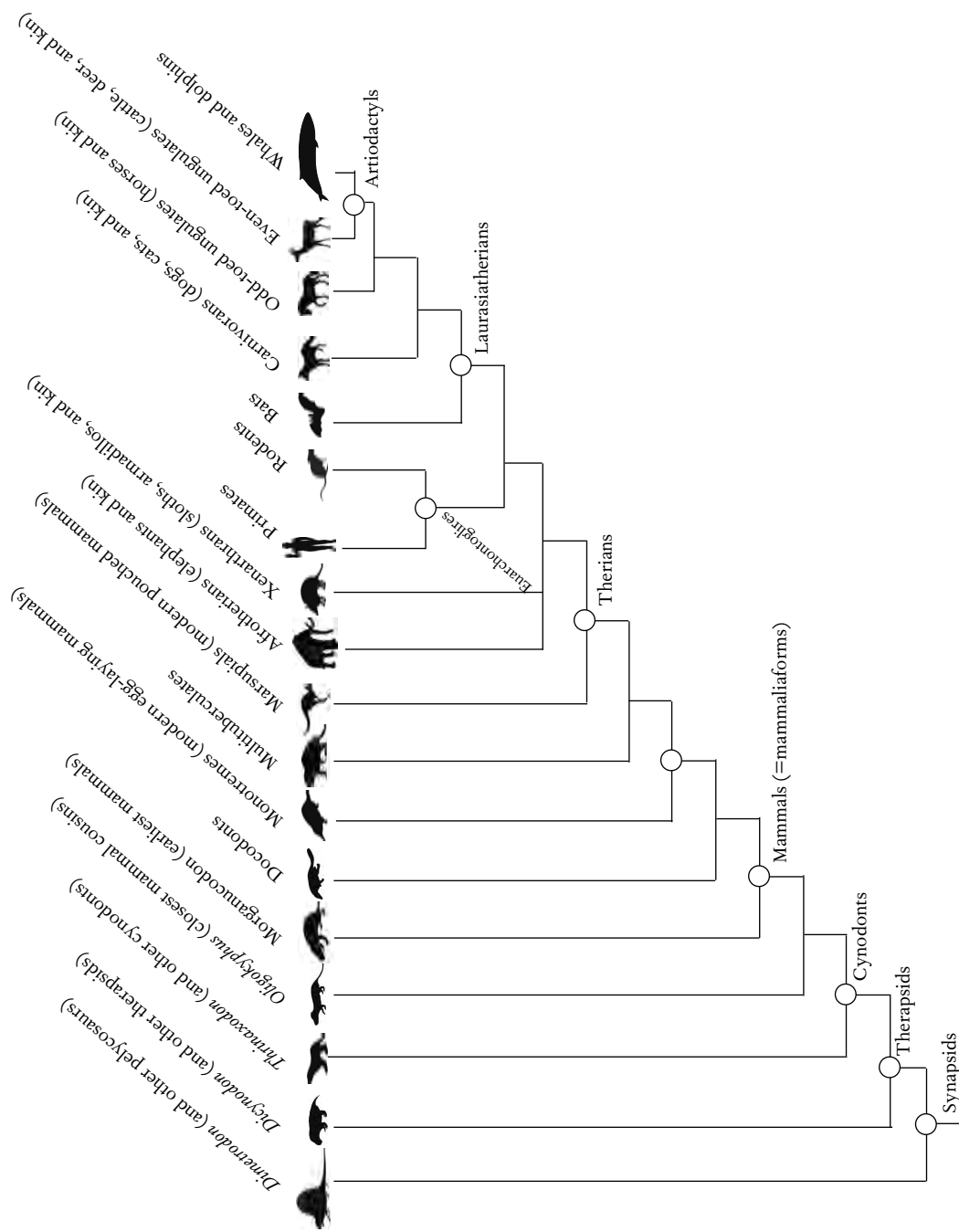
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TIMELINE OF MAMMALS

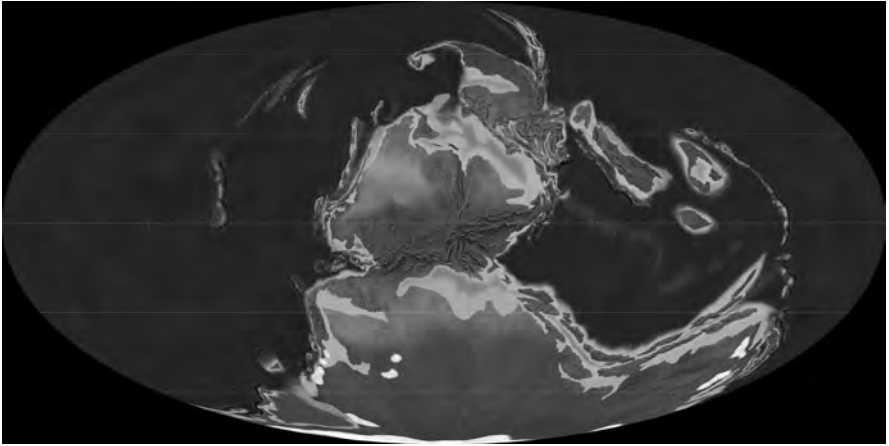


numerical age

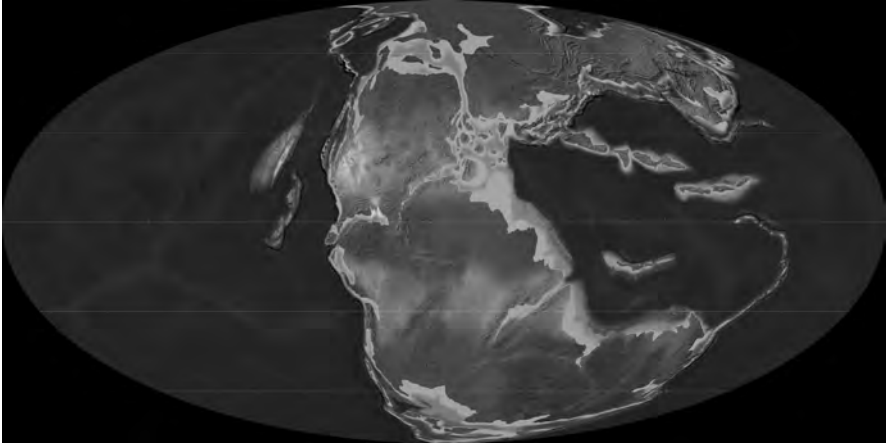
MAMMAL FAMILY TREE



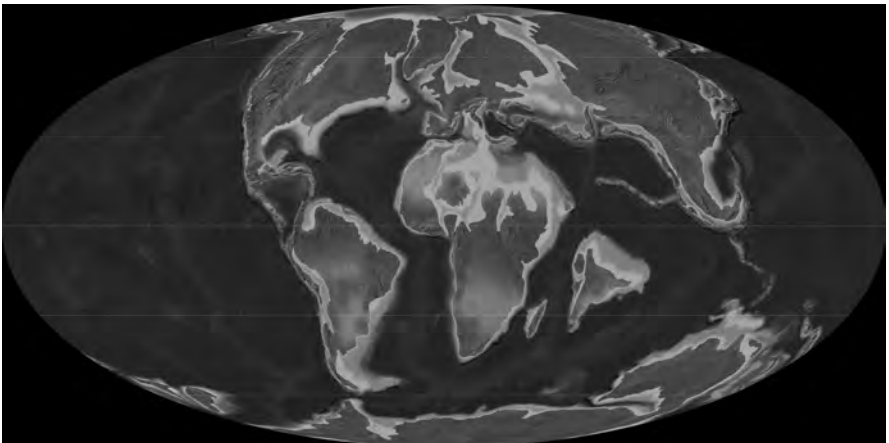
MAPS OF EARTH OVER TIME



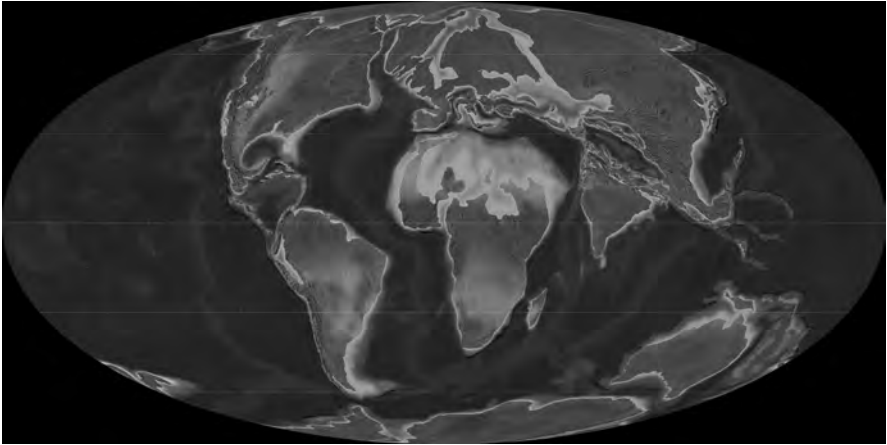
320 million years ago, Carboniferous (Pennsylvanian)



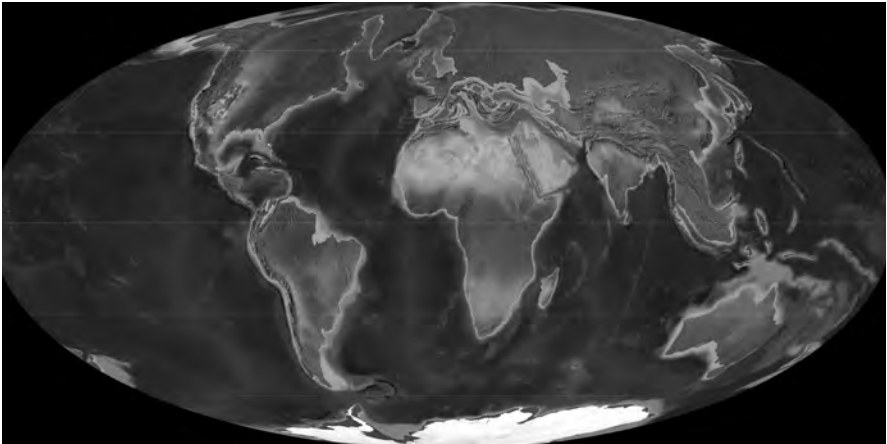
200 million years ago, Triassic-Jurassic Boundary



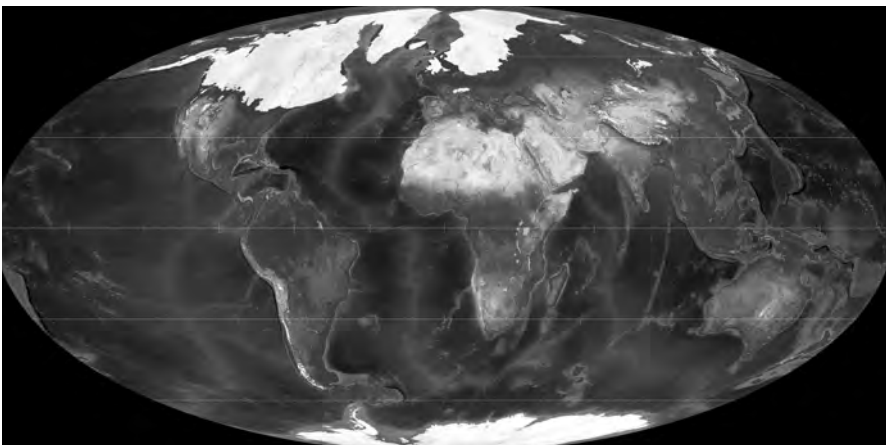
66 million years ago, end of the Cretaceous, time of asteroid impact



50 million years ago, Eocene



20 million years ago, Miocene



21,000 years ago, last advance of the Ice Age

INTRODUCTION

Our **Mammalian** Family





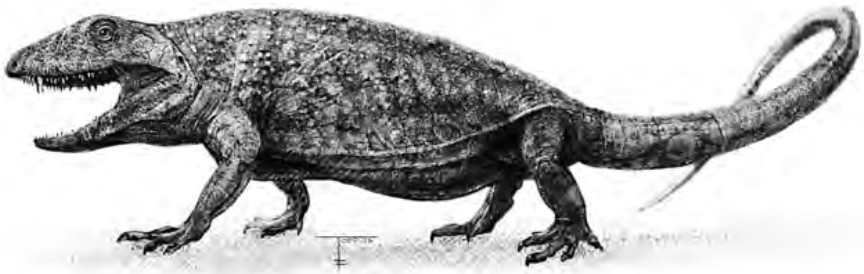
Sarah Shelley and me in New Mexico, collecting teeth from mammals that lived soon after the dinosaurs went extinct. (photo by Tom Williamson)

1

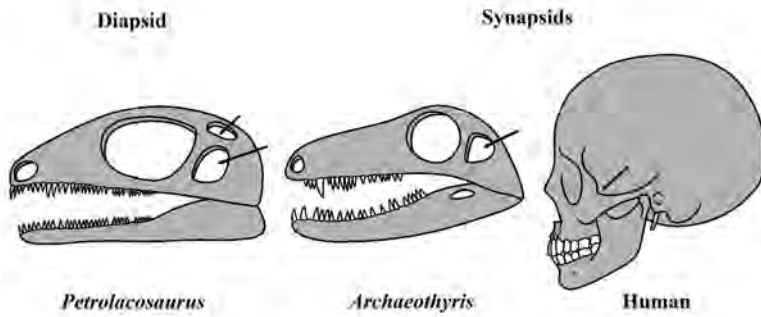
MAMMAL ANCESTORS



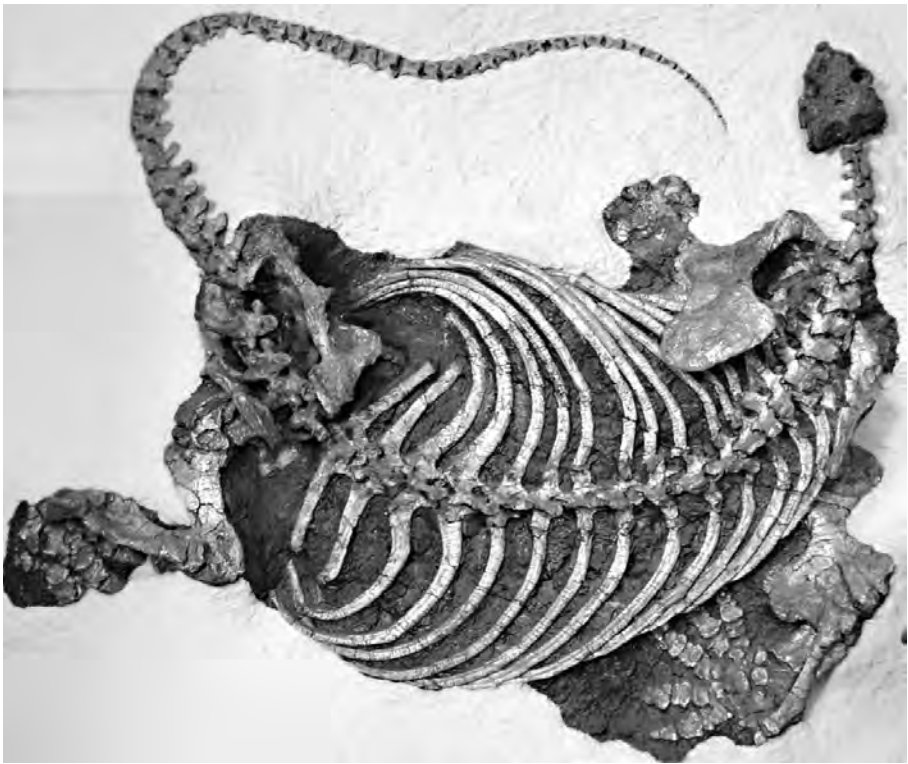
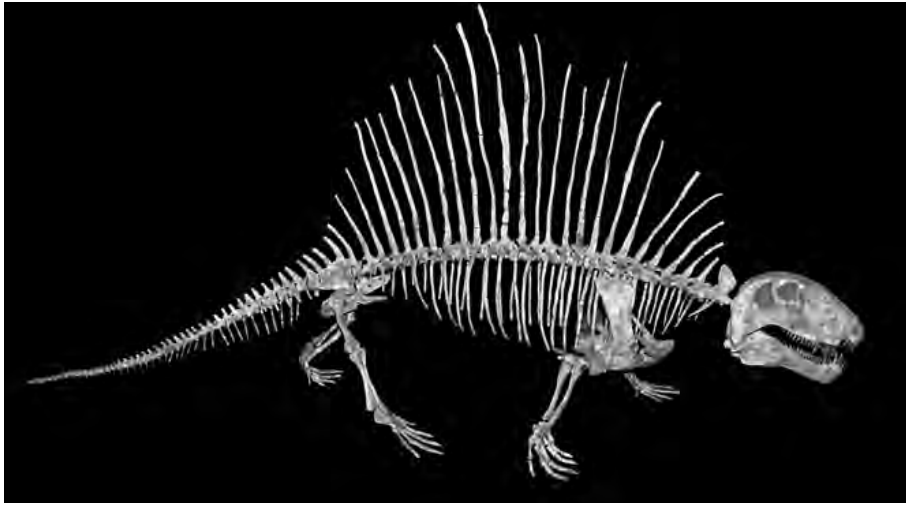
Dimetrodon



Archaeothyris (illustrated by Todd Marshall)

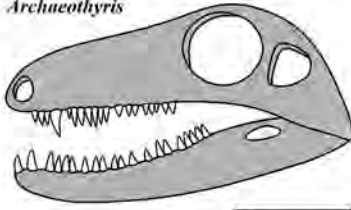


The two main skull types of land-living vertebrates: diapsids with two openings for jaw muscles behind the eye and synapsids—including humans—with a single opening. Arrows denote the jaw openings. (illustrated by Sarah Shelley)

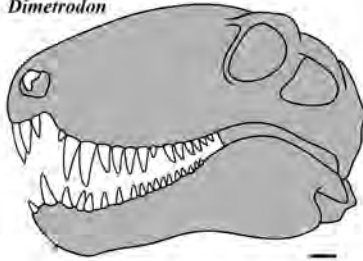


Pelycosaurs, primitive synapsid forebears of mammals: the sail-backed *Dimetrodon* (top) and a pot-bellied, plant-eating caseid (bottom).
(photos by H. Zell and Ryan Somma, respectively)

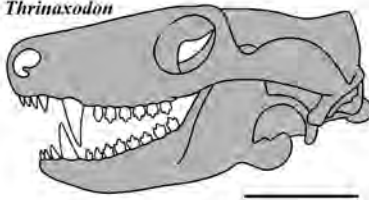
Archaeothyris



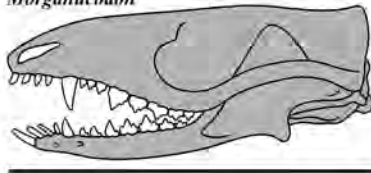
Dimetrodon



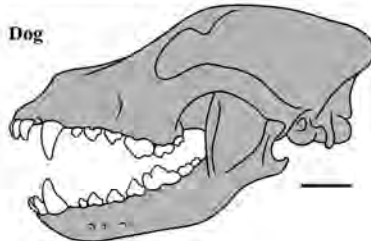
Thrinaxodon



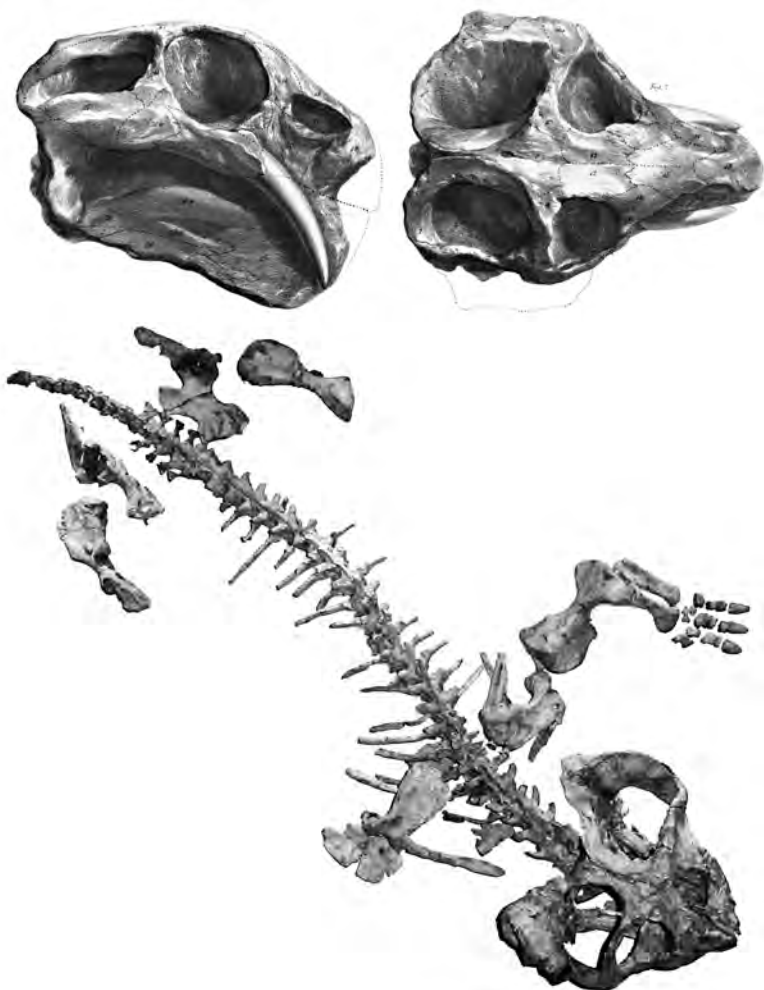
Morganucodon



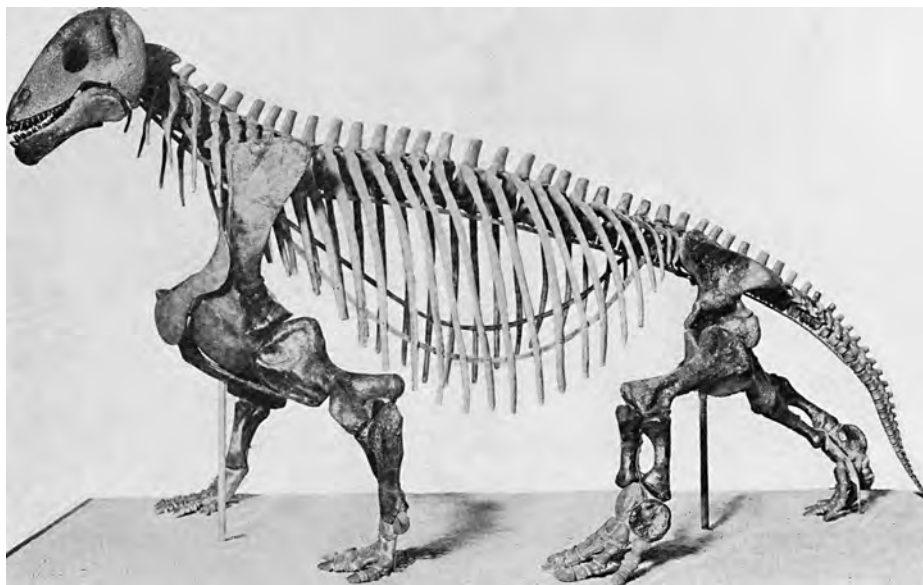
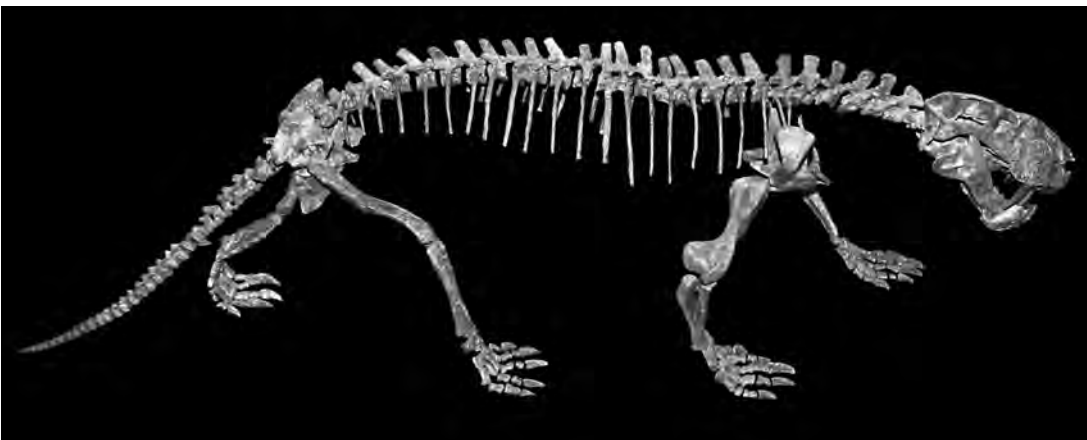
Dog



The evolution of skulls and teeth during synapsid history, illustrating how the teeth become more complex and split into incisors, canines, premolars, and molars in mammals. Scale = 3 cm. (illustrated by Sarah Shelley)



Dicynodonts, primitive synapsid forebears of mammals: skull of *Dicynodon* from Richard Owen's 1845 monograph (top) and skeleton (bottom). (photo by Christian Kammerer)



Therapsids, primitive synapsid forebears of mammals: a saber-toothed gorgonopsian (top) and the head-butting dinocephalian *Moschops* (bottom). (photos by H. Zell and AMNH Library, respectively)



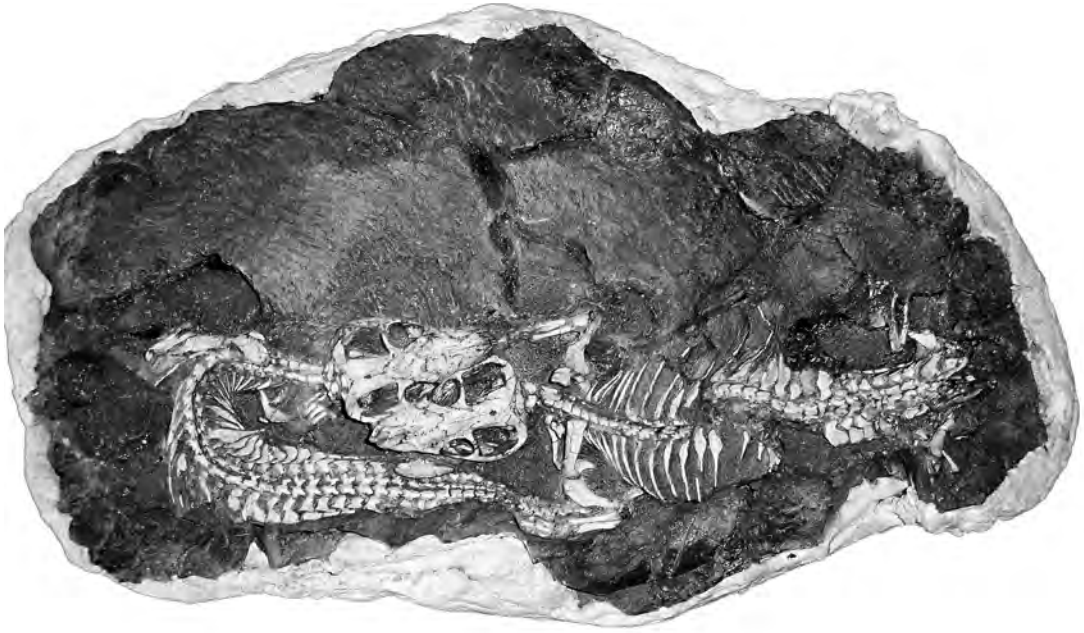
Anusuya Chinsamy-Turan studying microscopic images of bone in her lab. (photo courtesy of Anusuya Chinsamy-Turan)

2

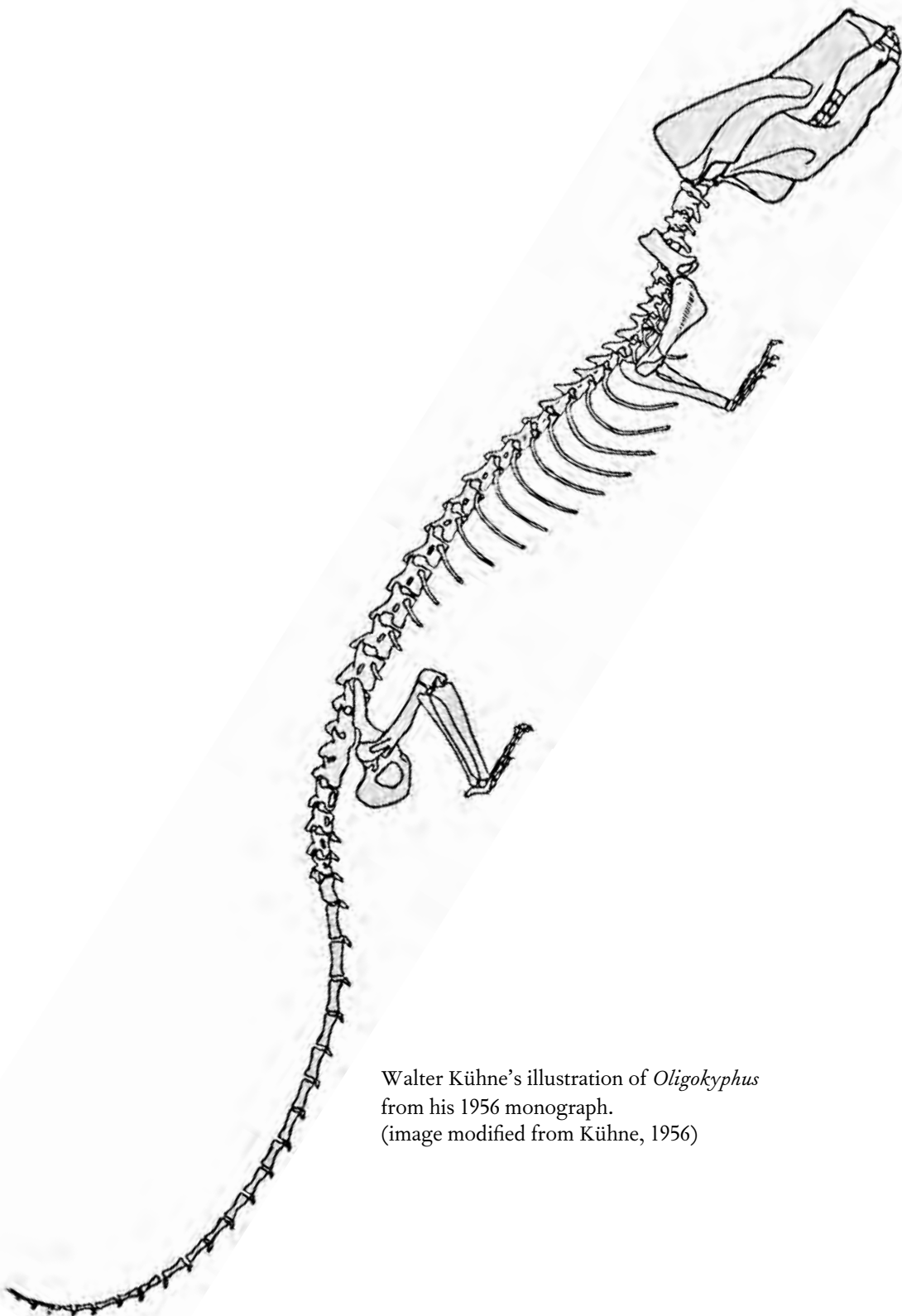
MAKING *a* MAMMAL



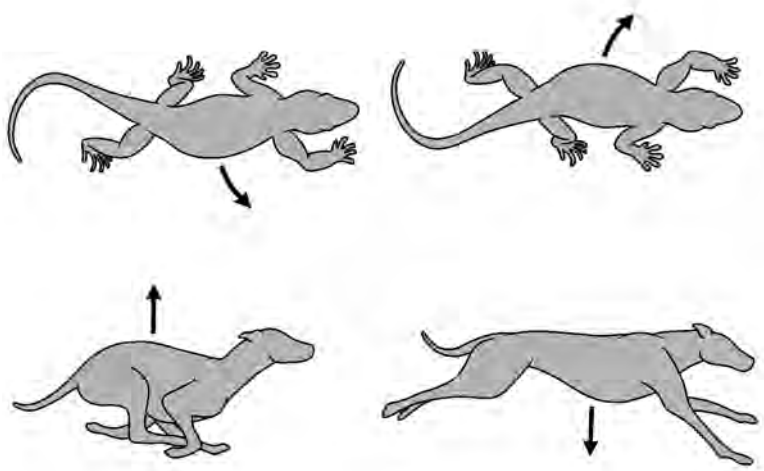
Thrinaxodon



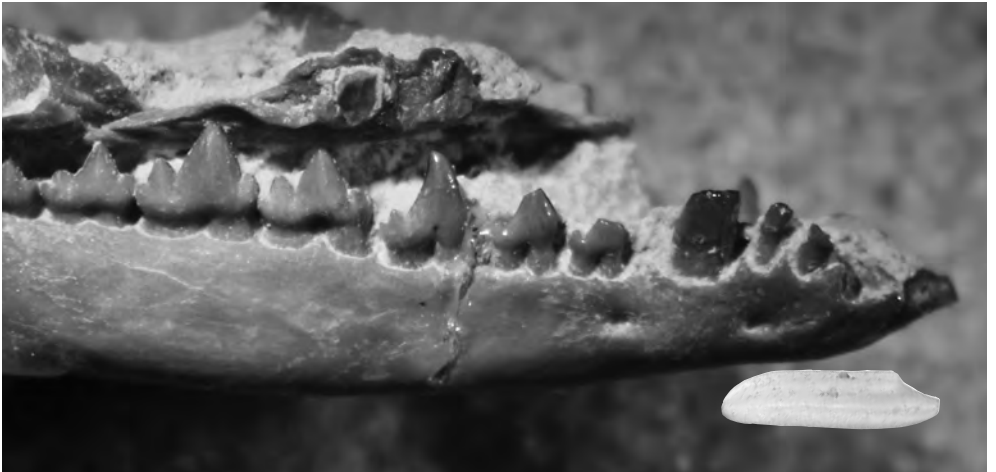
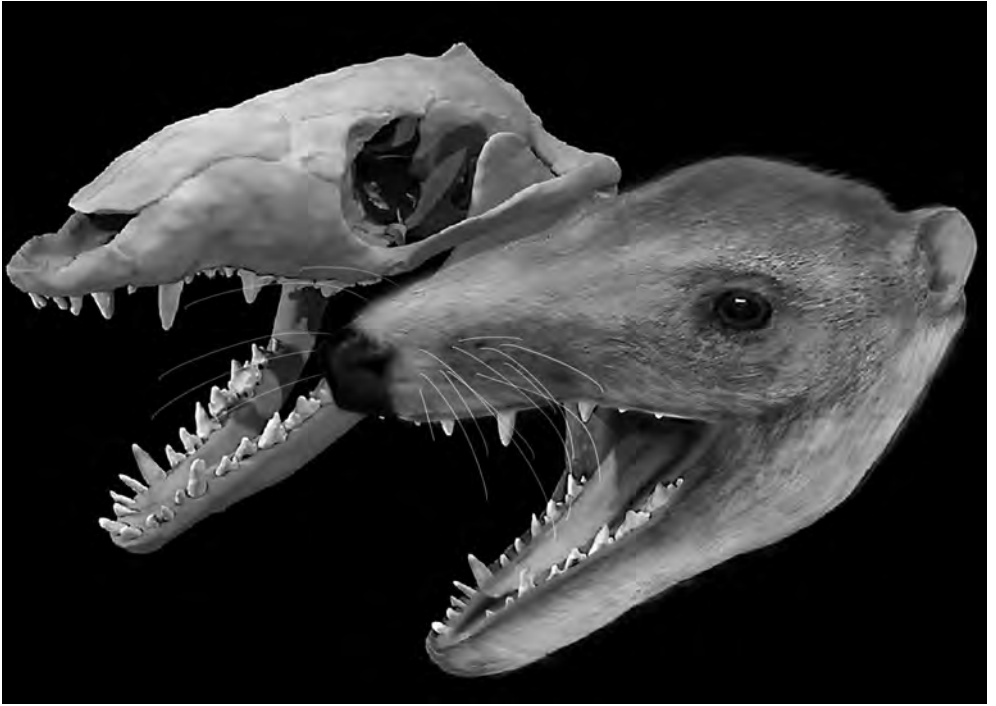
Thrinaxodon skeletons (top) and CT scan of a *Thrinaxodon* fossilized in a burrow next to an amphibian (bottom). (images by Christian Kammerer and from Fernandez et al., 2013, *PLoS ONE*, respectively)



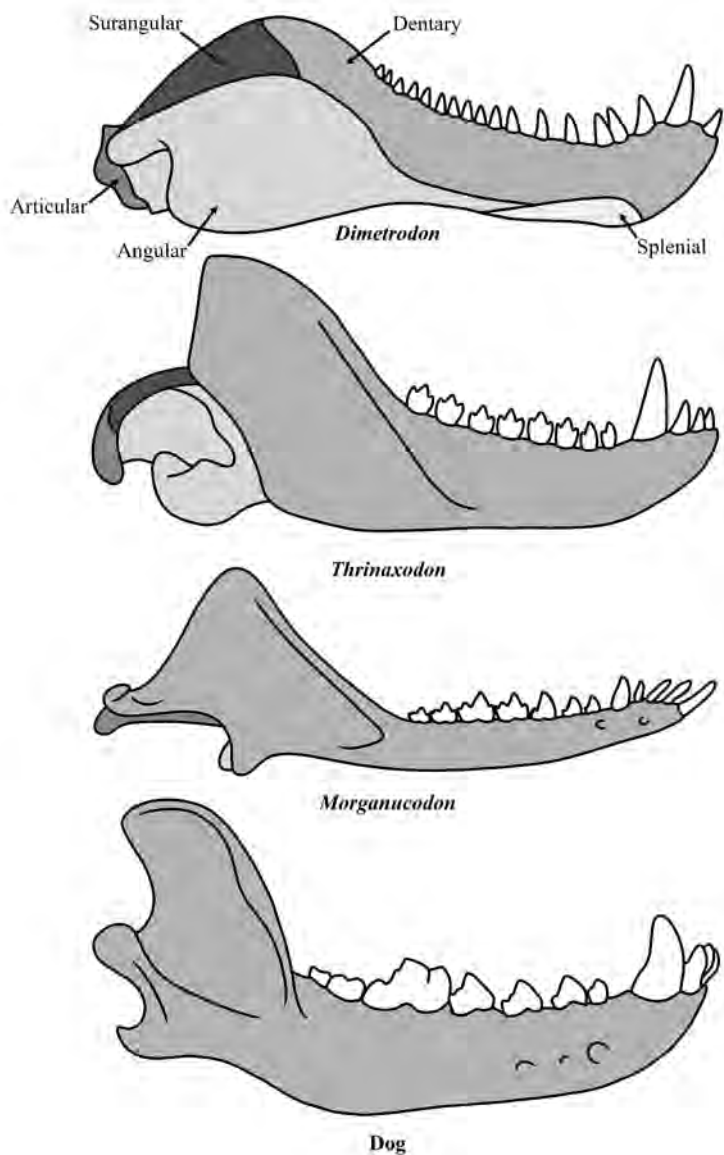
Walter Kühne's illustration of *Oligokyphus*
from his 1956 monograph.
(image modified from Kühne, 1956)



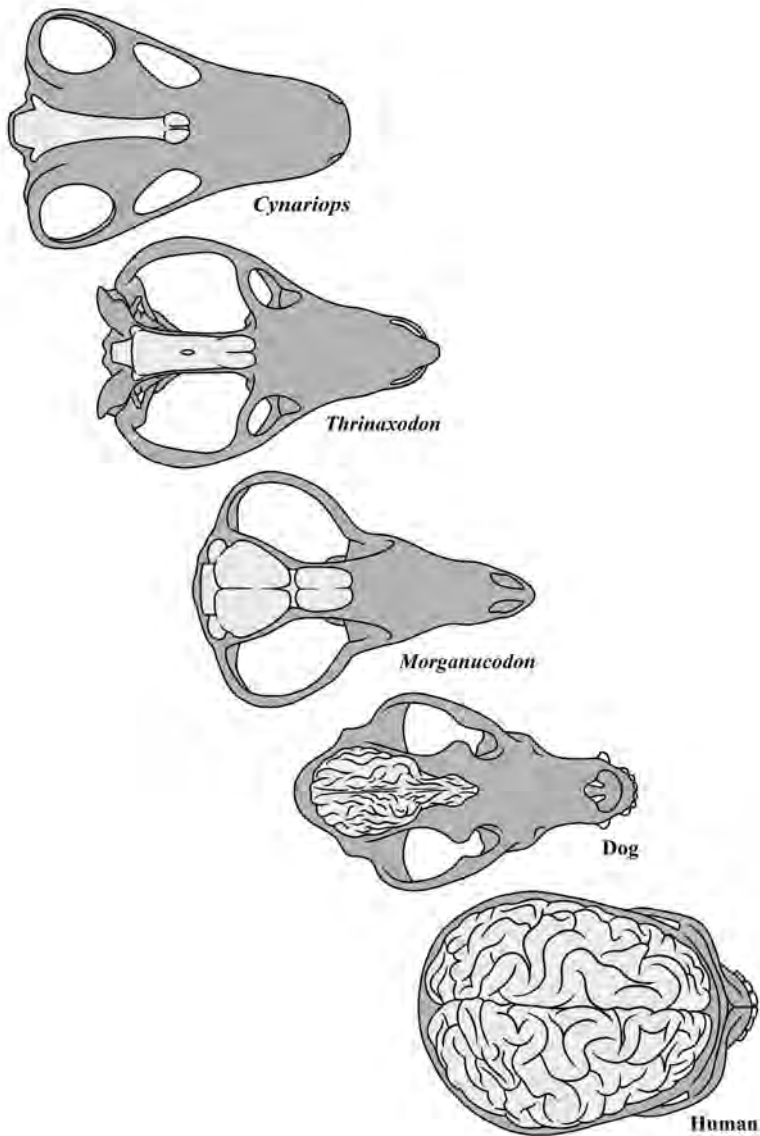
Differences in locomotion between reptiles that move side to side (top) and mammals that move up and down (bottom). Arrows show direction of movement. (illustrated by Sarah Shelley)



Morganucodon, one of the first mammals. Skull and head reconstruction based on CAT scans (top) and fossilized lower jaw with a grain of rice for scale (bottom). (images by Stephan Lautenschlager and Pamela Gill, respectively)



The reduction and simplification of synapsid jaws over time, culminating in the single lower jaw bone (dentary) of mammals. (illustrated by Sarah Shelley)



The enlargement of brain size in synapsids over time, culminating in the large brains of mammals, with a convoluted texture and enlarged neocortex of the cerebrum. Scale = 3 cm. (illustrated by Sarah Shelley)



Farish Jenkins's revolutionary image of the early mammal *Megazostrodon*. (image modified from Jenkins & Parrington, 1976)

3

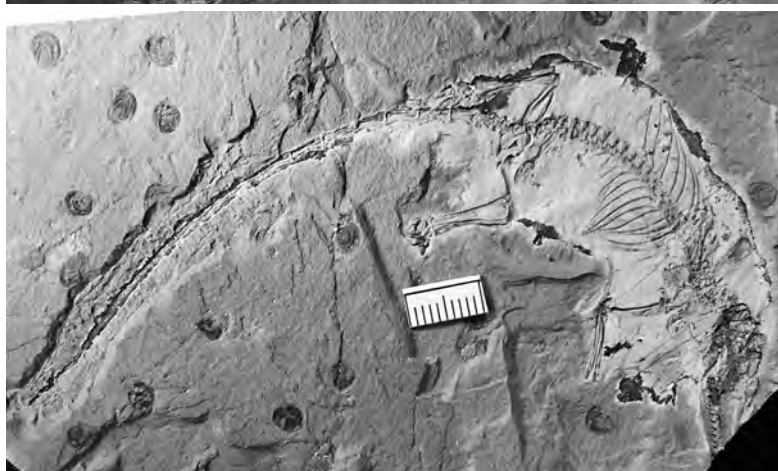
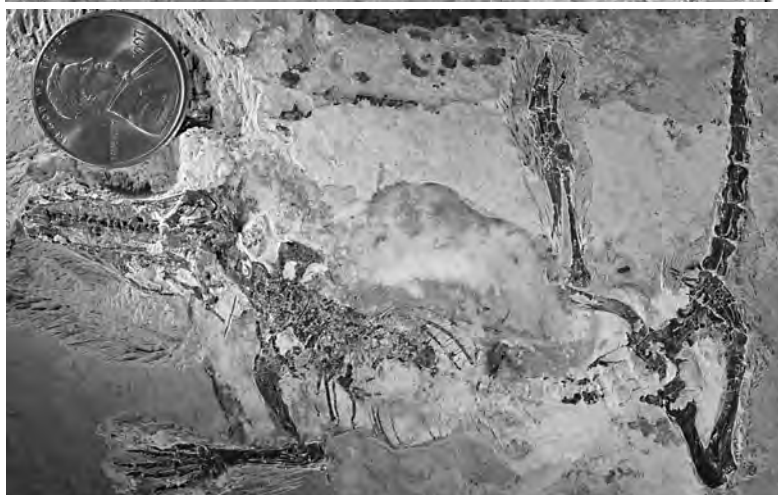
MAMMALS *and* DINOSAURS



Vilevolodon



Junchang Lü (center) and his team showing me the mystery mammal fossil in Beipiao, China. (photo by Steve Brusatte)



Stunningly preserved mammal fossils from Liaoning, China:
Jeholodens (top), *Agilodocodon* (middle), *Microdocodon* (bottom).
 (photos by Zhe-Xi Luo)



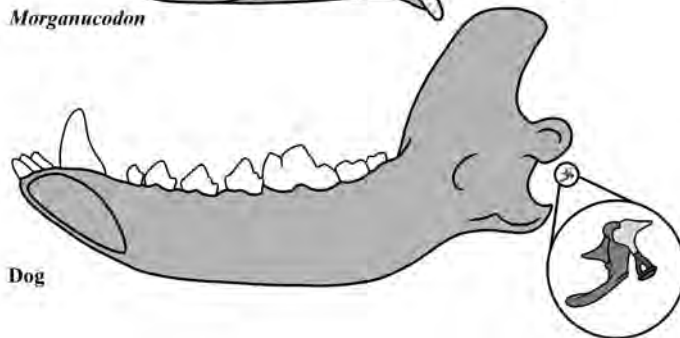
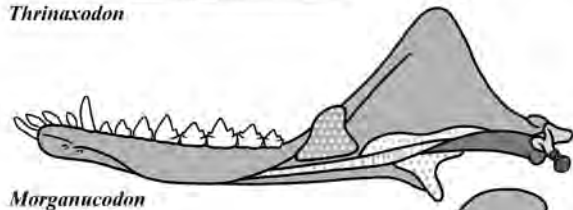
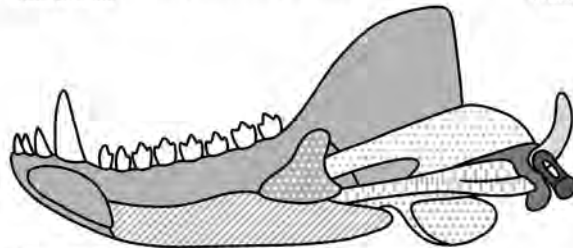
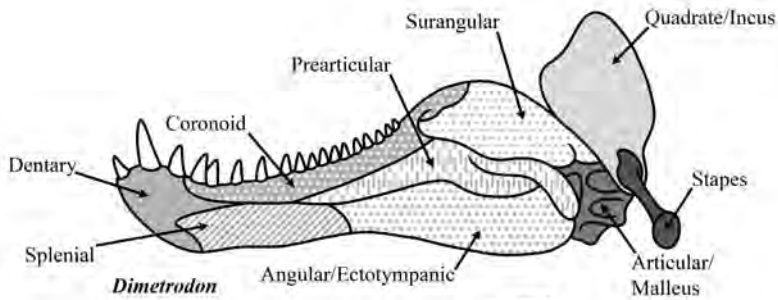
The gliding haramiyidan *Maiopatagium* from the Jurassic of Liaoning, China. (photo by Zhe-Xi Luo)



The dinosaur-eating mammal *Repenomamus* from the Cretaceous of Liaoning, China. (photo by Meng Jin)



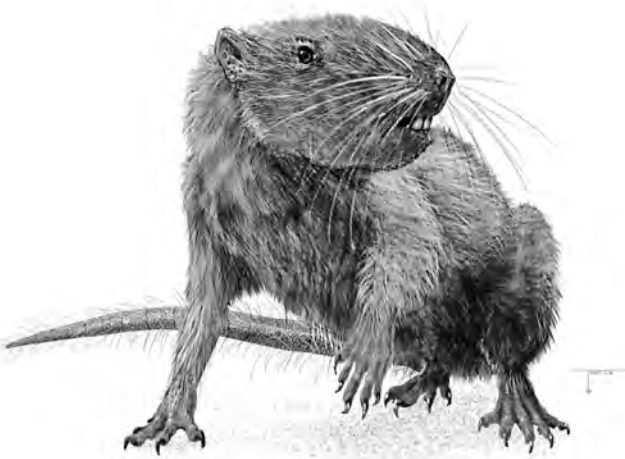
Moji Ogunkanmi, a member of our team, scrutinizing the Jurassic rocks of Skye, Scotland, for small fossils. (photo by Steve Brusatte)



The transformation of jaw bones of mammal ancestors into the tiny ear ossicles of mammals. (illustrated by Sarah Shelley)

4

The
**MAMMALIAN
REVOLUTION**



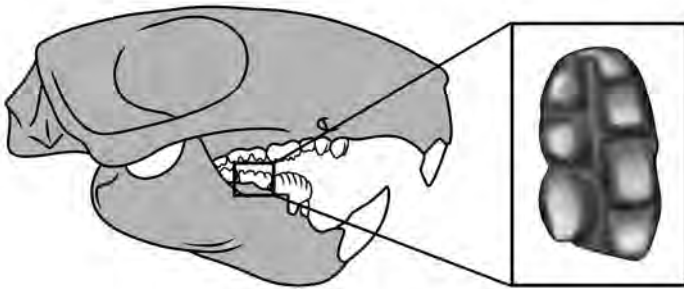
Kryptobaatar



Richard Butler and me meeting Zofia Kielan-Jaworowska at her home in Poland in 2010 (top) and Zofia in the Gobi Desert of Mongolia in 1970 (bottom). (photos by Tomasz Sulej and Institute of Paleobiology Warsaw, respectively)



Zofia Kielan-Jaworowska and team searching for tiny mammal fossils in the Gobi Desert in 1968. (photo courtesy of Institute of Paleobiology Warsaw)



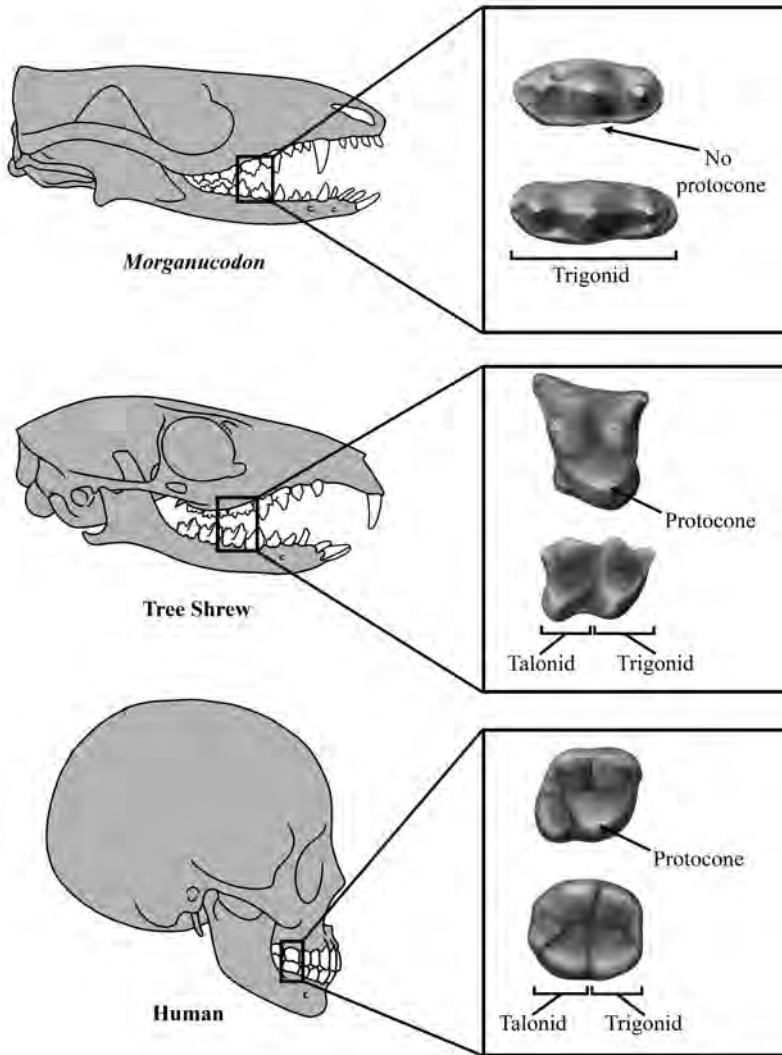
The skull of a Cretaceous multituberculate, with a close-up of the chewing surface of its Lego brick-shaped molar. (illustrated by Sarah Shelley)



Fieldwork in Romania:
collecting fossils from the
Multi-Bed (right), Mátyás
Vremir gathering fossils
from the river (left). (photos
by Akiko Shinya and Steve
Brusatte, respectively)



The pea-brained multituberculate *Litovoi*. (photo by Mick Ellison)



The evolution of tribosphenic molars. Inset boxes show the chewing (occlusal) surfaces of the upper and lower molars for each species. The simple three-peaked molars of early mammals (top) changed into the more complex molars of tribosphenic therians, with a large protocone on the upper molar that fits into a basin on the six-cusped lower molar (middle). We humans have these teeth (bottom)! (illustrated by Sarah Shelley)



Zalambdalestes and *Deltatheridium*



A platypus paddles in a creek in Tasmania. (photo by Klaus via Flickr)

5

DINOSAURS DIE, MAMMALS SURVIVE



Ectoconus



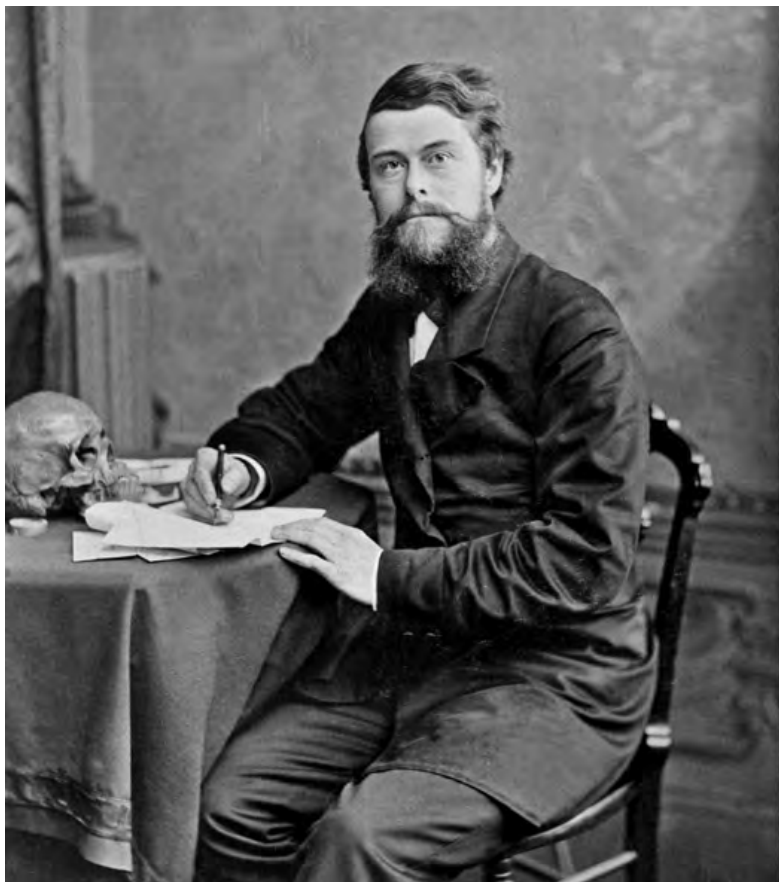
Kimbetopsalis, the “Primeval Beaver”: fossil skull and teeth (top) and Carissa Raymond and Ross Secord collecting the fossils a few moments after discovery in 2014 (bottom). (photos by Tom Williamson and Steve Brusatte, respectively)



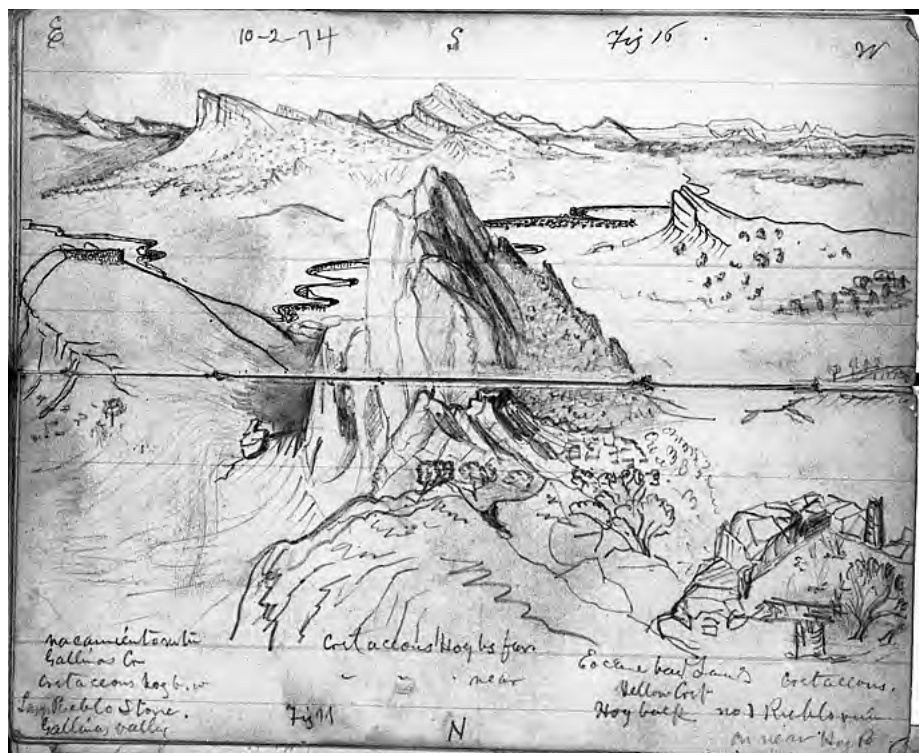
Sarah Shelley and Tom Williamson encasing the skeleton of the “archaic” placental *Ectoconus* in a protective plaster jacket in 2014.
(photo by Steve Brusatte)



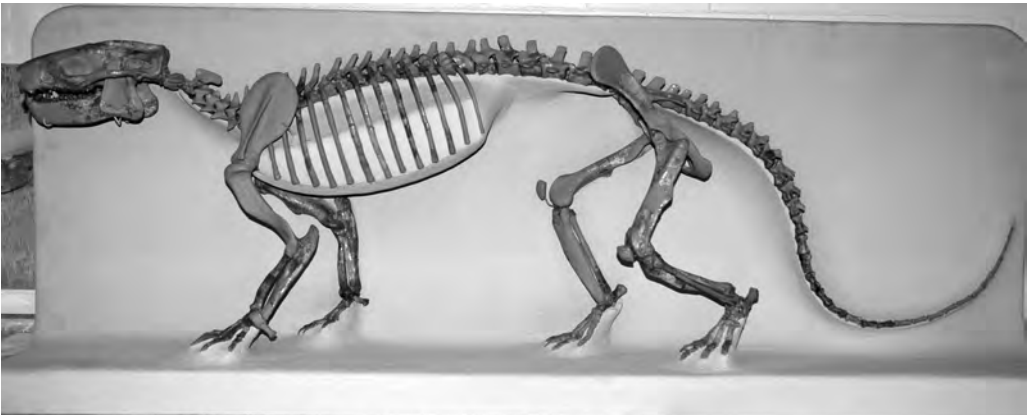
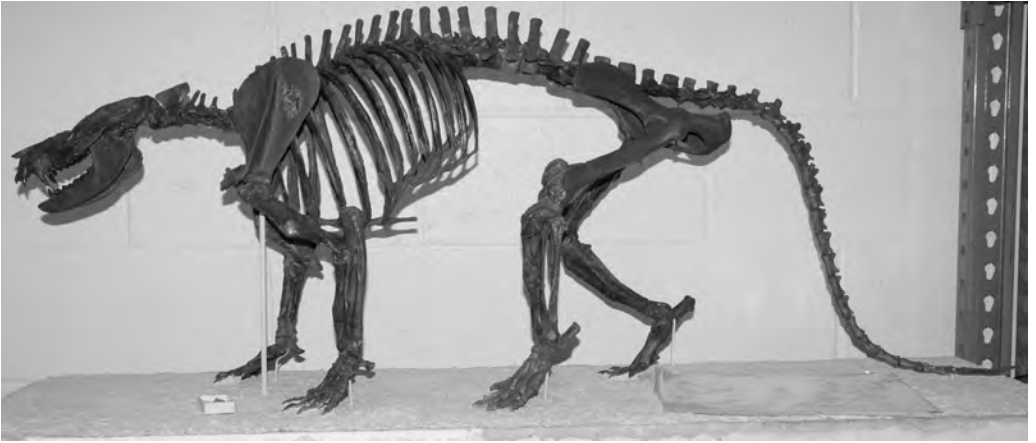
Greg Wilson Mantilla (back) and Bill Clemens (front) collecting mammal fossils in Montana. (photo by Diane Clemens-Knott and courtesy of Greg Wilson Mantilla)



Edward Drinker Cope in 1876, two years after discovering the “Puerco marls” in New Mexico. (photo by AMNH Library)



A page from Cope's 1874 field notebook, depicting the fossil- rich rocks of New Mexico. (photo by AMNH Library)



Two “archaic” placental mammals: *Ectoconus* (top), and *Pantolambda* (bottom). (photos by Tom Williamson)



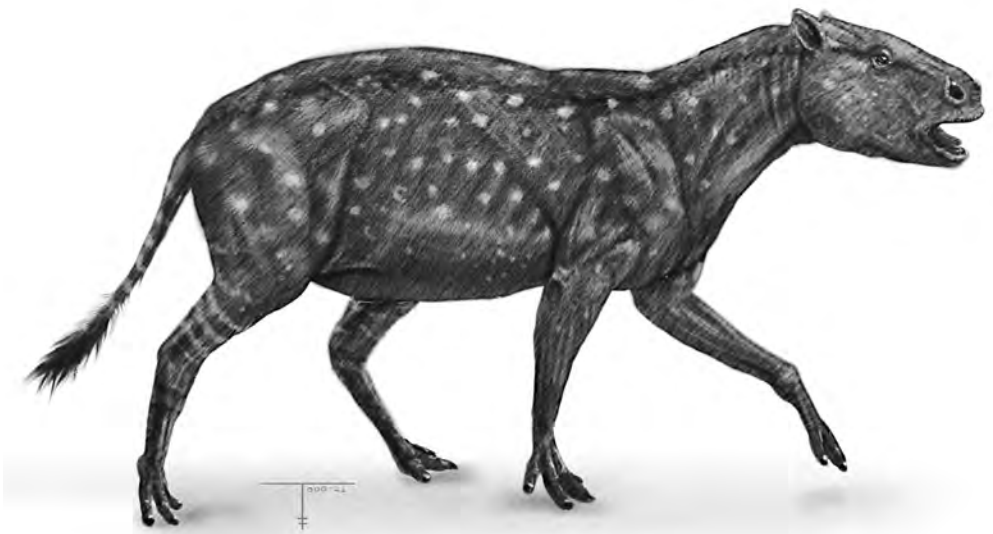
Skull of *Stylinodon* (a taeniodont cousin of *Wortmania*) and jaw of *Eoconodon* (bottom). (photos by Steve Brusatte and Tom Williamson, respectively)



Ornella Bertrand studying CAT scans of fossil mammal skulls (top). Digital models showing the small brain of the “archaic” placental *Arctocyon* (bottom left) and the much larger brain of the modern ground squirrel (bottom right). Scales = 1 cm. (photo by University of Toronto Scarborough; *Arctocyon* specimen curated at Royal Belgian Institute of Natural Sciences).

6

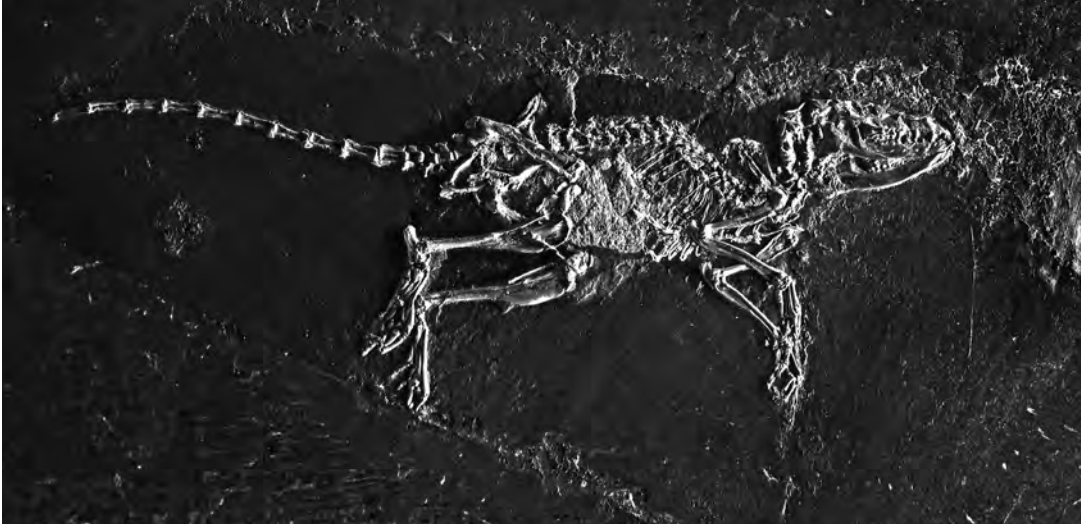
MAMMALS MODERNIZE



Eurohippus



The Messel mare *Eurohippus* with a preserved fetus (circled). (image from Franzen et al., 2015, *PLoS ONE*)

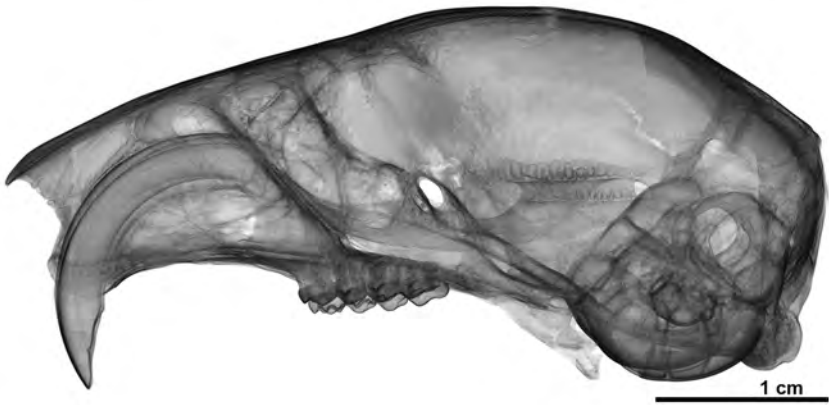


Montage of Messel mammal fossils: *Macrocranium* (top), *Lesmesodon* (bottom left), and *Messelobunodon* (bottom right). (photos by H. Zell, Norbert Micklich, and Ghedoghedo, respectively)



My team of students and colleagues studying mammal genealogy. Back row: Hans Püschel, Sarah Shelley, Sofia Holpin, Paige dePolo, Zoi Kynigopoulou, Tom Williamson. Front row: Jan Janecka, me, John Wible (and his favorite pangolin). (photo courtesy Steve Brusatte)

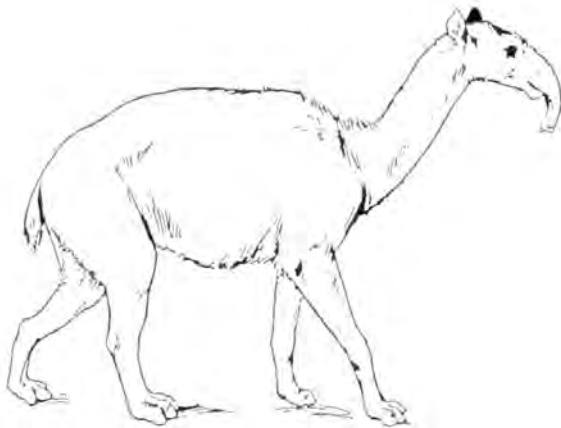




X-ray image of a red squirrel skull showing the extremely long and looping incisor, whose root extends far into the jaw. (photo by Ornella Bertrand)



Charles Darwin's bizarre South American Ungulates: *Toxodon* (above) and *Macrauchenia* (opposite). Drawings from William Scott's classic 1913 monograph. (photos by Hans Püschel)

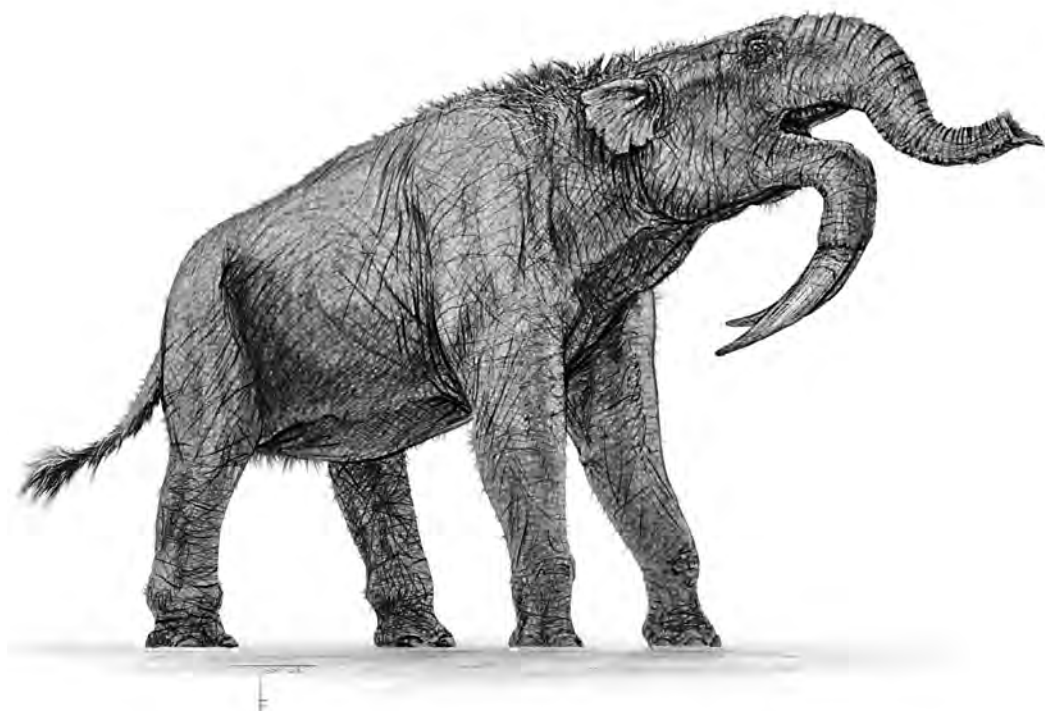




Predatory sparassodont marsupials: the saber-toothed *Thylacosmilus* (top) and *Lycopsis* (bottom). (photos by Jonathan Chen and Ghedoghedo, respectively)

7

EXTREME MAMMALS



Deinothereum





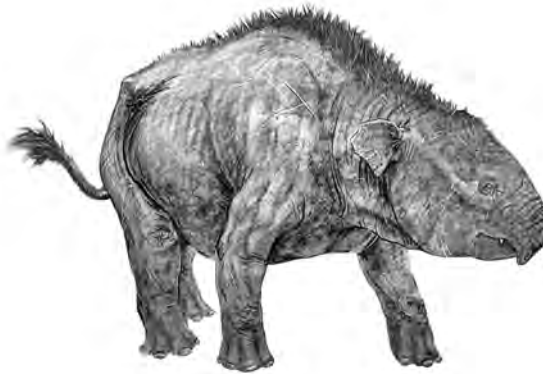
The blue whale, the largest animal to ever live on Earth. Skeleton on display at Natural History Museum London (opposite) and whale paleontologist Travis Park posing next to a skull (above). (photos by Jan Beránek and Travis Park, respectively)



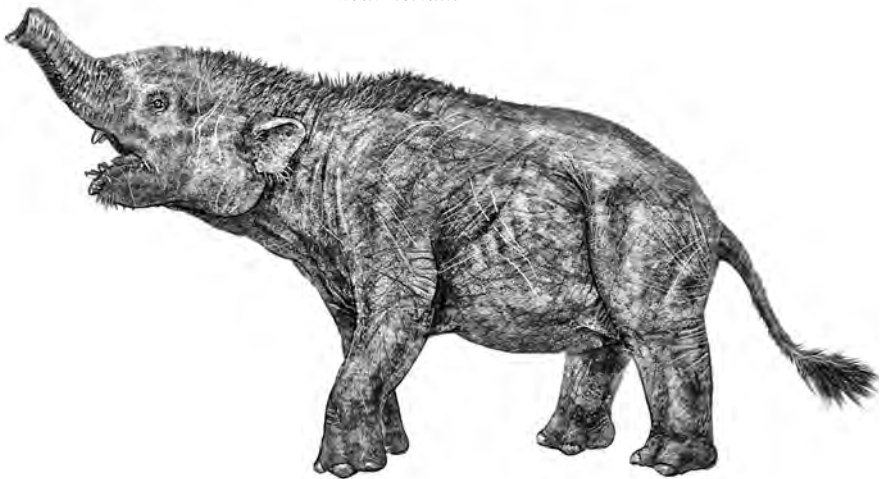
The outrageous extinct afrotherian *Arsinotherium*. (photo by Aram Dulyan)



Eritherium



Daouitherium



Numidotherium

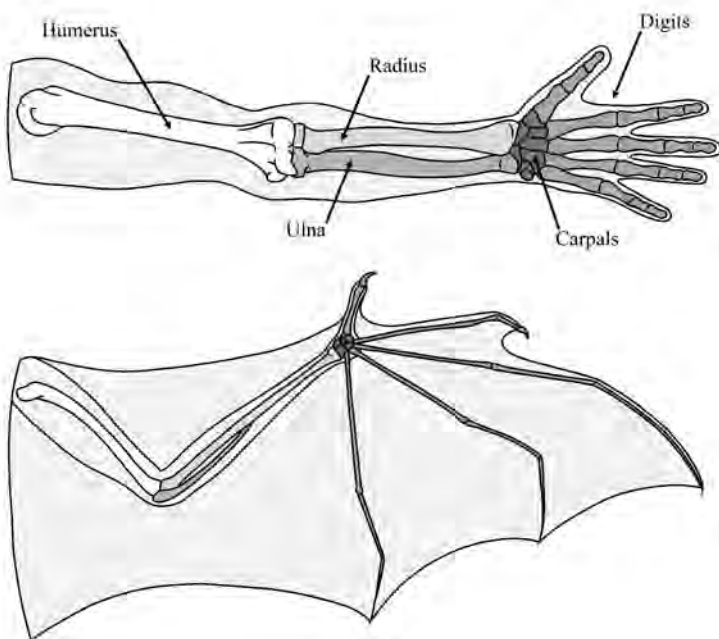
Sequence of elephant evolution. (illustration by Todd Marshall)



The extinct elephants *Palaeomastodon* (top) and *Deinotherium* (bottom). (photos by Egyptian Geological Museum and Alexxx 1979, respectively)



The fossil bat *Onychonycteris*, described by Nancy Simmons.
(photo by Matthew Dillon)



The wing of a bat next to the arm of a human. (illustrated by Sarah Shelley)





Indohyus



Pakicetus



Ambulocetus

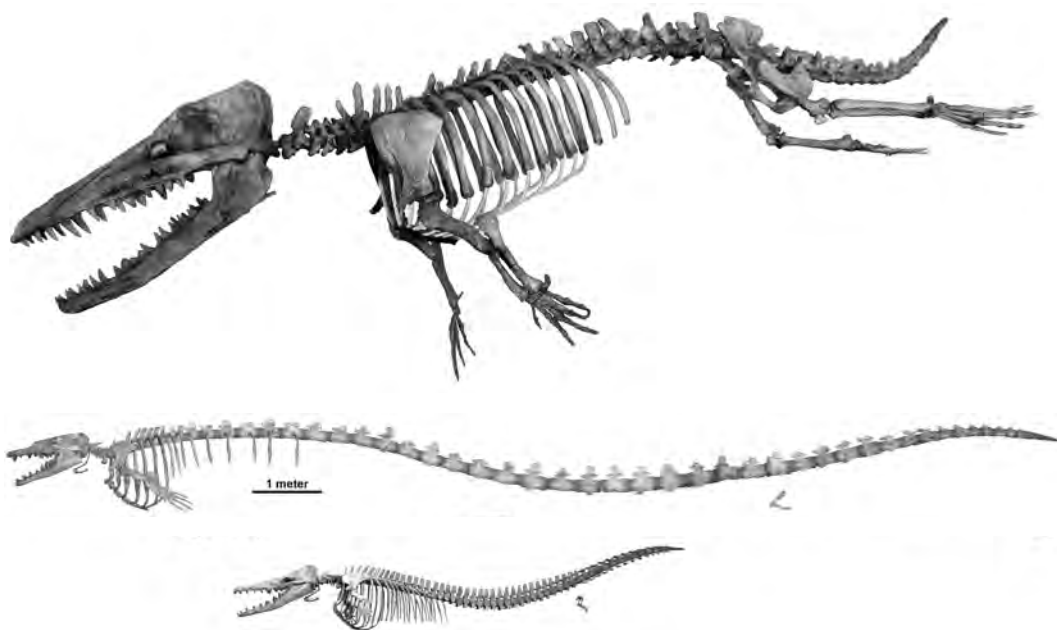


Rodhocetus

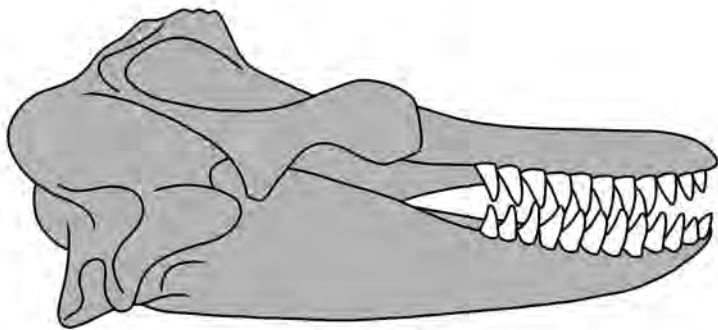


Basilosaurus

Sequence of whale evolution. (illustration by Todd Marshall)



Skeletons of fossil whales, showing their transition from land to sea, from top to bottom: *Pakicetus*, *Ambulocetus*, *Basilosaurus*, *Dorudon*. (photos by Kevin Guertin, Notafly, and from Voss et al., 2019, *PLoS ONE*) 1 meter scale bar for bottom two images only.



Toothed Whale

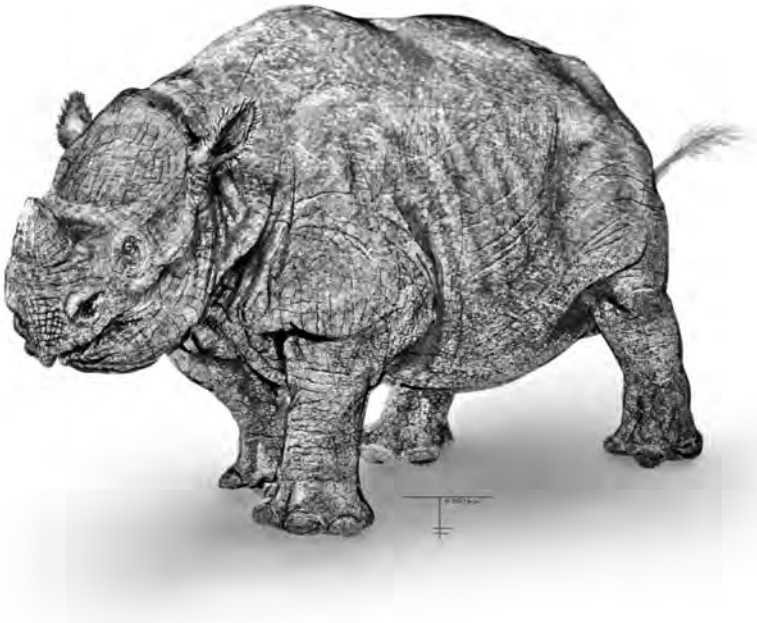


Baleen Whale

Skulls of toothed whales and baleen whales. (illustrated by Sarah Shelley)

8

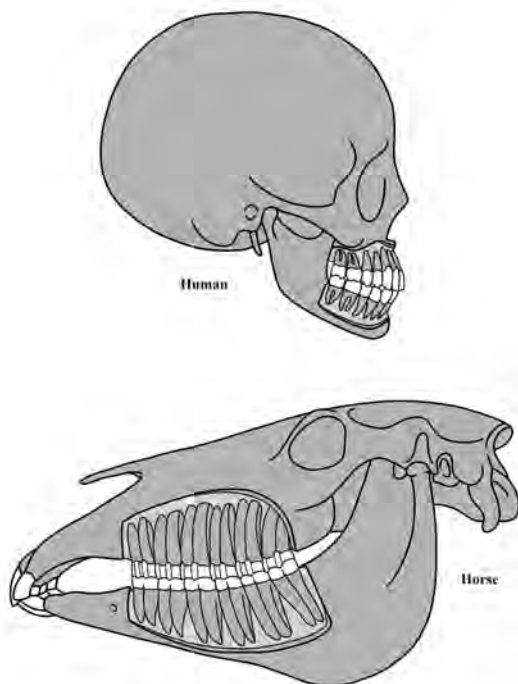
MAMMALS *and* CHANGING CLIMATES



Teleoceras



The skeleton of the rhino *Teleoceras* (top) and *Teleoceras* and the horse *Cormohipparion* preserved in ash at the Ashfall Fossil Beds (bottom). (photos by Ray Bouknight and Ammodramus, respectively)



The stretched hypsodont teeth of a horse, with long roots that extend deep into the jaw, compared to the shorter-rooted teeth of humans. Part of tooth exposed above the gumline shown in white. (illustrated by Sarah Shelley)

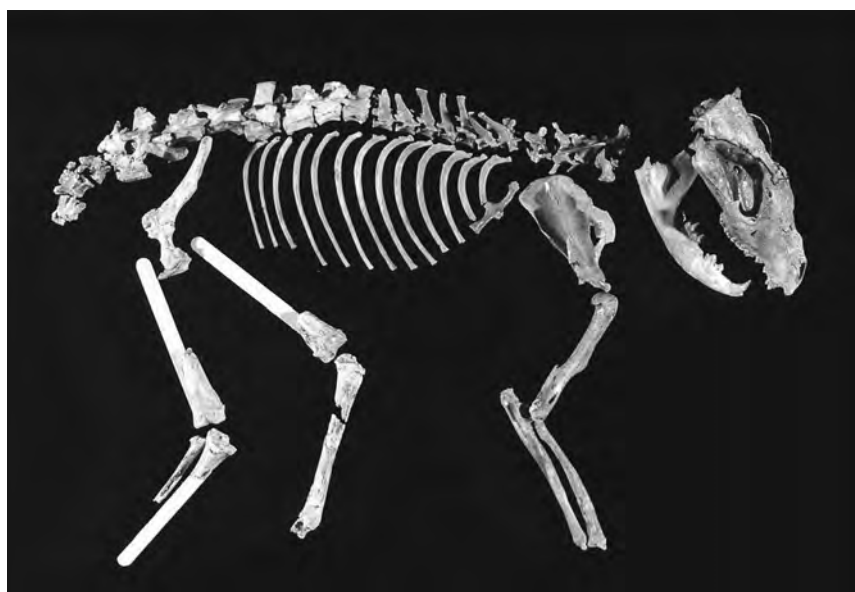
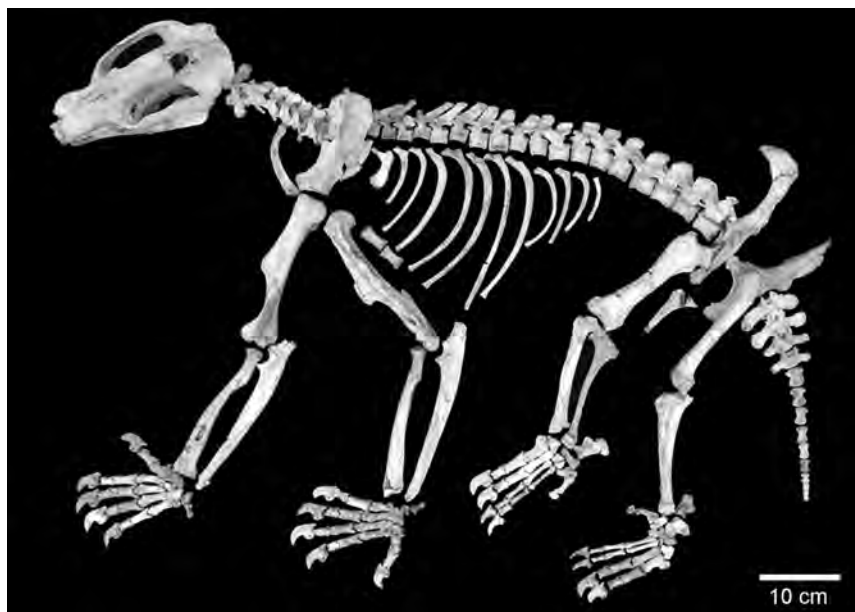


Predators of the American Savanna: the “hell pig” *Daeodon* (top) and the “bear dog” *Amphicyon* (bottom). (photos by James St. John and Clemens v. Vogelsang, respectively)



Collecting fossils at Riversleigh, Australia: team members prying out limestone blocks with mammal fossils (top), Mike Archer sitting on a box of used explosives (left), a helicopter delivering supplies (opposite). (photos courtesy of Mike Archer)





Riversleigh marsupial fossils: the wombat cousin *Nimbadon* (top) and the “marsupial wolf” cousin *Nimbacinus* (bottom). (photos from Black et al., 2012, *PLoS ONE* and Mike Archer, respectively)



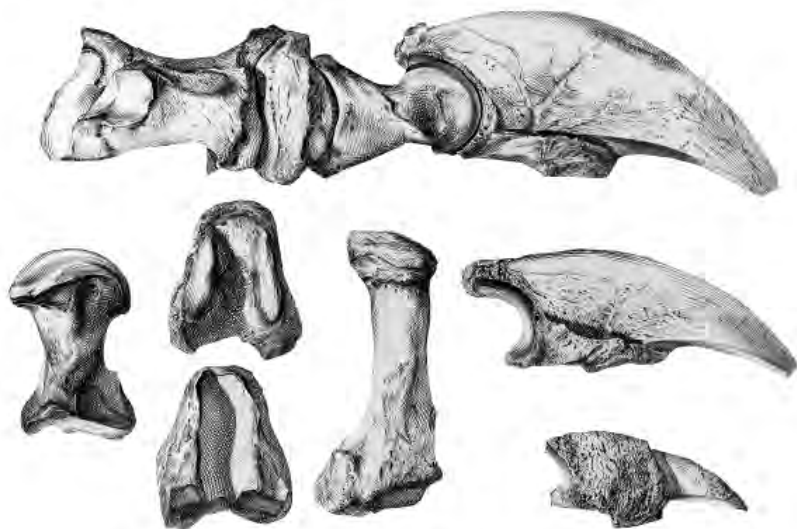
The “marsupial lion” *Thylacoleo*. (photo by Karora)

9

ICE AGE MAMMALS



Megalonyx



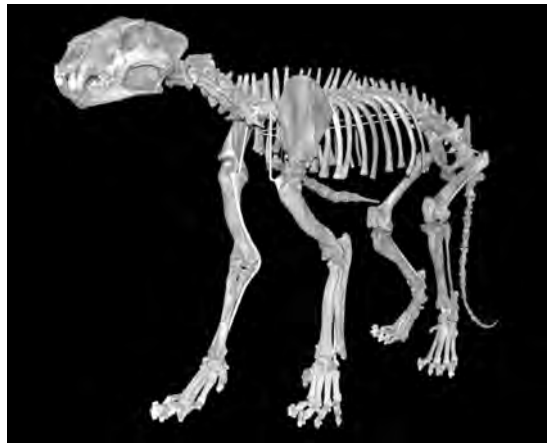
Thomas Jefferson's ground sloth *Megalonyx*. The opening lines from Jefferson's 1797 research paper, an early illustration of the bones, and a modern rendition of the skeleton. (skeleton photo by MCDinosaurhunter).



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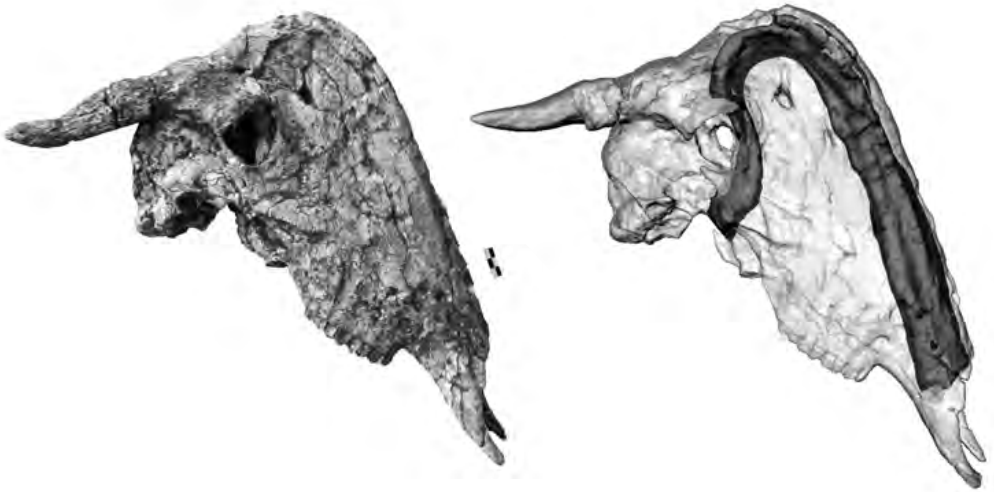
A Memoir on the Discovery of certain Bones of a Quadruped of the Clawed Kind in the Western Parts of Virginia.
By THOMAS JEFFERSON, Esq.

Read March 10, 1797. **I**N a letter of July 3d, I informed our late most worthy president that some bones of a very large animal of the clawed kind had been recently discovered within this state, and promised a communication on the subject as soon as we could recover what were still recoverable of them.



Montage of charismatic Ice Age megafauna: Irish elk (above left), cave lion (above right), dire wolf (opposite, top right), glyptodont (opposite, top left), woolly rhino (opposite, bottom). (photos by Franco Atirador, Tommy from Arad, Mariomassone & Momotarou2012, Ryan Somma, and Didier Descouens, respectively)

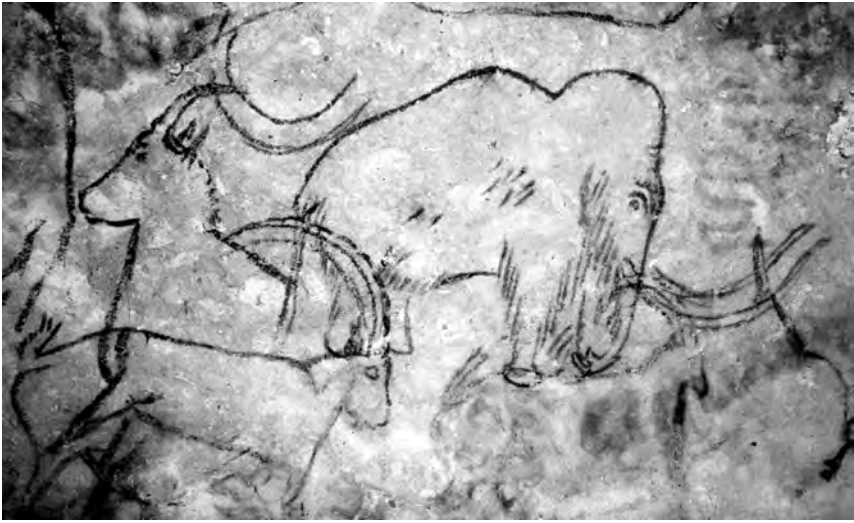




The African wildebeest *Connochaetus*: photo of skull and CAT scan showing its internal hollow structure and looping nasal passages. (images by Haley O'Brien)



Columbian mammoths. (Todd Marshall)



Mammoth and ibex drawn by Paleolithic humans at Rouffignac Cave in France, around 13,000-10,000 years ago.



Woolly mammoth mummies found frozen in Siberian permafrost:
Lyuba (top) and Yuka (bottom). (photos by Ruth Hartnup and
Cyclonaut, respectively)



The saber-toothed *Smilodon*. (Todd Marshall)



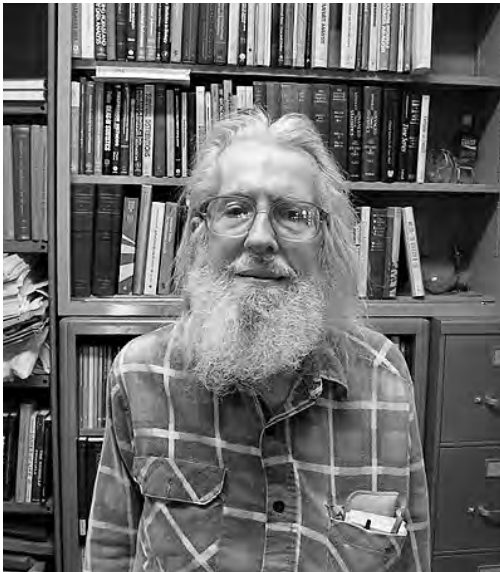
Smilodon skeleton and skull. (photos by Ninjatacoshell and Bone Clones)

10

HUMAN MAMMALS



Ardipithecus



Leigh Van Valen in his book- strewn office in Chicago (left), photocopied images of *Purgatorius* teeth printed in his self- published journal (top right), and a modern- day CAT scan rendering of *Purgatorius* teeth. (from Wilson Mantilla et al., 2021, Royal Society Open Science)



The early primate fossil *Darwinius* from Messel, Germany, showing its gracile fingers and toes and grasping thumbs and big toes. (photo from Franzen et al., 2009, *PLoS ONE*)



The joint Ethiopian-American team, of Tim White and colleagues, searching for fossil hominins at Aramis, Ethiopia. (photo by Kermit Pattison)



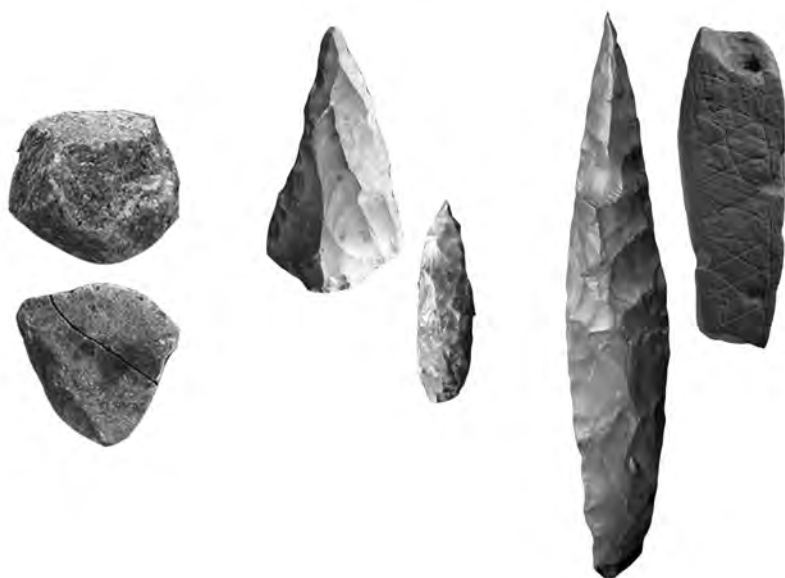
The skeletons of *Australopithecus* (Lucy) and Turkana Boy (an early member of our genus, *Homo*). (photo by AMNH Library)



Skull of *Australopithecus*, an early hominin and close human cousin of ours. (photo by José Braga and Didier Descouens)



Two *Australopithecus* leave their footprints in Tanzania, ca. 3.7 million years ago. (photo by AMNH Library)



Tools made by various species of humans: core and chopper likely made by primitive *Homo* species ca. 2 million years ago in Tanzania (left), tools likely made by Neanderthals ca. 42,000 years ago in Iran (middle), tool and engraved ochre fragment made by Middle Stone Age *Homo sapiens* in Africa (right). (photos from Mercader et al., 2021, *Nature Communications*; Heydari-Guran et al., 2021, *PLoS ONE*; Scerri et al., 2018, *Trends in Ecology & Evolution*, respectively)



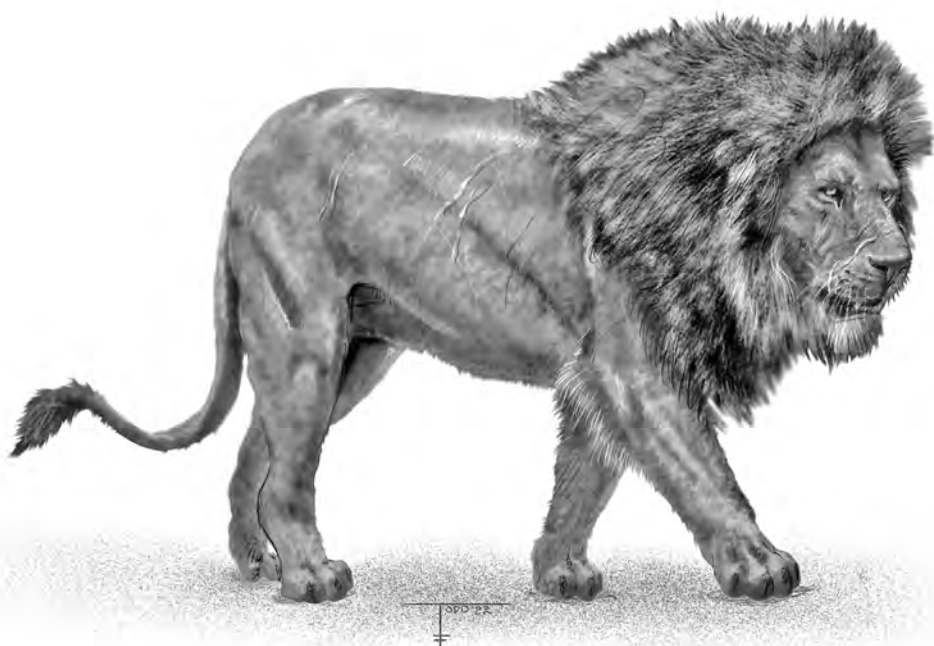
Evolution of the *Homo sapiens* brain region, from a flatter condition in a ca. 300,000-year-old skull from North Africa, to a more globular shape in a ca. 95,000-year-old fossil from the Levant. (photos from Scerri et al., 2018, *Trends in Ecology & Evolution*)



Neanderthals: reconstruction of a possible burial site at Chapelle-aux-Saints, France (top) and a skull from La Ferrassie, France (bottom). (photos by Wikipedia 120 & V. Mourre and Wikipedia 120, respectively)

EPILOGUE

Future Mammals



African lion

NOTES ON SOURCES

The following notes mention supplementary material and sources that I used, and which I direct you to for more information on the subjects covered in the chapters.

In general, I relied extensively on a handful of excellent books, including Tom Kemp's *The Origin and Evolution of Mammals* (Oxford University Press, 2005), Liam Drew's *I, Mammal* (Bloomsbury, 2017), David Rains Wallace's *Beasts of Eden* (University of California Press, 2004), Donald Prothero's *Princeton Field Guide to Prehistoric Mammals* (Princeton University Press, 2017), Donald Prothero and Robert Schoch's *Horns, Tusks, and Flippers* (The Johns Hopkins University Press, 2002), Kenneth Rose's *The Beginning of the Age of Mammals* (The Johns Hopkins University Press, 2006), Zofia Kielan-Jaworowska's *In Pursuit of Early Mammals* (Indiana University Press, 2012), and Ross MacPhee's *End of the Megafauna* (W.W. Norton & Company, 2019). When describing the paleogeography of ancient Earth, I used the industry-leading maps of Ron Blakey (<https://deephimemaps.com/>).

CHAPTER 1: MAMMAL ANCESTORS

The story of the “scaly critters” is set in a Carboniferous-aged coal forest. In some parts of the world, the Carboniferous is regarded as a single geological period spanning from about 359 to 299 million years ago; in other parts of the world, notably North America, it is split into separate Mississippian (359–323 million years ago) and Pennsylvanian (323–299 million years ago) periods. To bring the coal swamp to life, I relied on descriptions of the Mazon Creek fossil site in Illinois, most importantly the review of Clements et al. (*Journal of the Geological Society*, 2019, 176: 1–11), Shabica and Hay's influential book *Richardson's Guide to the Fossil Fauna of Mazon Creek* (Northeastern Illinois University Press, 1997), and Jack Whitry's books *The Mazon Creek Fossil Fauna* (2012) and *The Mazon Creek Fossil Flora* (2006), both published by the Earth Science Club of Northern Illinois. I supplemented this with information from another similar coal swamp fossil site, Joggins (Nova Scotia), as summarized by Falcon-Lang et al. (*Journal of the Geological Society*, 2006, 163: 561–76).

My description of the fictional “scaly critters,” which represent the most recent common ancestor of synapsids and diapsids, is based on *Hylonomus* (the oldest well-known unequivocal diapsid in the fossil record) and *Archaeothyris* (the oldest well-known unequivocal synapsid with reasonably complete fossils). The DNA molecular clock estimate for the synapsid-diapsid split is a mean of 326 million years ago (range of 354 to 311 million years ago), from Blair and Hedges (*Molecular Biology and Evolution*, 2005, 22: 2275–84). A very similar divergence estimate (mean 324.51, range 331–319 million years ago) was reported by Ford and Benson (*Nature Ecology & Evolution*, 2020, 4: 57–65), using morphological clocks on a phylogeny of extinct amniotes. The phylogenetic relationships reported in the Ford and Benson study are the framework I use to discuss the relationships of amniotes. This exciting new study, based on a comprehensive data set and analyzed with a variety of methods, finds some novel relationships compared to the long-held consensus view of early amniote genealogy. Most notably, the varanopids—long considered early synapsids—group with the diapsids. This is why I do not include varanopids in my narrative on early synapsid evolution, whereas older publications often do so.

For more information on the climate of the coal swamp world, and during the Carboniferous Rainforest Collapse, there are two excellent papers by Isabel Montañez and colleagues (Montañez et al., *Science*, 2007, 315: 87–91; Montañez and Poulsen, *Annual Review of Earth and Planetary Sciences*, 2013, 41: 629–56). For information on how oxygen has changed over Earth history, and how geologists calculate past oxygen levels, please consult David Beerling’s 2007 book *The Emerald Planet* (Oxford University Press) and Berner (*Geochimica et Cosmochimica Acta*, 2006, 70: 5653–64).

There is a huge literature on the origin of tetrapods and the early evolution of amniotes. There is no better source than the masterful book *Gaining Ground* (Indiana University Press, 2012) by Jennifer Clack, the world’s expert on the fish-tetrapod transition, who sadly passed away in the spring of 2020, as I was writing this book. There are also two outstanding pop-science books on the subject, by two of the finest science writers I know: *Your Inner Fish* by Neil Shubin (Pantheon, 2008) and *At the Water’s Edge* by Carl Zimmer (Free Press, 1998).

The Florence synapsids *Archaeothyris* and *Echinerpeton* were described by Robert Reisz in a 1972 paper (*Bulletin of the Museum of Comparative Zoology*, 144: 27–61). More recently, *Echinerpeton* has been redescribed by Mann and Paterson (*Journal of Systematic Palaeontology*, 2020, 18: 529–39). The Romer expeditions to Nova Scotia, including the discovery of the skeleton-bearing tree stumps, is recounted by Sues et al. (*Atlantic Geology*, 2013, 49: 90–103).

Robert Reisz's career is profiled in a touching biographical article by Laurin and Sues (*Comptes Rendus Palevol*, 2013, 12: 393–404).

Emma Dunne's paper on the Carboniferous Rainforest Collapse, written with several colleagues, was published in *Proceedings of the Royal Society, Series B* (2018: 20172730). It follows up—in some cases updating, in other cases contrasting with—an earlier study by Sarda Sahney and colleagues (*Geology*, 2010, 38: 1079–82). Another fascinating paper on climate changes across the Carboniferous-Permian transition, and its impact on vertebrate evolution and distribution, was recently published by Jason Pardo and colleagues in *Nature Ecology & Evolution* (2019, 3: 200–206). Extinctions and diversification in the plant fossil record—including the finding that there have been only two mass extinction events—is covered by Cascales-Miñana and Cleal (*Terra Nova*, 2014, 26: 195–200). For more information on the Carboniferous and Permian ice caps, and why they formed, consult the paper by Georg Feulner (*Proceedings of the National Academy of Sciences [USA]*, 2017, 114: 11333–37), and references therein.

The pelycosaurs are what paleontologists call a “grade” of species. They do not form a “clade,” which is defined as a group that includes a common ancestor and all of its descendants. Instead, a grade is a series of species on the line toward a clade—an ancestral stock. So when I talk about pelycosaurs I am talking about a succession of species on the line toward the more advanced therapsid clade (which includes mammals). I generally do not like to talk about grades, or give them names, but in this case, it is convenient because the pelycosaurs are generally similar in anatomy and biology and are the stock that the therapsids evolved from. In effect, the therapsid clade evolved from a single common ancestor that *was* part of the pelycosaur grade. There is a huge literature on *Dimetrodon* and other pelycosaurs, including papers by many of the leaders of nineteenth-century and early-twentieth-century paleontology: Cope, Case, Matthew, Olson, Sternberg, Romer, Vaughn, and so on. This is expertly summarized by Tom Kemp in his book *The Origin and Evolution of Mammals*, which I used extensively.

If you still doubt that *Dimetrodon* is more closely related to us than to dinosaurs, check out the clear and well-written essay by Ken Angielczyk—one of the world's leading experts on early synapsid evolution (*Evolution: Education and Outreach*, 2009, 2: 257–71). This essay is also an excellent introduction to “tree thinking”: how paleontologists construct and talk about family trees. The grade vs. clade issue should be a lot clearer after reading Ken's essay, as should the step-by-step sequence of changes across the mammal stem lineage, from pelycosaurs to therapsids to mammals.

The collapse of pelycosaurs around the Early-Middle Permian boundary is part of an extinction event called Olson's Extinction, named for the paleontologist (E. C. Olson) who first noted it (*Geological Society of America Special Papers*, 1982, 190: 501–12). Olson, a fellow alum (although many decades earlier) of the University of Chicago's geology program, was a prolific researcher on Permian synapsids, and published landmark papers such as his 1962 monograph comparing North American and Russian species (*Transactions of the American Philosophical Society*, 52: 1–224). There has been debate about whether Olson's Extinction was a real event or a mirage, caused by a biased and unevenly sampled fossil record (a view suggested by Benson and Upchurch, *Geology*, 2013, 41: 43–46). Recently, another young, statistically minded paleontologist of Emma Dunne's generation—Neil Brocklehurst—led a team that addressed this debate using big databases and statistical analyses, which found that the extinction was a real event (*Proceedings of the Royal Society, Series B*, 2017, 284: 20170231).

A key concept I try to articulate in this chapter is that the characteristics that today make mammals unique (compared to other tetrapods, like birds, lizards, and amphibians) did not all evolve at once but were acquired piecemeal over millions of years of evolution, along the mammal “stem lineage”: the series of synapsid groups on the line to mammals, including pelycosaurs, therapsids, and cynodonts (note that therapsids and cynodonts are both clades; so mammals are technically part of each group!). As usual, Tom Kemp does the best job of summarizing a long and deep literature on the subject. His book *The Origin and Evolution of Mammals*, particularly chapters 3 and 4, is required reading for anyone interested in the subject, as are two essay-style reviews (*Journal of Evolutionary Biology*, 2006, 19: 1231–47; *Acta Zoologica*, 2007, 88: 3–22) and his chapter in the 2012 book *The Forerunners of Mammals*. Bruce Rubidge and Chris Sidor have also written an influential review (*Annual Review of Ecology and Systematics*, 2001, 32: 449–80), and more recently Ken Angielczyk and Christian Kammerer have done a marvelous job of summarizing where the evidence stands now (in their chapter in the *Handbook of Zoology: Mammalian Evolution, Diversity and Systematics*, DeGruyter, 2018). For a more technical look at this issue, consult Sidor and Hopson (*Paleobiology*, 1998, 24: 254–73).

The Karoo Basin of South Africa is the world's premier place for preserving fossils of Permian therapsids. An accessible review of the basin, its rocks, and its fossils is given by Roger Smith and colleagues in their chapter in the 2012 book *The Forerunners of Mammals* (Indiana University Press). The story of Andrew Geddes Bain's first therapsid discoveries and Richard Owen's early work on these “mammal-like reptiles” (forgive my use of the term) are covered

by David Rains Wallace in his book *Beasts of Eden*. Owen's two most important works on therapsids, which I mention, were published in 1845 (*Transactions of the Geological Society of London*, 7: 59–84) and 1876 (*Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa in the Collection of the British Museum*, Taylor & Francis, London). Edward Drinker Cope outlined the link between “reptilian” ancestors like the Karoo fossils, pelycosaurs, and mammals in 1884, as recounted by Henry Fairfield Osborn (*The American Naturalist*, 1898, 32: 309–34), and Angielczyk and Kammerer in their review chapter cited above.

Robert Broom, his life, and his research are touchingly recalled in an obituary by D. M. S. Watson (*Obituary Notices of Fellows of the Royal Society*, 1952, 8: 36–70) and a review essay by Bruce Rubidge, the grandson of Broom's most productive farmer-collector, Sidney Rubidge (*Transactions of the Royal Society of South Africa*, 2013, 68: 41–52). Broom's magnum opus, his 1910 monograph linking pelycosaurs and therapsids, was published in the *Bulletin of the American Museum of Natural History* (28: 197–234). At this point, I must acknowledge that, while his work set the foundation for mammal origins, Broom was a vexing figure. He claimed that spirits guided him to fossils, argued that spirits inside animals acted on their chromosomes to cause evolutionary change, and most troubling, espoused racist ideas and was involved in grave robbing (in addition to mammal origins, he also studied human origins). For a discussion of the legacy of racism in human origins research, including Broom's work, see Christa Kuljian's book *Darwin's Hunch: Science, Race and the Search for Human Origins* (Jacana Media, 2016).

Many of my descriptions of dicynodonts, dinocephalians, and gorgonopsians are inspired by Tom Kemp's meticulous prose in *The Origin and Evolution of Mammals*. My description of the common ancestor of therapsids is taken from Kemp's 2006 paper, cited above.

Christian Kammerer's revision of *Dicynodon* was published in 2011 (*Society of Vertebrate Paleontology Memoir*, 11: 1–158). This monograph also includes a historical review of *Dicynodon* research (it is here where the term “taxonomic dumping ground,” which I use, was coined!), and a comprehensive genealogical analysis of dicynodonts, which Christian and colleagues updated in 2013 (*PLoS ONE*, 8: e64203), and continue to update, with the most recent version (as of this writing) published in 2021 (Kammerer and Ordoñez, *Journal of South American Earth Sciences*, 108: 103171). Two other essential works on dicynodonts were published by G. M. King, including a review article in the *Handbuch der Paläoherpetologie*, Gustav Fischer Verlag, 1988) and a book (*The Dicynodonts: A Study in Palaeobiology*, Chapman & Hall, 1990).

Dinocephalian head-butting was proposed by Barghusen (*Paleobiology*, 1975, 1: 295–311) and has recently been explored in more detail through synchrotron scanning of the internal skull anatomy of *Moschops*, which shows that its brain and other neural structures were encased in extra thick bone to protect from impact (Benoit et al., *PeerJ*, 2017, 5: e3496). Information on the giant *Anteosaurus* was gleaned from Boonstra (*Annals of the South African Museum*, 1954, 42: 108–48) and Van Valkenburgh and Jenkins (*Paleontological Society Papers*, 2002, 8: 267–88).

There is debate about the jaw mechanics of gorgonopsians. The wide-gape hypothesis is supported by the work of Tom Kemp (*Philosophical Transactions of the Royal Society of London, Series B*, 1969, 256: 1–83) and L. P. Tatarinov (*Russian Journal of Herpetology*, 2000, 7: 29–40), whereas a dissenting view was articulated by Michel Laurin (*Journal of Vertebrate Paleontology*, 1998, 18: 765–76). The brain anatomy and sensory systems of gorgonopsians were recently described by Ricardo Araújo and colleagues, using computed tomography (CT) scan data (*PeerJ*, 2017, 5: e3119).

For an excellent review on the origin of higher metabolisms and finer temperature control in therapsids, hypotheses for why this happened, and a thorough review of the diverse literature on this subject, check out the paper by James Hopson published in 2012 (*Fieldiana*, 5: 126–48).

Anusuya Chinsamy-Turan described her methods of making and studying bone thin sections in her 2005 book *The Microstructure of Dinosaur Bone* (Johns Hopkins University Press). She wrote or coauthored several chapters in the 2012 book *The Forerunners of Mammals* (which she edited), on the bone texture, growth, and metabolism of mammal antecedents. Other key papers on this subject are her coauthored study with Sanghamitra Ray and Jennifer Botha (*Journal of Vertebrate Paleontology*, 2004, 24: 634–48), and studies by Huttenlocker and Botha-Brink (*PeerJ*, 2014, 2: e325), Olivier et al. (*Biological Journal of the Linnean Society*, 2017, 121: 409–19), and Rey et al. (2017, *eLife*, 6: e28589). Details of Anusuya's life and career were taken from an interview with her, published online: <https://scibraai.co.za/anusuya-chinsamy-turan-breathing-life-bones-extinct-animals/>.

The evolution of more upright locomotion in therapsids is discussed by Blob (*Paleobiology*, 2001, 27: 14–38), and in the cynodont works of King cited above. A recent study by another brilliant PhD student, Jacqueline Lungmus, and her advisor, Ken Angielczyk, showed how therapsids developed a greater variety of forelimb shapes and motions, allowing them to ecologically diversify (*Proceedings of the National Academy of Sciences*, 2019, 116: 6903–07). Liam Drew's book *I, Mammal* has a fantastic chapter on the origin of hair, which has

a detailed description of the sensory, display, and waterproofing hypothesis, and of how hair became co-opted for physiological reasons. Permian coprolites with hairlike structures have been described by Bajdek et al. (*Lethaia*, 2016, 49: 455–77) and Smith and Botha-Brink (*Palaeogeography, Palaeoclimatology, Palaeoecology*, 2011, 312: 40–53). The blood vessels and nerves in the skull that innervate the hair are reviewed by Benoit et al. (*Scientific Reports*, 2016, 6: 25604). Currently, it seems as if the facial bones of early therapsids have equivocal evidence for hair, but there is no doubt that later therapsids like cynodonts and close relatives had evolved whiskers and hair.

CHAPTER 2: MAKING A MAMMAL

The story of the burrowing *Thrinaxodon*, waiting out the dry season and setting out to eat and mate when the rains came, is based on the fossil and rock record of the Karoo Basin across the Permian-Triassic boundary. My primary sources were papers by Smith and Botha-Brink (*Palaeogeography, Palaeoclimatology, Palaeoecology*, 2014, 396: 40–53) and Botha et al. (*Palaeogeography, Palaeoclimatology, Palaeoecology*, 2020, 540: 109467), along with work by Peter Ward and colleagues (*Science*, 2000, 289: 1740–43; *Science*, 2005, 307: 709–14).

The best pop-science book on mass extinctions is *The Ends of the World*, by Peter Brannen (Ecco, 2017). I think Peter is one of the finest science writers working today, and his earth science writing is on par with my favorite all-time geologizing author, John McPhee. There are two excellent pop-science books on the end-Permian extinction, one by my former master's advisor Michael Benton (*When Life Nearly Died*, Thames & Hudson, 2003) and the other by Douglas Erwin (*Extinction: How Life on Earth Nearly Ended 250 Million Years Ago*, Princeton University Press, 2006). Zhong-Qiang Chen and Mike Benton wrote an accessible review of the extinction and subsequent recovery for *Nature Geoscience* (2012, 5: 375–83). Updated information on the timing and nature of the volcanic eruptions that caused the extinction was published by Seth Burgess and colleagues (*Proceedings of the National Academy of Sciences USA*, 2014, 11: 3316–21; *Science Advances*, 2015, 1: e1500470). An important paper on climate change and warming during the extinction was published by Joachimski and colleagues (*Geology*, 2012, 40: 195–98); this is my source for the figure of 9–14 degrees Fahrenheit (5–8 degrees Celsius) warming.

The ecological collapse of the Karoo ecosystems, and the prolonged recovery, has been studied by Peter Roopnarine, Ken Angielczyk, and colleagues, using ecological food web modeling (*Proceedings of the Royal Society, Series B*, 2007, 274: 2077–86; *Science*, 2015, 350: 90–93; *Earth-Science Reviews*, 2019,

189: 244–63). Adam Huttenlocker’s work on the Lilliput effect was published in *PLoS ONE* (2014, 9: e87553), and Adam was part of a team led by Jennifer Botha-Brink that addressed the wider question of cynodont survival at the end-Permian, which proposed the hypothesis that growing young and breeding fast were key (*Scientific Reports*, 2016, 6: 24053). Other important work on body size evolution in early synapsids was published by Roland Sookias and colleagues (*Proceedings of the Royal Society, Series B*, 2012, 279: 2180–87; *Biology Letters*, 2012, 8: 674–77). Chris Sidor and colleagues published an important study on the distribution of species across Pangea during the Permian-Triassic transition (*Proceedings of the National Academy of Sciences, USA*, 2013, 110: 8129–33).

There is a wealth of literature on *Thrinaxodon*, the hero cynodont of the chapter. Tom Kemp, as usual, has a scrupulous summary in his book *The Origin and Evolution of Mammals*. One of the key descriptive papers is by Richard Estes (*Bulletin of the Museum of Comparative Zoology, Harvard University*, 1961, 125: 165–80), and an important study of its teeth was published by A.W. “Fuzz” Crompton (*Annals of the South African Museum*, 1963, 46: 479–521). Robert Broom himself described the cranial anatomy of *Thrinaxodon* in a 1938 paper (*Annals of the Transvaal Museum*, 19: 263–69), by cutting up a skull into eighteen slices from front to back. He grumbled that, while he wanted many more, thinner sections, a “medical practitioner has to be content with simpler and less perfect technique,” which is ironic because contemporary paleontologists use CAT scanners to make digital x-ray slices of fossil skulls, and often need to beg medical doctors and hospitals for access to scanners!

Important burrows with *Thrinaxodon* skeletons inside were described by Damiani et al. (*Proceedings of the Royal Society, Series B*, 2003, 270: 1747–51) and Fernandez et al. (*PLoS ONE*, 2013, 8: e64978); the latter paper describes the remarkable fossil of a *Thrinaxodon* and an amphibian crowded together into a single burrow. The posture of *Thrinaxodon* and other cynodonts was expertly studied by Farish Jenkins, and two of his most important works are his 1971 monograph *The Postcranial Skeleton of African Cynodonts* (*Peabody Museum of Natural History Bulletin*, 36: 1–216) and a review paper published in *Evolution* (1970, 24: 230–52). Further information on cynodont posture was gleaned from Richard Blob’s 2001 paper, cited above. Bone histology and growth of *Thrinaxodon* was described by Jennifer Botha and Anusuya Chinsamy (*Palaentology*, 2005, 48: 385–94). The teeth, jaws, and jaw-closing muscles of *Thrinaxodon*—including how they changed during growth—have been the focus of publications by Sandra Jasinowski, Fernando Abdala, and Vincent Fer-

nandez (*Journal of Vertebrate Paleontology*, 2013, 33: 1408–31; *The Anatomical Record*, 2015, 298: 1440–64), and Jasinoski and Abdala described social aggregations and parental care in a paper in *PeerJ* (2017, 5: e2875). The Antarctic fossils of *Thrinaxodon* were described by James Kitching (the son of the road-building Karoo fossil collector Croonie Kitching from chapter 1) and colleagues (*Science*, 1972, 175: 524–27; *American Museum Novitates*, 1977, 2611: 1–30).

I thank Christian Kammerer and his Twitter feed for drawing my attention to the remarkable life of Walter Kühne. Kühne’s 1956 monograph of *Oligokyphus* was published by the British Museum of Natural History and is freely available online (<https://www.biodiversitylibrary.org/item/206348#page/5/mode/lup>). Some details of Kühne’s life and incarceration are outlined in the monograph, but I sourced further information from Zofia Kielan-Jaworowska’s book *In Pursuit of Early Mammals* (Indiana University Press, 2012), Alfred Romer’s review of Kühne’s monograph in the *Quarterly Review of Biology*, and Rex Parrington’s paper on British Triassic mammals, which is a great general resource on the many cave discoveries such as *Morganucodon*, *Kuehneotherium*, and *Eozostrodon* (*Philosophical Transactions of the Royal Society, Series B*, 261: 231–72). The dismissive quote from the British Museum curator is paraphrased from Romer’s review.

The phylogenetic relationships of cynodonts have been the subject of extensive analysis, reanalysis, and debate over the last several decades. Tritylodontids like *Oligokyphus* are recognized as some of the closest relatives of mammals, along with two groups called the tritheledontids and brasilodontids. These are all advanced groups of cynodonts that were blossoming around the same time, in the Late Triassic. My conception of cynodont genealogy is based on a recent study by Marcello Ruta and colleagues, on which I was one of the peer reviewers (*Proceedings of the Royal Society, Series B*, 2013, 280: 20131865). Another important recent work was published by Jun Liu and Paul Olsen (*Journal of Mammalian Evolution*, 2010, 17: 151–76).

Changes on the cynodont lineage—linking *Thrinaxodon* to *Oligokyphus* and mammals—are expertly covered in Tom Kemp’s book. Fuzz Crompton and Farish Jenkins wrote an influential review on the subject in the very first volume of *Annual Review of Earth and Planetary Sciences* (1973, 1: 131–55). Changes in the vertebral column in cynodonts have been scrutinized by Katrina Jones—another winner of the Romer Prize, in 2014, the year after Adam Huttenlocker—and colleagues (*Science*, 2018, 361: 1249–52; *Nature Communications*, 2019, 10: 5071). The papers by Farish Jenkins and Richard Blob, cited

above, discuss the postural and locomotor changes in more detail, particularly the development of full mammalian-style upright walking through a semi-sprawling transitional phase.

When it comes to the story of dinosaur origins and early evolution, I will not so humbly point readers in the direction of my book *The Rise and Fall of the Dinosaurs* (William Morrow, 2018), and a review paper I wrote on the subject, with my colleagues Sterling Nesbitt, Randy Irmis, Richard Butler, Mike Benton, and Mark Norell (*Earth-Science Reviews*, 2010, 101: 68–100). In my book, I also provide a more detailed description of Pangea and its climate and outline the most important sources.

Several authors have opined about a “nocturnal bottleneck” in early mammal evolution, with some pinpointing this phase to the origin of mammals in the Triassic, and others using it to refer to the small, night-living mammals that may have preferentially survived the dinosaur extinction. An illuminating study by Ken Angielczyk and Lars Schmitz showed—using eye measurements—that nocturnal behaviors probably first evolved early in the synapsid line, and various pelycosaurs, therapsids, and cynodonts lived in the night (*Proceedings of the Royal Society, Series B*, 2014, 281: 20141642). Other papers to consider are those by Margaret Hall and colleagues (*Proceedings of the Royal Society, Series B*, 2012, 279: 4962–68), Jiaqi Wu and colleagues (*Current Biology*, 2017, 27: 3025–33), and Roi Maor and colleagues (*Nature Ecology & Evolution*, 2017, 1: 1889–95). My comment about mammals going “all in” for scent and touch was inspired by an interview with my PhD advisor, Mark Norell, published by, of all things, Marvel Comics in 2019.

The way I discuss warm-bloodedness (endothermy) relied extensively on Tom Kemp’s *The Origin and Evolution of Mammals*, and the discussion section in Katrina Jones and colleagues’ *Nature Communications* paper on mammal spine evolution, cited above. The figure that warm-blooded mammals can run eight times faster than lizards was cited in the latter paper, based on work by Kemp (*Zoological Journal of the Linnean Society*, 2006, 147: 473–88) and Bennett and Ruben (*Science*, 1979, 206: 649–54). The increasing prevalence of fibrolamellar bone in cynodonts is covered in two very readable chapters in *The Forerunners of Mammals*, one by Jennifer Botha-Brink and colleagues (ch. 9) and the other by Jørn Hurum and Anusuya Chinsamy (ch. 10). The decreasing size of bone cells, and by extension red blood cells, was noted by Adam Huttenlocker and Colleen Farmer (*Current Biology*, 2017, 27: 48–54). Kévin Rey and team published their oxygen isotope work in *eLife* (2017, 6: e28589). Carrier’s constraint was christened by Richard Cowen, named for the scientist who first articulated it: David Carrier, in *Paleobiology* (1987, 13: 326–

41). A nice paper on the evolution of nasal turbinates was written by Crompton and colleagues (*Journal of Vertebrate Paleontology*, 2017, e1269116). There is some uncertainty about exactly when respiratory turbinates covered in blood vessels first evolved. It seems like some nonmammal cynodonts may have had them, although they may have been made of cartilage rather than bone, but the oldest unequivocal bony evidence is from early mammals. It is very difficult to determine the size, shape, and blood vessel coverage of these delicate structures from fossils.

The evolution of the three-part mammalian jaw muscle system was comprehensively reviewed by Lautenschlager et al. (*Biological Reviews*, 2017, 92: 1910–40), with copious references to the historical literature on the subject. The same team followed with an important paper in *Nature* (2018, 561: 533–37) which used engineering software to test jaw function in a series of fossil species, leading them to argue that miniaturization was the primary driver for the evolution of the new dentary-squamosal jaw joint. As mammal ancestors got smaller, there was a sweet spot in which small size lowered stress and strain disproportionately to the loss of absolute bite force that came with a smaller jaw. Chris Sidor authored a study in *Evolution* (2001, 55: 1419–42) showing how the upper skull of mammal ancestors simplified (= fewer and more fused bones).

The definition of mammals that I use throughout the book—any descendant of the first cynodont to develop a robust dentary-squamosal jaw joint—is prevalent in the historical literature. It is more or less the definition used by Kielan-Jaworowska, Cifelli, and Luo in their magisterial overview of early mammals, *Mammals from the Age of Dinosaurs* (Columbia University Press, 2004). (Technically, they define mammals as “a clade defined by the shared common ancestor of *Sinoconodon*, morganucodontans, docodontans, Monotremata, Marsupialia, and Placentalia, plus any extinct taxa that are shown to be nested within this clade,” which is basically equivalent to the group on the family tree that developed the dentary-squamosal joint). This group—what I call “mammals”—is referred to as Mammaliaformes by those researchers who prefer a “crown group” definition for mammals, which limits the name “mammals” to the group on the family tree including the modern mammals (monotremes, marsupials, placentals) and all descendants of their most recent common ancestor. Timothy Rowe’s 1988 *Journal of Vertebrate Paleontology* (8: 241–64) paper first set out the crown-based definition of Mammalia and the new name Mammaliaformes for the larger group with the dentary-squamosal joint. And that’s all I’ll say about classification—an exercise in semantics more than science—before pleading again for my colleagues to forgive me in not using the crown group definition here.

There is a large literature on mammalian chewing, and once again, Tom Kemp's *The Origin and Evolution of Mammals* and Kielan-Jaworowska et al.'s *Mammals from the Age of Dinosaurs* were invaluable sources and are necessary reading for anyone interested in the subject. Kai Jäger and colleagues recently published a key paper on *Morganucodon* chewing and dental occlusion (*Journal of Vertebrate Paleontology*, 2019, 39: e1635135). Bhart-Anjan Bhullar and Armita Manafzadeh and team published an intriguing study in *Nature* (2019, 566: 528–32) that used x-ray analysis of actual living marsupials chewing food to argue that the rolling action of the lower jaw—which evolved around the same time as the dentary-squamosal jaw joint—was central to the chewing motions. David Grossnickle wrote a reply to this article (*Nature*, 2020, 582: E6–E8), which mostly addressed other aspects of the paper. My discussions with Dave greatly helped me understand the evolution of mammalian chewing. I should also mention here that Anjan Bhullar used the term “internal furnace” when describing endothermy in an interview, so I borrowed that phrase in this chapter.

There is a huge literature on *Morganucodon*, the exemplar for early mammals. It was first described and named by Kühne in 1949 (*Proceedings of the Zoological Society of London*, 119: 345–50), and more complete fossils were later described by Kenneth Kermack, Frances Mussett, and Harold Rigney in two *Zoological Journal of the Linnean Society* papers (1973, 53: 86–175; 1981, 71: 1–158). Rigney described the Chinese *Morganucodon* skull, the source of so much trouble, in *Nature* (1963, 197: 1122–23). His autobiography, *Four Years in a Red Hell*, was published by Henry Renery, Chicago. Diphyodonty—two generational tooth replacement—in *Morganucodon* was described by Rex Parrington (*Philosophical Transactions of the Royal Society, Series B*, 261: 231–72), and the postcranial skeleton was described by Jenkins and Parrington (*Philosophical Transactions of the Royal Society, Series B*, 1976, 273: 387–431).

Tim Rowe has published two important studies on the brain evolution of early mammals, including the development of larger olfactory bulbs and the neocortex. The first in *Science* (1996, 273: 651–54) and the second coauthored with Ted Macrini and Zhe-Xi Luo in *Science* (2011, 332: 955–57). These present CT scans of *Thrinaxodon*, *Morganucodon*, and other key species on the cynodont-mammal line.

Relevant literature on other, non-*Morganucodon* early mammals include Parrington's description of *Eozostrodon* (*Annals and Magazine of Natural History*, 1941, 11: 140–44), Diane Kermack's description of *Kuehneotherium* (*Journal of the Linnean Society [Zoology]*, 1968, 47: 407–23), Crompton and Jenkins's description of Ione Rudner's *Megazostrodon* (*Biological Reviews*, 1968,

43: 427–58), and Luo et al.’s description of *Hadrocodium* (*Science*, 2001, 292: 1535–40). Pam Gill and her team published their study of diet in *Morganucodon* and *Kuehneotherium*—using not only tooth wear, but also engineering models of the jaws—in *Nature* (2014, 512: 303–5). A related paper, also supporting feeding differences between these species, was written by Conith et al. (*Journal of the Royal Society Interface*, 2016, 13: 20160713).

Farish Jenkins is a legend in my field, and although I didn’t know him personally, I will always remember being in attendance when he won the Romer-Simpson medal of the Society of Vertebrate Paleontology in 2009, while he was battling cancer. He passed away three years later, in 2012, reportedly telling friends that he was at peace because, as a paleontologist, he was familiar with extinction. I gleaned this quote, along with other biographical details, from obituaries published in the *New York Times*, the *Economist*, the *Boston Globe*, and *Nature* (written by Neil Shubin)—a sign of his prominence. The famous illustration of *Megazostrodon* was published by Jenkins and Parrington in their 1976 paper, cited above. In their acknowledgments, they credit the final artistic reconstructions to Laszlo Meszoly, an artist at Harvard’s Museum of Comparative Zoology who was profiled in a *Harvard Gazette* article in 2003.

The idea that diversification of major new mammal groups often begins in the small-bodied insect-eating niche was presented by Dave Grossnickle and colleagues in a wonderfully written 2019 review paper, published in *Trends in Ecology and Evolution* (2019, 34: 936–49).

CHAPTER 3: MAMMALS AND DINOSAURS

The fascinating life of William Buckland is recounted in many books on the early history of paleontology, including my favorite: Deborah Cadbury’s *The Dinosaur Hunters* (Fourth Estate, 2000), which was also published internationally under the title *Terrible Lizard*. Buckland’s role in the study of early mammals was recounted in Wallace’s *Beasts of Eden*, and I also gleaned additional details from a biography in the University of Oxford’s online “Learning More” series, and an article in the *Guardian* about Buckland’s gastronomic proclivities (“*The Man Who Ate Everything*,” February 2008). Buckland described *Megalosaurus* and the tiny mammal jaws in a written version of his Geological Society address (*Transactions of the Geological Society of London*, 1824, 2: 390–96). Several decades later, Richard Owen published a landmark review of Mesozoic mammals known at the time (Monograph of the Fossil Mammalia of the Mesozoic Formations, *Monographs of the Palaeontographical Society*, 1871).

The stereotype of Mesozoic mammals as small, dull generalists was articulated in the two most important reviews of the early twentieth century, both

written by the eminent mammal expert and evolutionary biologist George Gaylord Simpson (*A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum*, Oxford University Press, 1928; *American Mesozoic Mammalia*, *Memoirs of the Peabody Museum*, 1929, 3: 1–235).

For more information on the end-Triassic extinction, I point readers to the discussion in my book *The Rise and Fall of the Dinosaurs*, and the references cited therein. The book *Triassic Life on Land: The Great Transition* (Columbia University Press, 2010) by Nicholas Fraser and Hans-Dieter Sues is a great summary of the Triassic world, its inhabitants, its physical geography, and the extinction. The lava erupting at the end of the Triassic created a huge amount of basaltic rock that covers part of four continents today, called the Central Atlantic Magmatic Province (or CAMP), which has been well described by Marzoli and colleagues (*Science*, 1999, 284: 616–18). The timing of the CAMP eruptions has been studied by Blackburn and colleagues (*Science*, 2013, 340: 941–45), which shows the eruptions took place in four large pulses over 600,000 years. Work by Jessica Whiteside, Paul Olsen, and colleagues shows that the extinctions on land and in the sea happened at the same time at the end of the Triassic, and that the first hints of extinction are synchronous with the first lava flows in Morocco (*Proceedings of the National Academy of Sciences USA*, 2010, 107: 6721–25). Changes across the Triassic-Jurassic boundary in atmospheric carbon dioxide, global temperature, and plant communities have been studied by, among others, McElwain et al. (*Science*, 1999, 285: 1386–90; *Paleobiology*, 2007, 33: 547–73) and Belcher et al. (*Nature Geoscience*, 2010, 3: 426–29).

The new image of Jurassic-Cretaceous mammals as diverse, dynamic, and exciting was first articulated to a big readership by Zhe-Xi Luo's review in *Nature* (2007, 450: 1011–19), which summarized the first decade of discoveries from Liaoning. In 2014, Meng Jin wrote an updated review of the Chinese fossils, further demonstrating their unexpected diversity (*National Science Review*, 1: 521–42). Roger Close and colleagues applied a variety of statistical methods to family trees of mammals, demonstrating that they underwent rapid rates of evolution in the Middle Jurassic (*Current Biology*, 2015, 25: 2137–42). One of these methods—a way of calculating rates of skeletal evolution—I helped develop with my colleagues Graeme Lloyd and Steve Wang (*Evolution*, 2012, 66: 330–48). Close et al. hypothesized that the breakup of Pangea may have caused these increased rates of evolution, and the overall explosive diversification of mammals in the Middle Jurassic.

The first fossil mammal reported from Liaoning, called *Zhangheotherium*, was described by Zhe-Xi Luo and his colleagues Yaoming Hu and Yuanqing

Wang et al. in 1997 (*Nature*, 390: 137–42). Two years later Luo, Ji Qiang, and Ji Shu-an described *Jeholodens*, also in *Nature* (1999, 398: 326–30). The dinosaur-eating *Repenomamus* was described in 2005 by Meng Jin and his team, led by first author Yaoming Hu (*Nature*, 433: 149–52).

Docodonts and haramiyidans are reviewed in books such as Kemp’s *The Origin and Evolution of Mammals* and Kielan-Jaworowska et al.’s *Mammals from the Age of Dinosaurs*, but these are by now quite outdated, because of the rush of new discoveries from China. It’s fun to read passages in these books—written in the early- to mid-2000s—bemoaning both groups as enduring mysteries, represented almost exclusively by fragmentary fossils. How things have changed! More information on the species mentioned in the text can be found in the papers describing them: *Microdocodon* (Zhou et al., *Science*, 2019, 365: 276–79), *Agilodocodon* (Meng et al., *Science*, 2015, 347: 764–68), *Docofossor* (Luo et al., *Science*, 2015, 347: 760–64), *Castorocauda* (Ji et al., *Science*, 2006, 311: 1123–27), *Vilevolodon* (Luo et al., *Nature*, 2017, 548: 326–29), *Maiopatagium* (Meng et al., *Nature*, 2017, 548: 291–96) and *Arboroharamiya* (Zheng et al., 2013, *Nature*, 500: 199–202; Han et al., *Nature*, 2017, 551: 451–56). There was also an intriguing, late-surviving haramiyidan recently described from the Cretaceous of North America: *Cifelliodon*, named by Adam Huttenlocker and colleagues, in honor of the eminent fossil mammal expert Rich Cifelli (*Nature*, 2018, 558: 108–12).

As a brief pause, I note that there is currently huge debate about the placement of haramiyidans on the mammal family tree. There are two camps. One, led by Zhe-Xi Luo, argues that they are primitive mammals, placed on the stem of the family tree not too far from *Morganucodon*. The other camp, headed by Meng Jin, argues for a much more derived placement, within the crown group of mammals (the group that includes all the modern species and all descendants of their most recent common ancestor), as the sister group to the multituberculates, a group of plant-eating mammals that were diverse in the Cretaceous. I don’t have a firm opinion either way. It may seem like a purely academic debate, but it does have one broad implication: because haramiyidans first appear in the Triassic, if they are crown mammals that means that the modern-type mammals go back further in time, to about 208 million years ago. If they are earlier stem mammals, then the crown group most likely first appeared in the Early Jurassic, around 178 million years ago.

We’ve described our dinosaur discoveries from Skye in a series of papers (Brusatte and Clark, *Scottish Journal of Geology*, 2015, 51: 157–64; Brusatte et al., *Scottish Journal of Geology*, 2016, 52: 1–9; dePolo et al., *Scottish Journal of Geology*, 2018, 54: 1–12; Young et al., *Scottish Journal of Geology*, 2019, 55:

7–19; dePolo et al., *PLoS ONE*, 2020, 15[3], e0229640). My work on Skye has been conducted with a great team of colleagues and students: Tom Challands, Mark Wilkinson, Dugald Ross, Paige dePolo, Davide Foffa, Neil Clark, and many others. Neil Clark has written several important papers on Skye dinosaurs, and Dugie Ross has discovered many of the most important fossils.

Hugh Miller's book *The Cruise of the Betsey* was published in 1858 in Edinburgh and can be found online here: https://minorvictorianwriters.org.uk/miller/b_betsey.htm. A fascinating biography of Miller was published by my colleague at the National Museum of Scotland, the paleontologist Michael Taylor (*Hugh Miller: Stonemason, Geologist, Writer*, National Museum of Scotland, 2007). Waldman and Savage published their description of *Borealestes* in 1972 (*Journal of the Geological Society*, 128: 119–25). Elsa's description of the *Borealestes* skull was published in 2021 (Panciroli et al., *Zoological Journal of the Linnean Society*, zla144), and she published a separate paper on the jaws and teeth (*Journal of Vertebrate Paleontology*, 2019, 39: e1621884) and another on the petrosal bone that encases the cochlea (*Papers in Palaeontology*, 2018, 5: 139–56). She's also written other papers on Skye mammals, which turn out to be quite diverse. There's *Stereognathus*, a tritylodontid: a member of the group of not-quite-mammals that also includes *Oligokyphus* and *Kayentatherium*; it was described initially by Waldman and Savage in their 1972 paper, and then redescribed by Elsa, myself, and colleagues in a 2017 paper (*Journal of Vertebrate Paleontology*, e1351448). There's *Wareolestes*, a primitive *Morganucodon*-type mammal (Panciroli et al., *Papers in Palaeontology*, 2017, 3: 373–86), and *Palaeoxonodon*, a more derived mammal closely related to the therians (placental and marsupials) (Panciroli et al., *Acta Paleontologica Polonica*, 2018, 63: 197–206).

Liam Drew has an excellent discussion of the origin of lactation in his book *I, Mammal*. While writing this section, I also relied extensively on Olav Oftedal's fascinating review of mammary glands and lactation, published in 2002 (*Journal of Mammary Gland Biology and Neoplasia*, 7: 225–52). Eva Hoffman and Tim Rowe described their sublime *Kayentatherium* fossil family in *Nature* (2018, 561: 104–8). Zhou et al.'s paper on *Microdocodon*, cited above, is the best source for information on hyoid and throat musculature evolution.

There is a vast literature on mammalian middle ear bones, and I point readers to four papers to begin. First, Zhe-Xi Luo wrote a fantastic review of ear evolution in 2011 (*Annual Review of Ecology, Evolution, and Systematics*, 42: 355–80), which covers the anatomy of the ear, the homologies of the ear bones, the evolutionary sequence between many-jaw-boned cynodonts and mammals, and the genetic, developmental, and embryonic data that help us

understand how the ear evolved. Second, Neal Anthwal and colleagues presented a review that blends a historical recounting of important work on the mammalian ear and the anatomical, genetic, and embryological evidence for ear evolution (*Journal of Anatomy*, 2012, 222: 147–60). Third, Wolfgang Maier and Irina Ruf wrote a historical piece explaining how researchers—dating back to the sixteenth century—studied the mammalian ear bones and came to understand their origins and evolutionary trajectory (*Journal of Anatomy*, 2015, 228: 270–83). Finally, the landmark paper of Edgar Allin—which laid out the evolutionary sequence of mammalian ear evolution—is well worth a read (*Journal of Morphology*, 1975, 147: 403–38).

Other important papers to consider, which expand on species I mention in the text, are Meng et al.’s description of *Liaoconodon*, the mammal with a transitional middle ear (*Nature*, 2011, 472: 181–85); Mao et al.’s description of *Origolestes*, the mammal with a middle ear detached from the bony strip, technically called the Meckelian element (*Science*, 2019, 367: 305–8; I note here that Zhe-Xi Luo has proposed an alternative explanation that the “detachment” of the cartilage is actually a fracture in the fossil and not genuine); Wang et al.’s description of the multituberculate *Jeholbaatar*, which revealed that the ear joint reflects the shape of the ancestral chewing motions when it was a jaw joint (*Nature*, 2019, 576: 102–5); Rich et al.’s description of the ears and jaws of early monotremes, which revealed that they evolved their detached middle ears independently of marsupials and placentals (*Science*, 2005, 307: 910–14); and Han et al.’s description of *Arboroharamiya allinhopsoni*, the haramiyidan with ear ossicles separated from the jaw (*Nature*, 2017, 551: 451–56). Some of these papers can be quite opaque to a nonspecialist (or to a paleontologist originally trained to study dinosaurs), so this reader was grateful to the commentary pieces by Anne Weil—a leading expert on multituberculate mammals—that accompanied some of these *Nature* papers.

I note that several months after drafting the chapter in the text, my former PhD student Sarah Shelley, my colleague and mentor John Wible, and their colleagues published an important paper on a haramiyidan ear, with broader implications for understanding the multiple ear bone detachments in mammalian history (Wang et al., *Nature*, 2021, 590: 279–83). They redefined some terms with historical baggage, and I follow their terms here. Most importantly, they use the term “detached middle ear” to refer to middle ear bones completely lacking any bony or cartilaginous attachment to the jaw; this is what many previous workers called a Definitive Mammalian Middle Ear (or DMME). Finally: the Wang et al. (2021) paper presented a new hypothesis to explain the differently shaped middle jaw joints of monotremes and the marsupial plus

placental group: instead of being differently shaped because they reflect different chewing motions of the ancestral jaw bones (as proposed by the Wang et al. [2019] paper cited above, and as I outline in the text of chapter 3), they propose that the overlapping-type joint of monotremes is an evolutionary precursor to the more intricate interlocking joint of ours. This is an active debate!

Two recent studies, by the same team of embryologists and paleontologists, show how straightforward it is to sever the Meckel's cartilage from the ear bones in living mammals. One, by Anthwal et al. (*Nature Ecology & Evolution*, 2017, 1: 0093) focuses on chondroclasts in mice (a placental mammal), and the other, by Urban et al. (*Proceedings of the Royal Society, Series B*, 2017, 284: 20162416) focuses on cell death in possums (a marsupial mammal). Although I didn't cover it in the main text, there is another fascinating aspect of the jaw-ear story: some of the same genes that are expressed in the jaws of reptiles are expressed in the ears of mammals (for instance, the gene *Bapx1*), more definitive proof that jaw bones became ear bones. This work was published in 2004 by Abigail Tucker and team, including my Edinburgh colleague, the legendary geneticist Bob Hill (*Development*, 131: 1235–45).

CHAPTER 4: THE MAMMALIAN REVOLUTION

Zofia Kielan-Jaworowska tells her own life story in her book *In Pursuit of Early Mammals* (Indiana University Press, 2012), which also provides succinct overviews of the origin of mammals, the cynodont-mammal transition, and Mesozoic mammal groups. Other aspects of Zofia's biography come from my discussion with her on that summer afternoon in 2010, as recorded in my field notes. She also wrote a firsthand account of the first few Polish-Mongolian expeditions in her 1969 book *Hunting for Dinosaurs* (MIT Press). The Polish-Mongolian team's discoveries were described in a vast series of papers, which are extensively cited in Zofia's 2012 book. Many of these appeared in *Palaeontologia Polonica*—a quick perusal of this journal's back catalog online or in a library will reveal a wealth of information. Among these are her critical 1970 and 1974 papers on multituberculates.

Roy Chapman Andrews's life, and his Central Asiatic Expeditions, are the subject of Charles Galkenamp's book *Dragon Hunter* (Viking, 2001). The American Museum of Natural History-Mongolian Academy of Sciences expeditions of the early 1990s are chronicled by Mike Novacek in his addictively readable book *Dinosaurs of the Flaming Cliffs* (Anchor Books, 1996), one of my favorite reads as a high school fossil enthusiast. The Ukhaa Tolgod locality—the site of so many multituberculate fossil discoveries—was initially described by Dashzeveg, Novacek, Norell, and colleagues (*Nature*, 1995, 374: 446–49).

Information on the geology of the site, and the detailed forensic evidence that fossils were formed in flood-collapsed sand dunes, can be found in papers by Loope et al. (*Geology*, 1998, 26: 27–30) and Dingus et al. (*American Museum Novitates*, 2008, 3616: 1–40).

Details of the Jurassic-Cretaceous transition are covered in my book *The Rise and Fall of the Dinosaurs*, with relevant references cited. The most useful general description of the climate and environmental changes is a review paper by Jon Tennant and colleagues (*Biological Reviews*, 2017, 92: 776–814). Jon, a young paleontologist and outspoken advocate of open science and open access publishing, tragically died in a motorbike accident in spring 2020, while I was writing this chapter.

Good general resources on multituberculates can be found in Zofia’s 2012 book (cited above), Tom Kemp’s *The Origin and Evolution of Mammals*, and the magnificent encyclopedia that Zofia edited with Zhe-Xi Luo and Richard Cifelli (*Mammals from the Age of Dinosaurs*, also cited above). The number I cite—that multituberculates constitute 70 percent of Gobi mammal faunas—comes from a paper by Chinsamy and Hurum on the bone microstructure and growth of early mammals (*Acta Palaeontologica Polonica*, 2006, 51: 325–38).

Important work on multituberculate feeding was published by Philip Gingerich, who presented evidence for the backward chewing stroke in a 1977 chapter in the book *Patterns of Evolution* (Elsevier); Zofia and her colleague Peter Gambaryan, who described the cranial musculature (*Acta Palaeontologica Polonica*, 1995, 40: 45–108); and David Krause (*Paleobiology*, 1982, 8: 265–313). Regarding multituberculate locomotion, Farish Jenkins and Krause described the reversible ankle and tree-climbing abilities (*Science*, 1983, 220: 712–15; *Bulletin of the Museum of Comparative Zoology*, 1983, 150: 199–246); my undergraduate advisor Paul Sereno and Malcolm McKenna described more advanced, fast-moving capabilities (*Nature*, 1995, 377: 144–47); and Zofia and Gambaryan published other important work (*Fossils and Strata*, 1996, 36; *Acta Palaeontologica Polonica*, 1997, 42: 13–44).

The Jurassic multituberculate *Rugosodon*—currently the oldest well preserved fossil of the group—was described by Chong-Xi Yuan, Luo, and their team (*Science*, 2013, 341: 779–83). Greg Wilson’s study of multituberculate dental evolution was published in *Nature* (2012, 483: 457–60), and another study by David Grossnickle and David Polly found similar patterns of increasing tooth diversity with a different data set (*Proceedings of the Royal Society, Series B*, 2013, 280: 20132110). Our team—Zoltán Csiki-Sava, Mátyás Vremir, Meng Jin, Mark Norell, and myself—described *Litovoi* in 2018 (*Proceedings of the National Academy of Sciences [USA]*, 115: 4857–62), a paper that also

reviews the Romanian island-living kogaionids more broadly. In 2021, Luke Weaver—a PhD student at the time—led a team describing the discovery of a social group of multituberculates in Montana (*Nature Ecology & Evolution*, 5: 32–37), work that in part earned him the Romer Prize of the Society of Vertebrate Paleontology.

A good source of general information on angiosperm origins and evolution is the book *Early Flowers and Angiosperm Evolution*, by Friis, Crane, and Pedersen (Cambridge University Press, 2011). The oldest good angiosperm vegetation fossils—called *Archaeofructus*—were described from Liaoning by Sun et al. (*Science*, 2002, 296: 899–904). Important references that I consulted on early angiosperms, and why they eventually proved so adaptable, included papers by: Wing and Boucher (*Annual Review of Earth and Planetary Sciences*, 1998, 26: 379–421), Boyce et al. (*Proceedings of the Royal Society, Series B*, 2009, 276: 1771–76), Feild et al. (*Proceedings of the National Academy of Sciences [USA]*, 2011, 108: 8363–66), Coiffard et al. (*Proceedings of the National Academy of Sciences [USA]*, 2012, 109: 20955–59), deBoer et al. (*Nature Communications*, 2012, 3: 1221), Chaboureau et al. (*Proceedings of the National Academy of Sciences [USA]*, 2014, 111: 14066–70). One of these paleobotanists—Kevin Boyce—was an undergraduate instructor of mine at the University of Chicago. A few years after I took his class, he won a MacArthur Genius Grant!

The term “Cretaceous Terrestrial Revolution” was coined by some of my closest friends and colleagues in the field: Graeme Lloyd, Marcello Ruta, Mike Benton (my three MScR supervisors at the University of Bristol) and their colleagues in a 2008 paper on dinosaur evolution (*Proceedings of the Royal Society, Series B*, 275: 2483–90). Discussions with Mike Benton provided additional information on the Revolution, particularly the evolution of insects.

There is a vast literature on the anatomy, function, and evolution of the tribosphenic molar of therians—a complex topic that, by necessity, I had to greatly abridge in the main text so as not to dull everyone to boredom with pages after pages of molar cusp descriptions (as I tried to do in my first draft, before the red pens of my editor and wife set me straight). Two classic studies are Bryan Patterson’s 1956 paper “Early Cretaceous mammals and the evolution of mammalian molar teeth,” published in *Fieldiana* (13, 1–105), and Fuzz Crompton’s 1971 paper “The Origin of the Tribosphenic Molar,” published in *Zoological Journal of the Linnean Society* (50, supplement 1: 65–87). More recently, Brian Davis published a key paper on the origin and function of the tribosphenic molar, which also lays out the different wear patterns in the “tribosphenic-like” molars of the southern australosphenidans (*Journal of Mammalian Evolution*, 2011, 18: 227–44), and Julia Schultz and Thomas

Martin used 3-D models to describe how tribosphenic molars chew, in detail (*Naturwissenschaften*, 2014, 101: 771–871). Although I don't go into detail in the main text, the tribosphenic molars—with their complex interlocking shearing and grinding surfaces—would have required very precise chewing motions to function properly. There is currently debate about the jaw mechanics of the early tribosphenic therians, and it seems like they had either enhanced rotational movements (Bhullar et al., *Nature*, 2019, 566: 528–32) or enhanced yaw (side-to-side pivoting) motions (Grossnickle, *Scientific Reports*, 2017, 7: 45094), or possibly both. The description of the currently oldest known tribosphenic therian—*Juramaia*—was published by Zhe-Xi Luo and colleagues in 2011 (*Nature*, 476: 442–45).

David Grossnickle has published several important studies on how the evolution of the tribosphenic molar affected therian evolution, and mammalian evolution more generally. These include his review paper (written with Stephanie Smith and Greg Wilson) arguing that mammalian innovation often originates in the small-bodied insectivore niche (*Trends in Ecology and Evolution*, 2019, 34: 936–49); his paper with David Polly on mammal tooth and jaw shape evolution over time (*Proceedings of the Royal Society, Series B*, 2013, 280: 20132110); and his study with Elis Newham on the diversification of tribosphenic therians during and after the Cretaceous Terrestrial Revolution (*Proceedings of the Royal Society, Series B*, 2016, 283: 20160256; note that they argue most of this diversification was after the “Revolution” and not necessarily during it). I first met Dave when he joined our New Mexico fieldwork crew in 2013, on the invitation of the multituberculate expert Anne Weil. Dave went on to do his PhD with Zhe-Xi Luo in Chicago and has quickly become a leading expert on the evolution of mammals during the Jurassic and Cretaceous. He's also one of the funniest and most subversive people in the field (in a good way).

The genetic underpinning of therian tribosphenic tooth versatility has been studied by many developmental biologists and paleontologists. Key papers are by Jernvall et al. (*Proceedings of the National Academy of Sciences [USA]*, 2000, 97: 14444–48), Kavanagh et al. (*Nature*, 2007, 432: 211–14), Salazar-Ciudad et al. (*Nature*, 2010, 464: 583–86), and Harjunmaa et al. (*Nature*, 2014, 512: 44–48).

The effects of tribosphenic molar evolution (and many other mammal innovations) on community structure and ecology was covered in a recent paper by Meng Chen, Caroline Strömberg, and Greg Wilson, in *Proceedings of the National Academy of Sciences [USA]* (2019, 116: 9931–40).

Many Cretaceous eutherians and metatherians have been described in recent years, ranging from gorgeous Liaoning skeletons to fragmentary—but

very important—teeth from North America (many of which have been studied by Richard Cifelli, Brian Davis, and colleagues). The problematic *Sinodelphys* from Liaoning was described as the oldest metatherian by Luo and colleagues (*Science*, 2003, 302: 1934–1940), but recently reinterpreted as a basal eutherian by Shundong Bi and his team, in their description of a new Liaoning eutherian called *Ambolestes* (*Nature*, 2018, 558: 390–95). A key resource on early metatherian evolution is a review paper that I contributed to, led by Tom Williamson and also including Greg Wilson as an author (*ZooKeys*, 2014, 465: 1–76). This is a follow-up to a genealogical analysis of Cretaceous–Paleogene metatherians that Tom and I published with a larger team (*Journal of Systematic Palaeontology*, 2012, 10: 625–51). The books *Mammals from the Age of Dinosaurs* and *In Pursuit of Early Mammals* (cited above) have great summaries of Gobi eutherians and metatherians, with references to all the important historical literature. More recently, the American Museum team published several important new *Deltatheridium* specimens, affirming their link to metatherians (Rougier et al., *Nature*, 1998, 396: 459–63). Another interesting recent paper focuses on the North American Late Cretaceous metatherian *Didelphodon*, also a fierce hunter in the small-size niche (Wilson et al., *Nature Communications*, 2017, 7: 13734).

The first encounters between humans and monotremes (platypuses and echidnas) in Australia is unrecorded by history, and the Aboriginal peoples had many thousands of years of experience with these peculiar animals. But the first European dealings with these animals has been covered in many retellings. I base my story on Brian Hall’s 1999 paper on the platypus (*BioScience*, 49: 211–18) and Liam Drew’s compelling storytelling in his book *I, Mammal*. I gleaned information on John Hunter from many online sources, including a nice Wikipedia biography (yes, even scientists click on Wikipedia sometimes, especially for an entry point to subjects outside of our immediate expertise). A more thorough reference is a 2009 biography of Hunter written by Robert Barnes (*An Unlikely Leader: The Life and Times of Captain John Hunter*, Sydney University Press).

Key references on the fossil monotremes and monotreme-line australosphenidans include papers on *Obdurodon* (Woodburne and Tedford, *American Museum Novitates*, 1975, 2588: 1–11; Archer et al., *Australian Zoologist*, 1978, 20: 9–27; Archer et al., *Platypus and Echidnas*, 1992, Royal Zoological Society of New South Wales; Musser and Archer, *Philosophical Transactions of the Royal Society of London, Series B*, 1998, 353: 1063–79); *Steropodon* (Archer et al., *Nature*, 1985, 318: 363–66; Rowe et al., *Proceedings of the National Academy of Sciences [USA]*, 2008, 105: 1238–42); *Ausktribosphenos* (Rich et al., *Science*,

1997, 278: 1438–42); *Ambondro* (Flynn et al., *Nature*, 1999, 401: 57–60); *Asfaltomylos* (Rauhut et al., *Nature*, 2002, 416: 165–68). There’s another important one that I don’t mention in the main text since: *Teinolophos*, named by the Rich and Vickers-Rich team in 1999 (*Records of the Queen Victoria Museum*, 106: 1–34), and more recently described in detail (*Alcheringa*, 2016, 40: 475–501).

Zhe-Xi Luo, Zofia Kielan-J aworowska, and Richard Cifelli published their genealogical analysis, finding separate groups of northern tribosphenic therians and southern false-tribosphenic australosphenidans, in *Nature* (2001, 409: 53–57). I acknowledge here that not all mammal workers accept this phylogeny, and there have been arguments from the Rich and Vickers-Rich team that some of the southern species are closely related to therians and have true tribosphenic teeth. The nuances of this debate are outside of the scope of this book, but I feel the preponderance of evidence is on the side of separate northern and southern lineages. The independent origin of tribosphenic-like molars is supported by some astounding fossils that I do not talk about in the main text: the so-called pseudotribosphenic mammals, like *Shuotherium* (Chow and Rich, *Australian Mammalogy*, 1982, 5: 127–42) and *Pseudotribos* (Luo et al., *Nature*, 2007, 450: 93–97), which have backward tribosphenic-like teeth, with the talonid basin in front of the trigonid crests. These strange mammals—which might cluster with the southern australosphenidans on the family tree—are strong proof that different groups of mammals were evolving tribosphenic-like teeth independently, possibly many times. This is a classic case of convergent evolution: when similar ecological or other selective pressures lead to the independent evolution of similar-looking anatomical structures (like teeth) in distantly related groups.

The skull of *Vintana* was described by Krause and colleagues in 2014 in *Nature* (515: 512–17), and then later monographed in exceptional detail in a series of papers published as a *Memoir of the Society of Vertebrate Paleontology* in 2014, with contributions from several authors. Later, Krause’s team described *Adalatherium* in a short report (*Nature*, 2020: 581, 421–27) and a series of papers in another *Memoir of the Society of Vertebrate Paleontology* in 2020. Broader information on gonwanatherians can be found in *Mammals from the Age of Dinosaurs* and *In Pursuit of Early Mammals*. The Argentine dryolestoid *Cronopio* was described by Rougier and team (*Nature*, 2011, 479: 98–102).

I also note here that in the final paragraph of this chapter, I state that there were different groups of mammals eating different foodstuffs at the end of the Cretaceous (e.g., insectivorous eutherians, herbivorous multituberculates). This was true—but it’s not the case that all eutherians were insectivorous, for example. Most of the groups mentioned exhibited at least some dietary diversity.

CHAPTER 5: DINOSAURS DIE, MAMMALS SURVIVE

We described *Kimbetopsalis*, the new multituberculate species Carissa Raymond discovered, in 2016 (Williamson et al., *Zoological Journal of the Linnean Society*, 177: 183–208). The quotes I used in this chapter were taken from my field notes and recordings, a press release put out by the University of Nebraska, and Carissa and Tom’s National Public Radio interview. Further information on the New Mexico fossils is given later in this section.

There is a huge literature on the end-Cretaceous extinction. I describe what the asteroid impact may have been like for dinosaurs and mammals in North America in *The Rise and Fall of the Dinosaurs* and also cite many pertinent references therein. The hypothesis that an asteroid caused the extinction was first proposed by the father-and-son team of Luis and Walter Alvarez and their colleagues (*Science*, 1980, 208: 1095–1108), and also independently by Dutch geologist Jan Smit around the same time. Walter Alvarez wrote a fantastic pop-science book, *T. rex and the Crater of Doom* (Princeton University Press, 1997), that tells the story of how he found the chemical fingerprint of iridium in end-Cretaceous rocks that pointed to an asteroid, and how over the next decade evidence for his theory continued to accumulate, until the Chicxulub Crater was discovered in Mexico, definitively proving that an asteroid (or comet) hit the earth circa 66 million years ago. Walter’s book has references to all the key literature up until the time it was written.

There does remain some debate about whether the asteroid caused the extinction of the non-bird dinosaurs and other animals at the end of the Cretaceous. Critics of the asteroid theory instead implicate the Deccan volcanic eruptions in India—megavolcanoes on the scale of the eruptions that caused extinctions at the end of the Permian and Triassic. When it comes to dinosaurs, I led a team of paleontologists that reviewed all the evidence and firmly concluded that the asteroid was the main culprit (*Biological Reviews*, 2015, 90: 628–42), a view that I also articulated in a *Scientific American* article (Dec. 2015, 313: 54–59). Recent work by Pincelli Hull and colleagues—a large team of authors including my fellow Edinburgh professor Dick Kroon and fieldwork compatriots Dan Peppe and Jessica Whiteside—forcefully argues that the asteroid was responsible for the entire extinction, and that the Indian volcanism played little if any role (*Science*, 2020, 367: 266–72), and a similar argument was made by Ale Chiarenza and colleagues based on climate and ecological modeling (*Proceedings of the National Academy of Sciences [USA]*, 2020, 117: 17084–93). Although I doubt this will be the last word on the subject, for me, there is little doubt that if no asteroid impact had occurred, there would have been no extinction, although it may be the case that the volcanism made the

extinction worse, or prolonged the recovery. Another recent study, published as I was writing this chapter, found that the angle the asteroid impacted the earth made it even deadlier (Collins et al., *Nature Communications*, 2020, 11: 1480).

Bill Clemens was a warm and kind gentleman, who I knew from many pleasant chats at Society of Vertebrate Paleontology meetings. He was also generous with his time and expertise in communicating with my PhD student Sarah Shelley, when she was writing her thesis. Bill has published numerous papers on the mammals of the Hell Creek and Fort Union formations of Montana. Among the most important is a chapter in the 2002 edited volume *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains* (*Geological Society of America Special Paper*, 361: 217–45). Bill and Joseph Hartman wrote a review of the history of fossil collecting in the Hell Creek Formation, which was part of the 2014 edited volume *Through the End of the Cretaceous in the Type Locality of the Hell Creek Formation in Montana and Adjacent Areas* (*Geological Society of America Special Paper*, 503: 1–87). Early in his career, Bill wrote a three-part magnum opus on the mammals of the Late Cretaceous Lance Formation of Wyoming, which is roughly equivalent in age to the Hell Creek Formation; these were published in the *University of California Publications in Geological Sciences* (1964, 1966, and 1973). The details of how Bill strangely came into the orbit of the Unabomber were gleaned from a discussion with Anne Weil, whose admiration for her PhD advisor runs deep. Anne also told me another story of a weird brush with violence: one of the ranches in Montana on which Anne and Bill collected fossils was owned by the casino magnate Ted Binion, who was sadly murdered in a high-profile incident in 1998.

Greg Wilson Mantilla and his students and colleagues have written many important papers on mammal evolution across the end-Cretaceous extinction in Montana, which reveals what died and what survived, and why. These include sole-authored papers in *Journal of Mammalian Evolution* (2005, 12: 53–75), *Paleobiology* (2013, 39: 429–69), and in the 2014 edited volume cited above (*Geological Society of America Special Paper*, 503: 365–92). Greg and colleagues described the stunning new fossils of *Didelphodon* in 2016 (*Nature Communications*, 7:13734). Most recently, Greg and Bill were part of a team led by Greg's PhD student Stephanie Smith—one of the leading young mammal paleontologists today—that in 2018 described the Z-Line Quarry site and other Paleocene-aged localities from soon after the extinction—these are the best glimpses at the mammal communities that lived after the asteroid impact (*Geological Society of America Bulletin*, 130: 2000–2014). In unrelated studies,

Longrich and colleagues looked at Cretaceous and Paleocene mammals across all of western North America (*Journal of Evolutionary Biology*, 2016, 29: 1495–512), and Pires and colleagues looked at rates of extinction in multituberculates, metatherians, and eutherians in North America (*Biology Letters*, 2018, 14: 20180458).

There is more detailed discussion of why dinosaurs died at the end-Cretaceous in *The Rise and Fall of the Dinosaurs*. I credit my colleague Greg Erickson with using the term “dead man’s hand”—borrowed from the sad tale of Wild Bill Hickok (who was actually born very close to my hometown of Ottawa, Illinois)—to describe the bad luck of the dinosaurs when the asteroid hit.

The historical story of Cope, the Wheeler Survey, Baldwin, and other discoveries in the San Juan Basin was based on discussion with Tom Williamson and Sarah Shelley, and a series of engrossing papers by the eminent mammal expert and writer George Gaylord Simpson, who did his own fieldwork in New Mexico, although mostly focused on younger, Eocene-aged mammals. These include works published in 1948 (*American Journal of Science*, 246: 257–82), 1951 (*Proceedings of the Academy of Natural Sciences of Philadelphia*, 103: 1–21), 1959 (*American Museum Novitates*, 57: 1–22), and 1981 (a chapter in *Advances in San Juan Basin Paleontology*, University of New Mexico Press). I discuss the “Bone Wars” rivalry of Cope and Marsh in *The Rise and Fall of the Dinosaurs*. There is a wealth of further information in John Foster’s excellent book *Jurassic West: The Dinosaurs of the Morrison Formation and Their World* (Indiana University Press, 2007).

Cope published so many papers on the mammals from the “Puerco marls” that it is impossible to cite them all here. Tom Williamson’s magisterial study of the Nacimiento Formation mammals, the subject of his PhD and published in 1996 (*New Mexico Museum of Natural History and Science Bulletin*, 8: 1–141), has references to all the important historical literature. Key papers are Cope’s 1875 Wheeler Survey report (*Annual Report of the Chief of Engineers for 1875*, pp. 61–97) that first noted the “Puerco marls,” several short papers he published in *The American Naturalist* during the 1880s, and his lengthy (that’s putting it mildly) tome—often referred to as Cope’s Bible—published in 1884 (*The Vertebrata of the Tertiary Formations of the West*. Book 1. Report of the U.S. Geological Survey of the Territories [Hayden Survey], pp. 1–1009). Another critical study of the New Mexico mammals was published by W. D. Matthew in 1937 (*Transactions of the American Philosophical Society*, 30: 1–510).

The best general source of information on Paleocene mammals like condylarths, taeniodonts, and pantodonts is the book *The Beginning of the Age of Mammals*, written by the eminent mammal paleontologist Kenneth Rose

(Johns Hopkins University Press, 2016). Sarah Shelley completed her PhD thesis at the University of Edinburgh in 2017 and published a large chunk of it—a monographic description of the condylarth *Periptychus*, a close relative of *Ectoconus*, also from New Mexico—in 2018 (*PLoS ONE*, 13[7]: e0200132). Other chapters will be published soon! Taeniodonts were comprehensively studied by Robert Schoch (*Bulletin of the Peabody Museum of Natural History, Yale University*, 1986, 42: 1–307), and Tom Williamson and I described fossils of *Wortmania* from New Mexico in 2013 (*PLoS ONE*, 8[9]: e75886). Pantodonts were comprehensively studied by Elwyn Simons (*Transactions of the American Philosophical Society*, 1960, 50: 1–99). I have current PhD students studying condylarths (Sofia Holpin, Hans Püschel), taeniodonts (Zoi Kynigopoulou), and pantodonts (Paige dePolo), so keep an eye on them and their publications!

Mammal placentas are fascinating and complex, and worthy of much more space than I was able to give them in this chapter. The best place to start learning about how they work and how they evolved is Liam Drew’s book *I, Mammal*. In his book *Some Assembly Required*, Neil Shubin has a fascinating discussion of how placentas co-opted virus DNA to prevent themselves from being expelled by the mother, and how the mother’s uterine cells developed ways to allow the placenta to literally invade the walls of the uterus. Interesting papers on placenta evolution include those by Chavan et al. (*Placenta*, 2016, 40: 40–51), Wildman et al. (*Proceedings of the National Academy of Sciences [USA]*, 2006, 103: 3203–08), and Roberts et al. (*Reproduction*, 2016, 152: R179–R189). Zofia Kielan-Jaworowska first reported the probable presence of epipubis bones in Cretaceous eutherians, based on her team’s discovery of the pelvises of the eutherians *Barunlestes* and *Zalambdalestes* with articular notches for an epibuis bone (*Nature*, 1975, 255: 698–99). Actual epipubis bones were later found in the skeletons of the Gobi eutherians *Ukhaatherium* and a species that is most likely *Zalambdalestes*, by Novacek et al. (*Nature*, 1997, 389: 483–86). My description of the egg as a “care package” and the placenta as a multitasking organ were inspired by quotes from researcher Kelsey Coolahan, from a January 2020 interview on the Pulse radio program.

My research group has published several recent papers on the brains and senses of Paleocene mammals. This work was led by Ornella Bertrand, who was a postdoc in my lab (*Journal of Anatomy*, 2020, 236: 21–49); Joe Cameron, who was a master’s student in my lab (*The Anatomical Record*, 2019, 302: 306–24); and James Napoli, who was an undergraduate student in my lab (*Journal of Mammalian Evolution*, 2018, 25: 179–95). Just as this book was going to press, Ornella’s master study on early placental brain evolution was accepted

for publication in *Science*! Among the most important work on mammal brain evolution is the pioneering research of Harry Jerison, most notably his 1973 book *Evolution of the Brain and Intelligence* (Academic Press).

There have been several important studies on body size evolution in Paleocene mammals, showing that they rapidly exploded in mass after the end-Cretaceous extinction. Two of the most influential are papers by the illustrious paleo-statistician John Alroy (*Systematic Biology*, 1999, 48: 107–18) and Graham Slater, an expert on using statistical models to study evolutionary trends (*Methods in Ecology and Evolution*, 2013, 4: 734–44). A number of young paleontologists have recently studied how various aspects of mammal biology changed across the Cretaceous–Paleocene extinction boundary: David Grossnickle and Elis Newham on molar shapes, a proxy for diet (*Proceedings of the Royal Society, Series B*, 2016, 283: 20160256), Gemma Benevento on jaw shape, another proxy for diet (*Proceedings of the Royal Society, Series B*, 2019, 286: 20190347), and Thomas Halliday on skeletal characteristics, a proxy for overall anatomy (*Biological Journal of the Linnean Society*, 2016, 118: 152–68).

CHAPTER 6: MAMMALS MODERNIZE

All the animals that I mention in my story are known from the Messel fossil site, and many of the details (such as the single fetus in the mare’s womb, the anatomical features of the animals, and what they ate) are informed from actual fossils. In writing this story, I relied on the best source of information on Messel, the book *Messel: An Ancient Greenhouse Ecosystem*, edited by Krister Smith, Stephan Schall, and Jörg Habersetzer (Senckenberg Museum, Frankfurt, 2018), which has chapters on all the mammal groups, plus the other animals (birds, crocodiles, turtles, etc.), the plants, the environment, and details on how the lake was formed from a volcanic eruption and how gases most likely killed the many fossilized animals. Other important sources were UNESCO’s website (<https://whc.unesco.org/en/list/720/>); Gerhard Storch’s article in *Scientific American* (1992, 266[2]: 64–69); and Ken Rose’s short review of Messel mammals (*Palaeobiodiversity and Palaeoenvironments*, 2012, 92: 631–47).

There are several excellent papers on our hero, the mare *Eurohippus*. It was named by Jenz Lorenz Franzen, one of the deans of Messel research, in 2006 (*Senckenbergiana Lethaea*, 86: 97–102). For many years, until Franzen’s paper, it was thought that *Eurohippus* was synonymous with another Messel horse, *Propalaeotherium*. Franzen and colleagues described a gorgeous skeleton of *Eurohippus* with a fetus inside in a series of papers (*PLoS ONE*, 2015, 10[10]: e0137985; *Palaeobiodiversity and Palaeoenvironments*, 2017, 97: 807–32). Franzen and his colleagues—including Phil Gingerich, who we meet later in

the chapter—described the primate *Darwinius* to international fanfare in 2009 (*PLoS ONE*, 4[5]: e5723).

Mammal phylogenetics—the construction of their family trees—has a long and convoluted history. For general overviews of the current state of knowledge, and how we got there through many decades of debate, I recommend the relevant sections in Liam Drew’s book *I, Mammal*, a general overview of mammal genealogy by Nicole Foley and colleagues (*Philosophical Transactions of the Royal Society, Series B*, 2016, 371: 20150140), and a more detailed summary of mammal relationships written by Robert Asher—an expert on early mammal evolution and a fantastic writer—published in *Handbook of Zoology: Mammalian Evolution, Diversity and Systematics* (DeGruyter, 2018). George Gaylord Simpson’s famous 1945 family tree was published in the *Bulletin of the American Museum of Natural History* (85: 1–350), and Michael Novacek’s later tree was published in *Nature* (1992, 356: 121–25). The stories about Simpson’s life were gleaned from David Rains Wallace’s *Beasts of Eden*, and you can read more about Simpson in a biography written by Léo Laporte (*George Gaylord Simpson: Paleontologist and Evolutionist*, Columbia University Press, 2000).

Over the past twenty-five years, there have been numerous DNA-based family trees of mammals, some surveying mammals as a whole, others focusing in on the detailed species-level relationships of individual groups like primates or rodents. The key early papers that established the DNA tree of mammals—and recognized the four main clusters of Afrotheria, Xenarthra, Euarchontoglires, and Laurasiatheria—were published by Mark Springer and his colleagues, including Ole Madsen, Michael Stanhope, William Murphy, Stephen O’Brien, Emma Teeling, and many others. The most important include: Springer et al. (*Nature*, 1997, 388: 61–64), Stanhope et al. (*Proceedings of the National Academy of Sciences, USA*, 1998, 95: 9967–72), Madsen et al. (*Nature*, 2001, 409: 610–14), Murphy et al. (*Nature*, 2001, 409: 614–18), and Murphy et al. (*Science*, 2001, 294: 2348–51). More recent workers have started to combine DNA and anatomical features to build “total evidence” trees, most prominently the genealogy of placentals published by Maureen O’Leary and her colleagues on the NSF-funded Mammal Tree of Life project (*Science*, 2013, 339: 662–67). In my description of the unexpected groupings in the DNA tree, I say that Afrotheria was “a most unusual union that nobody had ever predicted from anatomy”—which is true, although it should be noted that Edward Cope himself, in the late 1800s, used anatomical features to argue that golden moles (now known to be members of the Afrotheria group with elephants and tenrecs) were very different than European moles.

Anatomy-only trees are becoming less common; one was recently published

by Thomas Halliday and colleagues, which attempted to untangle the relationships of the Paleocene “archaic” placentals (*Biological Reviews*, 2017, 92: 521–50). My European Research Council–funded team is working independently, to try to use anatomy and DNA to clarify these relationships further—particularly how the “archaic” species slot in with the modern species. We have so far published preliminary results as abstracts, but the research is still ongoing as I write this. A special thanks here to my co-PIs John Wible and Tom Williamson, who have also received funding for our big project through the National Science Foundation. Stay tuned for our publications!

There is a vast literature using the DNA clock to predict the origin times of placental mammals as a whole, and constituent subgroups. It is looking more and more likely that Placentalia itself originated back in the Cretaceous, during the time of dinosaurs, and that some subgroups did, too, but that the most explosive phase of their evolution occurred after the asteroid impact, in the Paleocene. However, this is all based on the DNA clock, as nobody, anywhere, has yet to find a convincing fossil of a Cretaceous placental. It might be that they were rare or localized to particular parts of the world at the time, or that they were common but we just have a hard time recognizing them as placentals . . . or that the DNA clock is wrong. For good overviews of this debate, consult the review papers of Archibald and Deutschmann (*Journal of Mammalian Evolution*, 2001, 8: 107–24) and Goswami (*EvoDevo*, 2012, 3:18).

The Paleocene-Eocene Thermal Maximum (PETM)—the global warming spurt circa 56 million years ago—has been the subject of intense study, from geologists, climatologists, biologists, and many other scientists. The best general summary of the PETM, its causes, and its duration is a review paper written by Francesca McInerney and Scott Wing (*Annual Review of Earth and Planetary Sciences*, 2011, 39: 489–516). It cites all the important work on the PETM up until 2011. There has been more recent geological and climatological work, which has convincingly (in my view) identified the North Atlantic volcanoes and their rock-baking magmas as the culprit (Gutjahr et al., *Nature*, 2017, 548: 573–77; Jones et al., 2019, *Nature Communications*, 10: 5547). These new studies essentially corroborate the hypotheses of Svensen et al. (*Nature*, 2004, 429: 542–45) and Storey et al. (*Science*, 2007, 316: 587–89), who noted that the PETM happened at the same time that volcanoes tore open the North Atlantic. For a more popular and poetic look at the PETM, the science writer extraordinaire Peter Brannen penned an evocative article for the *Atlantic* (August 2018).

The PETM had innumerable effects on the environment. Globally, the obscenely high arctic land temperatures were identified by Weijers et al. (*Earth*

and *Planetary Science Letters*, 2007, 261: 230–38) and Eberle et al. (*Earth and Planetary Science Letters*, 2010, 296: 481–86); midlatitude temperatures were measured by Naafs et al. (*Nature Geoscience*, 2018, 11: 766–71); and the boiling tropical temperatures were studied by Aze et al. (*Geology*, 2014, 42: 739–42). Locally in the Bighorn Basin of Wyoming, Kraus and Riggins described evidence for transient drying (*Palaeogeography, Palaeoclimatology, Palaeoecology*, 2007, 245: 444–61); Ross Secord and colleagues described in detail the temperature increase (*Nature*, 2010, 467: 955–58); and Scott Wing and colleagues described floral changes (*Science*, 2005, 310: 993–96).

The Bighorn Basin mammal record, and how it responded to the PETM, has been the subject of Philip Gingerich's life work, and the work of many of his students. For a brief look at Gingerich's background, including his upbringing as a Mennonite in Iowa, see Tom Mueller's article in the August 2010 issue of *National Geographic*. In 2006 Gingerich published an accessible overview of the issue (*Trends in Ecology and Evolution*, 21: 246–53), which followed from two more technical papers that detailed how mammal diversity and body size changed during the PETM: one that was led by his graduate student William Clyde (Clyde and Gingerich, *Geology*, 1998, 26: 1011–14) and one that he wrote (*Geological Society of America Special Papers*, 2003, 369: 463–78). Gingerich also edited two important volumes on Bighorn Basin geology and paleontology (*University of Michigan Papers on Paleontology*, 1980, 24; *University of Michigan Papers on Paleontology*, 2001, 33).

Key papers on local Bighorn Basin exposures that record the PETM and mammal response were published by Gingerich (*University of Michigan Papers on Paleontology*, 1989, 28), Gingerich and his Belgian colleague Thierry Smith (*Contributions from the Museum of Paleontology*, The University of Michigan, 2006, 31: 245–303) and Kenneth Rose and colleagues (*University of Michigan Papers on Paleontology*, 2012, 24). Ross Secord presented his exceptional work on PETM horse dwarfing in *Science* (2012, 335: 959–62), and later work by Abigail D'Ambrosia and team found that mammals dwarfed in a similar way during later global warming events (*Science Advances*, 2017, 3: e1601430). Other important papers are those on the forest environments of the Eocene Bighorn Basin (Secord et al., *Paleobiology*, 2008, 34: 282–300) and Amy Chew's longer-term study of the Eocene mammals of the area (*Paleobiology*, 2009, 35: 13–31).

The migration of the PETM Trinity—primates, artiodactyls, and perissodactyls—during the temperature spike is clear in the fossil record: these animals show up all across the northern continents, essentially simultaneously. The primates have been studied by Thierry Smith and colleagues

(*Proceedings of the National Academy of Sciences, USA*, 2006, 103: 11223–27) and Chris Beard (*Proceedings of the National Academy of Sciences, USA*, 2008, 105: 3815–18). General dispersal between Asia and other continents has been assessed by Bowen et al. (*Science*, 2002, 295: 2062–65) and Bai et al. (*Communications Biology*, 2018, 1: 115), and European faunas are discussed by Smith et al. (*PLoS ONE*, 2014, 9[1]: e86229).

For more information on the actual members of the PETM Trinity that spread around the world, I recommend the following sources.

Primates: One of the most enjoyable and accessible guides to early primate evolution is a book by the eminent paleontologist Chris Beard, a recipient of a MacArthur Genius Grant (*The Hunt for the Dawn Monkey*, University of California Press, 2004). The PETM primate *Teilhardina* has been described by Ni et al. (*Nature*, 2004, 427: 65–68), Rose et al. (*American Journal of Physical Anthropology*, 2011, 146: 281–305), and Morse et al. (*Journal of Human Evolution*, 2019, 128: 103–31). Other interesting primates from around the same time are *Cantius* (Gingerich, *Nature*, 1986, 319: 319–21) and *Archicebus* (Ni et al., *Nature*, 2013, 498: 60–64).

Artiodactyls: The pioneering artiodactyl *Diacodexis* was named by Cope and described by Ken Rose, one of the world’s most respected experts on early mammal anatomy and evolution (*Science*, 1982, 216: 621–23). Further descriptions of its postcranial anatomy were written by Thewissen and Hussain (*Anatomia, Histologia, Embryologia*, 1990, 19: 37–48), and Maëva Orliac and colleagues have used CT scans to describe its brain (*Proceedings of the Royal Society, Series B*, 2012, 279: 3670–77) and inner ear (*Journal of Anatomy*, 2012, 221: 417–26).

Perissodactyls: In many older publications, *Sifrhippus* is referred to as *Hyracotherium*—a well-known genus of early horse that became a wastebasket grouping many distinct species, which was clarified by David Froehlich, who created the name *Sifrhippus* (*Zoological Journal of the Linnean Society*, 2002, 134: 141–256). The anatomy of *Sifrhippus*—under the name *Hyracotherium*—was described by Wood et al. (*Journal of Mammalian Evolution*, 2011, 18: 1–32). Ken Rose and colleagues proposed a provocative theory that perissodactyls may have originated in India, and then spread across Asia when the two continents collided in the Eocene (*Nature Communications*, 2011, 5: 5570; *Society of Vertebrate Paleontology Memoir*, 2020, 20: 1–147). The idea of India as a “Noah’s Ark” is intriguing, but what is not clear is how the ancestors of perissodactyls would have reached the then-island of India, in the Cretaceous or Paleocene.

One of the best sources of information on Eocene primates, perissodactyls,

artiodactyls, and other mammals generally is Don Prothero's *Princeton Field Guide to Prehistoric Mammals* (Princeton University Press, 2017), which I used extensively. Also useful for the hoofed species is a book that Don wrote with Robert Schoch: *Horns, Tusks, and Flippers* (The Johns Hopkins University Press, 2002). Both these books have copious information on the bizarre bronotheres and chalicotheres. The single best technical resource on bronotheres is Matthew Mhlbachler's magisterial monograph, published in the *Bulletin of the American Museum of Natural History* (2008, 311: 1–475), which cleans up over a century of sloppy descriptive and taxonomic work on the group and presents an updated classification.

The historian Adrienne Mayor tells the tale of the Thunder Beasts and other Native American fossil discoveries in her 2005 book *Fossil Legends of the First Americans* (Princeton University Press) and a 2007 article (*Geological Society of London, Special Publications*, 273: 245–61).

Did rodents really outcompete multituberculates, and drive them to extinction? Or was it more of an opportunistic replacement? This was assessed using a clever biomechanical approach by the young paleontologist Neil Adams, while a master's student, and published in 2019 (*Royal Society Open Science*, 6: 181536). The verdict: maybe. Rodents actually have higher stresses on their skull bones when they bite compared to multituberculates, but they are able to optimize their bite forces, meaning the two groups didn't chew in exactly the same way, and it's not really clear if one or the other was "superior."

The best source of information—and real facts—about Charles Darwin's *Beagle* journey come from Darwin himself, in his books (both of which I quote): *The Voyage of the Beagle* (1839) and *The Origin of Species* (1859). Darwin's mammal discoveries were reviewed by the paleontologist Juan Fernicola and colleagues (*Revista de la Asociación Geológica Argentina*, 2009, 64: 147–59) and were celebrated for a more popular audience in David Quammen's *National Geographic* article (February 2009). Fernicola's paper also recounts stories of South American Indigenous peoples coming into contact with large fossil bones.

Darwin's South American Ungulates were recently reviewed by Darin Croft and colleagues (*Annual Review of Earth and Planetary Sciences*, 2020, 48: 11.1–11.32) and are also covered in both of Don Prothero's books cited above. Information on Richard Owen and the Ameghinos was gleaned from Wallace's *Beasts of Eden*. The "paternity test" studies linking them to perissodactyls are based on proteins (Welker et al., *Nature*, 2015, 522: 81–84; Buckley, *Proceedings of the Royal Society, Series B*, 2015, 282: 20142671) and DNA (Westbury et al., *Nature Communications*, 2017, 8: 15951). It should be noted that only two

subgroups of Darwin's Ungulates—notably the litopterns (the *Macrauchenia* group) and notoungulates (the *Toxodon* group)—have been subjected to the paternity test, so it is not yet clear if the other subgroups are linked to perisodactyls too. The dispersal of Darwin's Ungulates from South America to Antarctica is examined by Reguero et al. (*Global and Planetary Change*, 2014, 123: 400–413).

The insular South American mammal fauna is expertly profiled by Darin Croft in his book *Horned Armadillos and Rafting Monkeys* (Indiana University Press, 2016). George Gaylord Simpson's views were featured in his book *Splendid Isolation* (Yale University Press, 1980). Important papers on sparassodonts include those by: Argot (*Zoological Journal of the Linnean Society*, 2004, 140: 487–521), Forasiepi (*Monografías del Museo Argentino de Ciencias Naturales*, 2009, 6: 1–174), Goswami et al. (*Proceedings of the Royal Society, Series B*, 2011, 278: 1831–39), Prevosti et al. (*Journal of Mammalian Evolution*, 2013, 20: 3–21), Croft et al. (*Proceedings of the Royal Society, Series B*, 2017, 285: 20172012), Muizon et al. (*Geodiversitas*, 2018, 40: 363–459), and Janis et al. (*PeerJ*, 2020, 8:e9346). The latter paper uses biomechanical analysis to argue that the “marsupial saber tooth” *Thylacosmilus* used its canines differently than true saber-toothed cats, more as belly-opening tools than throat slashers. Sparassodont bite marks on Darwin's Ungulate bones were described by Tomassini et al. (*Journal of South American Earth Sciences*, 2017, 73: 33–41).

The improbable but true story of primates and rodents rafting from Africa to South America is covered in several important papers. Mariano Bond and colleagues described the oldest New World monkey, *Perupithecus*, from the Eocene of South America (*Nature*, 2015, 520: 538–41). Stuningly, Seiffert and colleagues recently described a second lineage of South America primates, also nested within an African group, which may have rafted westward independent of the New World monkeys (*Science*, 2020, 368: 194–97). The rafting caviomorphs are discussed by Antoine et al. (*Proceedings of the Royal Society, Series B*, 2012, 279: 1319–26). The massive cow-size rodent *Josephaartigasia*—imagine that, a guinea pig-looking thing as big as some cars!—is examined by Rinderknecht and Blanco (*Proceedings of the Royal Society, Series B*, 2008, 275: 923–28) and Millien (*Proceedings of the Royal Society, Series B*, 2008, 275: 1953–55). Before rodents and primates went from Africa to South America, they needed to travel from Asia (or Europe) to Africa, which is discussed by Sallam et al. (*Proceedings of the National Academy of Sciences, USA*, 2009, 106: 16722–27), Jaeger et al. (*Nature*, 2010, 467: 1095–98), and Chris Beard in his book, cited above.

CHAPTER 7: EXTREME MAMMALS

The chapter title “Extreme Mammals” was inspired by an exhibit of the same name, originally shown at the American Museum of Natural History and curated by one of my PhD committee members and mentors, the widely admired mammal expert John Flynn.

This chapter highlights elephants, bats, and whales. There are many sources of further reading for each group, expanded on below. The most engaging general resource that covers the evolution of all three groups is Don Prothero’s *Princeton Field Guide to Prehistoric Mammals* (Princeton University Press, 2017). For information on the evolutionary history and relationships of each group, Robert Asher’s chapter in the *Handbook of Zoology: Mammalian Evolution, Diversity and Systematics* (cited above) is an excellent summary.

Elephants: Emmanuel Gheerbrant and his colleagues have published several papers on their transitional sequence of elephant fossils, showing how they supersized over time. These include works on *Eritherium* (*Proceedings of the National Academy of Sciences, USA*, 2009, 106: 10717–21), *Phosphatherium* (*Nature*, 1996, 383: 68–70), and *Daouitherium* (*Acta Palaeontologica Polonica*, 2002, 47: 493–506). Gheerbrant has also described fossils of primitive afrotherians, on the ancestral lineage toward elephants and the other modern species, including *Ocepia* (*PLoS ONE*, 2014, 9: e89739). and *Abdounodus* (*PLoS ONE*, 2016, 11: e0157556), and he has done important work on the origin of the embrithopods, the extinct group that includes the bizarre huge-horned *Arsinotherium* (*Current Biology*, 2018, 28: 2167–73). Regarding other extinct afrotherians, three papers nicely exhibit the strange body types and large body sizes of prehistoric hyraxes (Schwartz et al., *Journal of Mammalogy*, 1995, 76: 1088–99; Rasmussen and Simmons, *Journal of Vertebrate Paleontology*, 2000, 20: 167–76; Tabuce, *Palaeovertebrata*, 2016, 40: e1–12). One final point on afrotherians, for clarity: while they seem to be African endemics, they would have had an ancestor that came from elsewhere in the latest Cretaceous or early Paleocene, and so it is possible that these earliest afrotheres were actually present—maybe even widespread—on other continents before they became restricted to Africa.

My discussion of elephant body sizes over time—including the size estimates for individual species—come from an important paper by Asier Larra-mendi (*Acta Palaeontologica Polonica*, 2016, 61: 537–74). This paper reviews the evidence for the massive body size estimates for *Palaeoloxodon*, which is admittedly based on extrapolating from fragmentary fossils. This paper also discusses the sizes of Eocene-Oligocene rhinos like *Paraceratherium*, and how

these animals compared to the largest elephants. From my reading of this and other literature, I don't think we can be confident (yet) about whether it was elephants like *Palaeoloxodon* or rhinos like *Paraceratherium* that held the "largest land mammal ever" title, but it doesn't matter that much: these animals got to be roughly the same size, and that size was monstrous.

My discussion of mammal body size evolution over time, and how it reached a peak around the Eocene-Oligocene boundary, was informed by two key papers from the same general research group, led by Felisa Smith (*Science*, 2010, 330: 1216–19) and Juha Saarinen (*Proceedings of the Royal Society of London Series B*, 2014, 281: 20132049), plus something of a rebuttal to the first paper by Roland Sookias and colleagues (*Biology Letters*, 2012, 8: 674–77).

For more information on how dinosaurs grew to enormous sizes, and which features of their anatomy enabled it, please see my book *The Rise and Fall of the Dinosaurs* and many references cited therein, including important work by Martin Sander and colleagues (*Biological Reviews*, 2011, 86: 117–55). For information on elephant brains, and how they got bigger over time, consult the study of Julien Benoit and team (*Scientific Reports*, 2019, 9: 9323).

Bats: When it comes to bats, Nancy Simmons and her colleagues described the oldest and most primitive fossil bat *Onychonycteris* on the cover of *Nature* (2008, 451: 818–21). They later published details on its throat and ear (*Nature*, 2010, 466: E8–E9, in response to the Vesekla et al. paper cited below), and on its wings and flying style, in a paper led by Lucila Amador (*Biology Letters*, 2019, 15: 20180857). Nancy was junior author on an engrossing review of bat origins, led by her late colleague Gregg Gunnell (*Journal of Mammalian Evolution*, 2005, 12: 209–46), and Nancy and Jonathan Geisler published a landmark monograph on bat genealogy in the *Bulletin of the American Museum of Natural History* (1998, 235: 1–182).

Other important Eocene bat fossils include *Icaronycteris* from the western United States (Jepsen, *Science*, 1966, 1333–39), *Australonycteris* from Australia (Hand et al., *Journal of Vertebrate Paleontology*, 1994, 14: 375–81), *Tanzanycteris* from Tanzania (Gunnell et al., *Palaeontologica Electronica*, 2003, 5[3]:1–10), an early Eocene specimen from Algeria (Ravel et al., *Naturwissenschaften*, 2011, 98: 397–405), several species from India (Smith et al., *Naturwissenschaften*, 2007, 94: 1003–09), and specimens from Portugal (Tabuce et al., *Journal of Vertebrate Paleontology*, 2009, 29: 627–30). The Messel bats from Germany are described in the book *Messel: An Ancient Greenhouse Ecosystem* (cited above), and in two papers by Jörg Habersetzer and colleagues (*Naturwissenschaften*, 1992, 79: 462–66; *Historical Biology*, 1994, 8: 235–60).

There is a rich literature on bat flight. One of the best resources on how bats

fly, and how this is enabled by their skeletons and wing shapes, is a landmark monograph by Norberg and Rayner (*Philosophical Transactions of the Royal Society Series B*, 1987, 316: 335–427). The 100 mph speed I mention was recorded by McCracken and colleagues (*Royal Society Open Science*, 2016, 3: 160398). Karen Sears and colleagues published an important study on how bat wings develop in an embryo, and what this means for how they evolved (*Proceedings of the National Academy of Sciences, USA*, 2006, 103: 6581–86).

There is also a rich literature on bat echolocation. Accessible review papers include those by Arita and Fenton (*Trends in Ecology and Evolution*, 1997, 12: 53–58), Speakman (*Mammal Review*, 2001, 31: 111–30), and Jones and Teeling (*Trends in Ecology and Evolution*, 2006, 21: 149–56). Mike Novacek showed how cochlea size is related to echolocation (*Nature*, 1985, 315: 140–41), and Nina Veselka and team showed how the connection between throat and ear bones is related to echolocation (*Nature*, 2010, 463: 939–42). Other authors have focused on how echolocation evolved in bats, informed by the family tree of modern bats and the distribution of different types of echolocation among the modern species; chief among these are papers by Emma Teeling and colleagues (*Nature*, 2000, 403: 188–92) and Mark Springer and team (*Proceedings of the National Academy of Sciences, USA*, 2001, 98: 6241–46). Teeling—who like Nancy Simmons is universally regarded as a leading expert on bats—led a milestone study on the genealogical relationships of today’s bats, using the DNA paternity test (*Science*, 2005, 307: 508–84).

I learned much about vampire bats, particularly about their hunting styles and how their brains are attuned to breathing rhythms, in papers by Gröger and Weigrebe (*BMC Biology*, 2006, 4: 18) and Schmidt et al. (*Journal of Comparative Physiology A*, 1991, 168: 45–51). The factoid about how much cow blood a vampire colony eats in a year comes from National Geographic (<https://www.nationalgeographic.com/animals/mammals/c/common-vampire-bat/>).

Whales: There is an enormous, broad, and deep literature on whales, covering how they evolved from walking ancestors and how these most extreme of mammals move, feed, reproduce, cognate, and communicate today. For a fast-paced, first-person account of the past, present, and future of whales, I cannot recommend enough Nick Pyenson’s pop-science book *Spying on Whales* (2018, Viking). Nick is a curator at the Smithsonian, and has seemingly done everything in the field of whaleontology, from excavating and describing fossil whales to dissecting modern-day whales and tagging living whales to study their migration and diving patterns. Carl Zimmer, the peerless science writer, wrote an earlier pop-science book focusing, in part, on how whales went from walking to swimming, called *At the Water’s Edge* (Simon & Schuster, 1999).

More recently, Hans Thewissen wrote a semitechnical, semipersonal account of whale evolution and his fossil discoveries, called *The Walking Whales* (University of California Press, 2019), and Annalisa Berta wrote a more general semitechnical book on all marine mammals, called *Return to the Sea* (University of California Press, 2012). The paleontologists Felix Marx, Olivier Lambert, and Mark Uhen teamed up to write a fantastic semitechnical review of whale evolutionary history, *Cetacean Paleobiology* (Wiley-Blackwell, 2016).

Before further diving into whales, a digression. If you want a quirky read, check out *The Stones of the Pyramids*, by Dietrich and Rosemary Klemm, which outlines what source rocks the Giza Pyramids, and other Egyptian monuments, were constructed from (De Gruyter, 2010).

When it comes to whale evolution—and the tale of how walkers turned into swimmers—there are several general review papers that tell the story well. Chief among these are essays by Hans Thewissen and E. M. Williams (*Annual Review of Ecology, Evolution, and Systematics*, 2002, 33: 73–90); Hans Thewissen, Lisa Noelle Cooper, and colleagues (*Evolution: Education and Outreach*, 2009, 2: 272–88); Sunil Bajpai and colleagues (*Journal of Biosciences*, 2009, 34: 673–86); Mark Uhen (*Annual Review of Earth and Planetary Sciences*, 2010, 38: 189–219); John Gatesy and colleagues (*Molecular Phylogenetics and Evolution*, 2013, 66: 479–506); and Nick Pyenson (*Current Biology*, 2017, 27: R558–R564). These reviews also cover the DNA and other molecular evidence linking whales to artiodactyls, and the history of this research, with citations to the key primary literature. Although I wish I could claim credit for it, the phrase “Bambi turning into Moby Dick” was inspired by the headline of Ian Sample’s *Guardian* article on the discovery of *Indohyus* (from which I also gathered details of the discovery of the *Indohyus* fossils).

Two papers published nearly simultaneously announced the discovery of the signature artiodactyl double-pulley astragalus in Eocene whales: one by Thewissen and colleagues (*Nature*, 2001, 413: 277–81) and one by Philip Gingerich and colleagues (*Science*, 2001, 293: 2239–42).

I want to be very clear about a potential pitfall of my narrative style. When I talk about transitional whales, I might give the impression that a single *Indohyus* individual fled into the water, and this one individual was the ancestor of whales. Similarly, I might give the impression that *Indohyus* evolved into *Pakicetus*, which evolved into *Ambulocetus*, which evolved into *Rodhocetus*, which evolved into today’s whales. These things are not strictly true. To the first point, there would have been a population of *Indohyus* (and/or closely related species) living on the Indian island, which began to experiment with living in the water. To the second point, the fossils I mention in the text form

successive branches on the family tree, on the line to whales. These species were not strictly ancestral to each other, but are the fossils that paleontologists have happened to find so far, which are links in a much bigger chain that would have included many other species that we have yet to find. Also, the particular species I highlight are members of larger groups: *Indohyus* is part of Raoellidae, *Pakicetus* part of Pakicetidae, *Ambulocetus* part of Ambulocetidae, *Rodhocetus* part of Protocetidae, and *Basilosaurus* part of Basilosauridae. It is these *groups*—plus another one called Remingtonocetidae that I don't discuss in the text—that form the series of ancestral steps on the line to whales. The species I discuss in the text are the best exemplars of these groups: they are known from the best fossils and have been the subject of most intensive study, so they are the easiest ones to profile. Thus, the fossils I mention *represent* the progressive stages that the deerlike ancestors of whales morphed through as they became ever-better swimmers. Each one is a clue that reveals part of the story; it is their step-by-step arrangement on the family tree, on the line to whales, that provides the directionality to the story, even though these specific species would not have formed a strict ancestor-descendant chain. Who knows what other links in the chain are still out there to be found?

Here are the most essential sources for the chain of transitional species on the line to whales:

Indohyus: A. Ranga Rao described the first, scrappy fossils of this mammal in 1971 (*Journal of the Geological Society of India*, 12: 124–34). Hans Thewissen and colleagues later described new fossil material that revealed a link to whales (*Nature*, 2007, 250: 1190–94), and these fossils were then described in more comprehensive detail by Lisa Noelle Cooper, Thewissen, and colleagues in 2012 (*Historical Biology*, 24: 279–310). Thewissen's team included Indian colleagues Sunil Bajpai and B. N. Tiwari.

Pakicetus: Phil Gingerich and colleagues first described *Pakicetus* in *Science* (1983, 220: 403–6). S. I. Madar described the skeleton of *Pakicetus* and other pakicetids in more detail (*Journal of Paleontology*, 2007, 81: 176–200).

Ambulocetus: Hans Thewissen and colleagues first described *Ambulocetus* in *Science* (1994, 263: 210–12), and then later published a comprehensive description of its skeleton (*Courier Forsch.-Inst. Senckenberg*, 1996, 191: 1–86). In 2016, Konami Ando and Shin-ichi Fujiwara published an important study arguing, based on postcranial anatomy, that *Ambulocetus* was a strong swimmer and poor walker, and probably spent most of its time in the water (*Journal of Anatomy*, 229: 768–77). Sunil Bajpai and Gingerich described another important ambulocetid: *Himalayacetus*, which at approximately 52.5 million years old is the oldest whale currently known in the fossil record, meaning that the

land-to-water transition had taken place by that time (*Proceedings of the National Academy of Sciences USA*, 1998, 95: 15464–68).

Protocetids: Phil Gingerich and colleagues described *Rodhocetus* in 1994 (*Nature*, 368: 844–47). The Belgian whale expert Olivier Lambert—with whom for a few years I coedited the journal *Acta Palaeontologica Polonica*—described the Peru pakicetid *Peregocetus* in a fascinating 2019 paper in *Current Biology* (29: 1352–59), which discusses the issue of early whale distribution and migration more generally. He was joined on the paper by several coauthors from Peru, Italy, and France—a global team studying the first global whales. There has been considerable work on the hearing abilities of whales in the pakicetid-ambulocetid-protocetid part of the family tree, most notably papers by Thewissen and Hussain (*Nature*, 1993, 361: 444–45), Nummella et al. (*Nature*, 2004, 430: 776–78), and Mourlam and Orliac (*Current Biology*, 2017, 27: 1776–81).

Basilosaurus and the Wadi al-Hitan Whales: *Basilosaurus* has a colorful history, first discovered in the southern United States in the 1830s and given its name—which means “king lizard”—because it looked like a sea serpent. It was our recurring villain, Richard Owen, who first realized that the animal was an early whale and not a reptile, but by the rules of zoological nomenclature, the name *Basilosaurus* had to stick. This history is chronicled in David Rains Wallace’s *Beasts of Eden* and Don Prothero and Robert Schoch’s *Horns, Tusks, & Flippers* (both cited above). Gingerich led a team that described the legs and feet of Egyptian specimens of *Basilosaurus* in 1990 (*Science*, 249: 154–57). In 1992, Gingerich published a scrupulous monograph on the Wadi al-Hitan whales, and other Egyptian Eocene whales, meticulously documenting where individual specimens were found both geographically and in the stratigraphic sequence of the Eocene rocks (*University of Michigan Papers on Paleontology*, 30: 1–84). Manja Voss led a team of authors (including Gingerich and Egyptian colleagues) describing the stunning fossil of a *Dorudon* inside a *Basilosaurus* (*PLoS ONE*, 2019, 14: e0209021). Tom Mueller’s article in the August 2010 issue of *National Geographic* is an evocative pop-science portrayal of the Wadi al-Hitan whales and Gingerich’s work.

Important references on the early evolution of odontocetes include papers on the three species mentioned by name in the text: *Cotylocara* (Geisler et al., *Nature*, 2004, 508: 383–86), *Echovenator* (Churchill et al., *Current Biology*, 2016, 26: 2144–49), and *Livyatan* (Lambert et al., *Nature*, 2010, 466: 105–8). Furthermore, other important studies on aspects of odontocete biology include a study of the origin and early evolution of echolocation by the early career paleontologist Travis Park and colleagues (*Biology Letters*, 2016, 12: 20160060),

and papers on the evolution of the enormous odontocete brain by Lori Marino and colleagues (*The Anatomical Record*, 2004, 281A: 1247–55; *PLoS Biology*, 2007, 5: e139).

Important references on the early evolution of mysticetes include papers on the two species mentioned by name in the text: *Mystacodon* (Lambert et al., *Current Biology*, 2017, 27: 1535–41) and *Llanocetus* (Mitchell, *Canadian Journal of Fisheries and Aquatic Sciences*, 1989, 46: 2219–35; Fordyce and Marx, *Current Biology*, 2018, 28: 1670–76), plus the key species *Maiabalaena*, which has neither teeth nor baleen on its jaws (Peredo et al., *Current Biology*, 2018, 28: 3992–4000). Furthermore, other important studies on aspects of mysticete biology include papers on the origin and early evolution of baleen (Peredo et al., *Frontiers in Marine Science*, 2017, 4: 67; Hocking et al., *Biology Letters*, 2017, 13: 20170348; see also a different hypothesis from Demere et al. [*Systematic Biology*, 2008, 57: 15–37] and Geisler et al. [*Current Biology*, 2017, 27: 2036–42]) and on their hearing abilities (Park et al., *Proceedings of the Royal Society, Series B*, 2017, 284: 20162528).

My main sources for the biological talents of blue whales and the evolution of mysticete gigantism include papers on blue whale weaning and calf sizes (Lockyer, *FAO Fisheries Series*, 1981, 3: 379–487. Mizroch et al., *Marine Fisheries Review*, 1984, 46: 15–19); feeding and engulfing krill (Goldbogen et al., *Journal of Experimental Biology*, 2011, 214: 131–46; Fossette et al., *Ecology and Evolution*, 2017, 7: 9085–97); and body size evolution (Slater et al., *Proceedings of the Royal Society, Series B*, 2017, 284: 20170546; Goldbogen et al., *Science*, 2019, 366: 1367–72). Nick Pyenson’s discussion of mysticete size evolution in his book *Spying on Whales* and his 2017 *Current Biology* review paper (cited above) is clear, gripping, and fascinating writing.

CHAPTER 8: MAMMALS AND CHANGING CLIMATES

My fictionalized tale of the ashfall apocalypse on the American Savanna was based on the fossils preserved at Ashfall Fossil Beds (the various species, how their skeletons were positioned in the ash, and the maladies observable on their bones), the geology of the site (the different layers of ash, their thicknesses and properties, and what that implies about the sequence of events), and a fun discussion with two of my volcanologist colleagues in Edinburgh, Eliza Calder and Isla Simmons.

The best sources of information on the Ashfall site have been written by the scientist who discovered it, Mike Voorhies. Particularly informative are his 1985 article in the *Research Reports of the National Geographic Society* (19: 671–88), his paper with Joseph Thomasson on the grass fossils preserved within the

mouths and rib cages of the rhinos (*Science*, 1979, 206: 331–33), a popular piece in the *University of Nebraska State Museum, Museum Notes* (1992, 81: 1–4), and a chapter he cowrote with S. T. Tucker and colleagues in the book *Geologic Field Trips along the Boundary between the Central Lowlands and Great Plains* (*Geological Society of America Field Guide*, 2014, 36). The Ashfall Fossil Beds website is also a font of information (<https://ashfall.unl.edu/>), as is an article by Terri Cook in *Earth Magazine* in 2017. The age of the Ashfall deposits, and the geological detective work tracing their source to a Yellowstone eruption in Idaho, are discussed by Smith et al. (*PLoS ONE*, 2018, 13: e0207103).

I used several references to flesh out the biology, behaviors, diets, and herd structure of the Ashfall rhinos. Chief among these are papers by Alfred Mead (*Paleobiology*, 2000, 26: 689–706), Matthew Mhlbachler (*Paleobiology*, 2003, 29: 412–28), Nicholas Famoso and Darren Pagnac (*Transactions of the Nebraska Academy of Sciences*, 2011, 32: 98–107), and my New Mexico field buddies Bian Wang and Ross Secord (*Palaeogeography, Palaeoclimatology, Palaeoecology*, 2020, 542: 109411). There is also a fascinating conference abstract by D. K. Beck on the pathologies of the Ashfall rhinos, caused by ash poisoning (*Geological Society of America Abstracts with Programs*, 1995, 27: 38).

There is copious literature on the hothouse-to-coolhouse shift at the Eocene-Oligocene boundary, what caused it, how severe it was in different parts of the world, and how the temperature change affected precipitation and other aspects of climate. The single best reference on how the Earth's climate has changed over the past 66 million years, postasteroid, was published in *Science* in 2020 by Thomas Westerhold and colleagues, including Edinburgh's Dick Kroon (369: 1383–87). This paper includes easy-to-follow plots of temperature over time, indicating major shifts and marking when the Earth was in hothouse, coolhouse, and icehouse phases (note that they divide what I call a hothouse into harsher hothouse and milder warmhouse phases). Other key references on the Eocene-Oligocene are papers by DeConto and Pollard (*Nature*, 2003, 421: 246–49), Cox et al. (*Nature*, 2005, 433: 53–57), Scher and Martin (*Science*, 2006, 312: 428–30), Zanazzi et al. (*Nature*, 2007, 445: 639–42), Liu et al. (*Science*, 2009, 323: 1187–90), Katz et al. (*Science*, 2011, 332: 1076–79), and Spray et al. (*Paleoceanography and Paleoclimatology*, 2019, 34: 1124–38).

There is a huge literature on the spread of grasslands during the Oligocene and Miocene, much of it by Caroline Strömberg and her colleagues. Two of the most useful and readable general reviews are Caroline's paper in *Annual Review of Earth and Planetary Sciences* (2011, 39: 517–44) and a paper she contributed to in *Science*, led by Erika Edwards (2010, 328: 587–91). Caroline's PhD thesis work on grassland and mammal coevolution in North America was published

in several key papers (*Palaeogeography, Palaeoclimatology, Palaeoecology*, 2004, 207: 239–75; *Proceedings of the National Academy of Sciences [USA]*, 2005, 102: 11980–84; *Paleobiology*, 2006, 32: 236–58), and with colleagues, she also studied grasslands in Turkey (*Palaeogeography, Palaeoclimatology, Palaeoecology*, 2007, 250: 18–49) and South America (*Nature Communications*, 2013, 4: 1478), including one study on South America led by her PhD student Regan Dunn (*Science*, 2015, 347: 258–61). Caroline and her Indian collaborators, led by Vandana Prasad, described their Late Cretaceous grass phytoliths in *Science* (2005, 310: 1177–80). Some details of Caroline’s career and early research were gleaned from a Society of Vertebrate Paleontology biography announcing her Romer Prize.

The effects of grassland evolution on mammals, and the development of tooth hypsodonty in response, has been studied for many years by the eminent paleontologist Christine Janis, with a team of colleagues. The best and most comprehensive review of the subject was written by Christine and John Damuth, and this paper is the source for the mechanical pencil analogy that I use, along with the statistics on how much grit modern grazers consume and how quickly their teeth wear down (*Biological Reviews*, 2011, 86: 733–58). This paper is, in many respects, a follow-up to a landmark review that Christine published with Mikael Fortelius in the same journal in 1988 (63: 197–230). Christine was also part of a team, led by Borja Figueirido, that broadly examined how mammal evolution related to climate over the last 66 million years (*Proceedings of the National Academy of Sciences [USA]*, 2019, 116: 12698–03), and another team, led by Phillip Jardine, that assessed patterns of hypsodonty evolution in horses and other high-toothed mammals on the American Savanna (*Palaeogeography, Palaeoclimatology, Palaeoecology*, 2012, 365–66: 1–10). The evolution of hypsodonty in South American mammals was assessed by Rodrigues et al. (*Proceedings of the National Academy of Sciences [USA]*, 2014, 114: 1069–74). The relationship between hypsodonty and tooth wear—and the remarkable finding that grazing-related tooth wear appeared in horses long before hypsodonty—was the subject of a scintillating 2011 paper in *Science* by Matthew Mhlbachler and colleagues (331: 1178–81). The relationship between grazing, hypsodonty, and tooth enamel complexity was illuminated by Nicholas Famoso and coworkers (*Journal of Mammalian Evolution*, 2016, 23: 43–47), and the evolution of cursorial running mammals on the savannas was addressed by David Levering and team (*Palaeogeography, Palaeoclimatology, Palaeoecology*, 2017, 466: 279–86).

George Gaylord Simpson laid out the story of the Great Transformation in his 1951 book *Horses: The Story of the Horse Family in the Modern World and*

through Sixty Million Years of History (Oxford University Press). The modern-day dean of horse research in North America is Bruce MacFadden, of the University of Florida. He published his own detailed book on horse evolution, *Fossil Horses: Systematics, Paleobiology, and Evolution of the Family Equinae* (1992, Cambridge University Press), along with reams of papers, including a brief but influential review in *Science* in 2005 (307: 1728–20). Other key works include his 1984 monograph on Miocene and Pliocene horses (*Bulletin of the American Museum of Natural History*, 179: 1–196), a 1988 paper with Richard Hulbert on the genealogy of early horses and the explosive radiation of Miocene grazers (*Nature*, 336: 466–68), a study of the diets and ecologies of horses during the waning days of their glory in the latest Miocene and early Pliocene (*Science*, 1999, 283: 824–27), and enjoyable reviews on the evolution of grazing mammals (*Trends in Ecology and Evolution*, 1997, 12: 182–87; *Annual Review of Ecology and Systematics*, 2000, 31: 33–59).

It wasn't only grass-grazers that thrived in the Miocene! Christine Janis, John Damuth, and Jessica Theodor wrote a provocative series of papers showing that leaf-eating browsers were still diversifying, too—and in fact were more diverse than in similar environments today (*Proceedings of the National Academy of Sciences [USA]*, 2000, 97: 7899–904; *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2004, 207: 371–98). When it comes to the predators eating all these grazers and browsers, my key sources were reviews by the renowned carnivorous mammal expert Blaire van Valkenburgh (*Annual Review of Earth and Planetary Sciences*, 1999, 27: 463–93; *Paleontological Society Papers*, 2002, 8: 267–88). An intriguing study by Figueirido and team showed that meat-eating mammals still were mostly ambush predators, or pounce-pursuit predators that could track their prey for a short distance, during the American Savanna times, and it was only very recently, during the Ice Age, that pure long-distance pursuit predators evolved (*Nature Communications*, 2015, 6: 7976). And we can't forget about the small mammals! Joshua Samuels and Samantha Hopkins beautifully outline their evolution on the grasslands in a 2017 paper (*Global and Planetary Change*, 149: 36–52).

The section on Riversleigh and the evolution of Australia's marsupial fauna was based on the literature and discussions with Mike Archer and Robin Beck. Mike and colleagues Sue Hand and Hank Godthelp wrote a book on Riversleigh in 1994 (*Riversleigh: The Story of Animals in Ancient Rainforests of Inland Australia*, Reed Books)—and they need to write another to update with all their recent discoveries! Other important general reviews include a chapter on the rise of Australian marsupials led by Karen Black, one of Mike's many PhD students, in the 2012 book *Earth and Life* (edited by John Talent, published by

Springer), and a chapter that Rob wrote for the *Handbook of Australasian Biogeography* in 2017 (329–66). Rob also led two important papers on the earliest Australian marsupials from the Eocene (*PLoS ONE*, 2008, 3: e1858; *Naturwissenschaften*, 2012, 99: 715–29). I also must mention Mike’s riveting and fun series of articles for *Nature Australia*, which cover so many of the Riversleigh finds and the general story of marsupial evolution; he really needs to update these and combine them into a pop-science book.

Mike, Sue, Hank, Rob, and their many Riversleigh compatriots—Derrick Arena, Marie Attard, Tim Flannery, Julien Louys, Anna Gillespie, Kenny Travouillon, Steve Wroe, and so many others—have published dozens and dozens of research papers on the Riversleigh fossils. The ones that I consulted to write this chapter include papers on: the Riversleigh rain forest environment (Travouillon et al., *Palaeogeography, Palaeoclimatology, Palaeoecology*, 2009, 276: 24–37; Travouillon et al., *Geology*, 2012, 40[6]: e273); the age of the Riversleigh fauna and its division into four zones spanning the Oligocene and Miocene (Arena et al., *Lethaia*, 2016, 49: 43–60; Woodhead et al., *Gondwana Research*, 2016, 29: 153–67); the preservation of Riversleigh fossils in cave settings (Arena et al., *Sedimentary Geology*, 2014, 304: 28–43); the overall diversity of Riversleigh mammals (Archer et al., *Alcheringa*, 2006, 30:S1: 1–17); and the Burdekin Plum fossil from Riversleigh (Rozeffelds et al., *Alcheringa*, 2015, 39: 24–39).

For information on specific Riversleigh mammals I mentioned in the text, please see the following references: the giant tree-climbing wombat-relative *Nimbadon* (Black et al., *Journal of Vertebrate Paleontology*, 2010, 30: 993–1011); the carnivorous thylacine *Nimbacinus* (Attard et al., *PLoS ONE*, 2014, 9[4]: e93088); the fierce marsupial-lions (Gillespie et al., *Journal of Systematic Palaeontology*, 2019, 17: 59–89); primitive kangaroos (Kear et al., *Journal of Paleontology*, 2007, 81: 1147–67; Black et al., *PLoS ONE*, 2014, 9[11]: e112705); the potentially meat-eating rat-kangaroo *Ekaltadeta* (Archer and Flannery, *Journal of Paleontology*, 1985, 59: 1331–49; Wroe et al., *Journal of Paleontology*, 1998, 72: 738–51); primitive koalas (Louys et al., *Journal of Vertebrate Paleontology*, 2009, 29: 981–92; Black et al., *Gondwana Research*, 2014, 25: 1186–201); the rain forest marsupial mole *Naraboryctes* (Archer et al., *Proceedings of the Royal Society, Series B*, 2011, 278: 1498–506; Beck et al., *Memoirs of Museum Victoria*, 2016, 74: 151–71); the hammer-toothed snail eater *Malleodectes* (Arena et al., *Proceedings of the Royal Society, Series B*, 2011, 278: 3529–33; Archer et al., *Scientific Reports*, 2016, 6: 26911); and “Thingodonta” itself, which goes by the scientific name *Yalkaparidon* (Archer et al., *Science*, 1988, 239: 1528–31; Beck, *Biological Journal of the Linnean Society*, 2009, 97: 1–17).

CHAPTER 9: ICE AGE MAMMALS

The story of the Stono slaves and their mammoth discovery is told by Adrienne Mayor, the leading historian of ancient and indigenous encounters with fossils, in her book *Fossil Legends of the First Americans* (Princeton University Press, 2005), and an article she wrote in 2014 for *Wonders & Marvels* magazine. She also provided further information during an email chat. Her book is excellent and covers a wealth of information on Native American fossil discoveries, and how they interpreted the giant bones they found—including the tale of Big Bone Lick.

Thomas Jefferson's mammoth obsession is well documented in many historical and scientific works. You can read Jefferson's 1797 address on *Megalonyx*, as it was published as a research paper (*Transactions of the American Philosophical Society*, 1799, 4: 246–60). As I'm writing this passage in mid-January 2021, I'm imagining how improbable it is that our outgoing vice president, Mike Pence, would publish a peer-reviewed scientific paper. Maybe Buffon was correct about American degeneracy? Other important sources on Jefferson include two articles by early-twentieth-century paleontologist Henry Fairfield Osborn (*Science*, 1929, 69: 410–13; *Science*, 1935, 82: 533–38). Osborn was an avowed white supremacist, so you'll find no mention of the Stono slaves in these works. I also gleaned information on Jefferson, Buffon, Lewis and Clark, and mammoths from several articles, including those by Richard Conniff in *Smithsonian*, Cara Giaimo in *Atlas Obscura*, Phil Edwards in *Vox*, Emily Petsko in *Mental Floss*, and Keith Thomson in *American Scientist*, along with the Monticello website, which has information on Jefferson's fossil collection. Finally: huge thanks to Ted Daeschler in Philadelphia, for showing me the *Megalonyx* bones as a grad student.

Much of my knowledge of Illinois's glacial topography comes from the class I took with Joe Jakupcak in high school, supplemented by countless conversations with him over the years. The Illinois State Geological Survey (ISGS) has a variety of resources on Ice Age Illinois, ranging from their website (<https://isgs.illinois.edu/outreach/geology-resources>) to their series of *Field Trip Guidebooks*. Of the latter, the most relevant to the story told here are guides 1986B (to my hometown of Ottawa), 1995C (to the Streator-Pontiac area, south of Ottawa), and 2002A (to the Hennepin area, east of Ottawa—a field trip I attended as a senior in high school, with Mr. Jakupcak). Other facts and figures in this section were taken from the 1942 ISGS Bulletin (number 66) on the *Geology and Mineral Resources of the Marseilles, Ottawa, and Streator Quadrangles*, and a United States Geological Survey report on the hydrogeology of LaSalle County (Scientific Investigations Report 2016-5154). The moraine

south of Ottawa, by the way, is the Farm Ridge Moraine, sometimes called the Grand Ridge Moraine, after the agricultural village of Grand Ridge perched on top of it.

One of the best, most lavishly illustrated, and most digestible summaries of the Ice Age and its megafauna is Ross MacPhee's book *End of the Megafauna* (W.W. Norton & Company, 2019). Along with Peter Schouten's stunning illustrations of megafauna in their environments, the book includes maps of glacial coverage during the last glacial advance (called the Wisconsin Glacial Advance in North America; the glaciers reached as far south as central Illinois, but in earlier glacial periods the ice sheets went even farther south), maps of the Mammoth Steppe and other Ice Age biomes, and plots showing changes in temperature and ice volume over time.

Important resources on Ice Age climate include works by Zhang et al. on carbon dioxide levels over time (*Philosophical Transactions of the Royal Society, Series A*, 2013, 371: 20130096), Sarinthein et al. on how changes in Atlantic Ocean circulation fed the ice caps (*Climate of the Past*, 2009, 5: 269–83), Bailey et al. on the start of the polar ice cap's advance onto North America (*Quaternary Science Reviews*, 2013, 75: 181–94), and Spray et al. on the timing of the Northern Hemisphere ice cap formation (*Paleoceanography and Paleoclimatology*, 2019, 34: 1124–38). The latest research on the celestial cycles and how they controlled glacial pulses—which is a bit more complicated than the musical analogy I gave in the text—can be found in Bajo et al.'s 2020 *Science* paper (367: 1235–39). There are three celestial cycles, which are technically called the Milankovitch Cycles: eccentricity (shape of Earth's orbit around the sun), obliquity (the tilt of Earth's axis), and precession (the wobble of Earth's axis). Bajo et al. found that obliquity, in particular, was a major driver of the initiation and duration of glaciations, with contributions from the other cycles.

Haley O'Brien's paper on the African dome-headed wildebeest *Rusingoryx* was published in *Current Biology* (2016, 26: 503–6), and additional information can be found in a paper by Tyler Faith and colleagues (*Quaternary Research*, 2011, 75: 697–707). Christine Janis and colleagues wrote an intriguing paper on the hopping abilities—or lack thereof—in the giant Australian Ice Age kangaroos (*PLoS ONE*, 2014, 9[10]: e109888).

Mammoths are an endless source of fascination, and thus an endless source of literature. A good general overview can be found in Adrian Lister and Paul Bahn's book *Mammoths: Giants of the Ice Age* (University of California Press, 2007) and Lister's sole-authored, similar-named *Mammoths: Ice Age Giants* (Natural History Museum, 2014). Other readable accounts can be found in Jordi Agustí and Mauricio Antón's book *Mammoths, Sabertooths, and Hominids*

(Columbia University Press, 2002), Don Prothero's *Princeton Field Guide to Prehistoric Mammals* and Prothero and Schoch's *Horns, Tusks, and Flippers*, both cited above.

The mad Mammoth Hunters of Siberia have been profiled in Helen Pilcher's book *Bring Back the King* (Bloomsbury, 2016), her article in BBC *Science Focus*, Sabrina Weiss's article in *Wired*, and a Radio Free Europe exposé, in which the photographer Amos Chapple accompanied a team on the ivory trail. In case modern-day mammoth hunting seems romantic, just stop. It's dangerous, it pollutes the environment, and it is illegal. Plus, there is the argument—which resonates with me—that selling mammoth tusks keeps the ivory market afloat, promoting the poaching of our last remaining African and Indian elephants.

The complete woolly mammoth genome was published by Eleftheria Palkopoulou and colleagues in *Current Biology* in 2015 (25: 1395–1400). Later that year, Vincent Lynch and colleagues published a paper in *Cell Reports* describing two additional mammoth genomes, which they used to identify genetic changes related to its cold habitat and frosty lifestyle (12: 217–28). Then, as I was finishing this chapter, a sensational study by Tom van der Valk et al. reported mammoth DNA more than one million years old—a record for ancient DNA (*Nature*, 2021, 591: 265–69)! These genetic studies follow over a decade of work on mammoth DNA. Other key papers over the years, sequentially building on each other, are those by: Poinar et al. (*Science*, 2006, 311: 392–94), Krause et al. (*Nature*, 2006, 439: 724–27), Rogaev et al. (*PLoS Biology*, 2006, 4[3]: e73), Gilbert et al. (*Proceedings of the National Academy of Sciences [USA]*, 2008, 105: 8327–32), Miller et al. (*Nature*, 2008, 456: 387–90), Debruyne et al. (*Current Biology*, 2008, 18: 1320–26), Campbell et al. (*Nature Genetics*, 2010, 42: 536–40; this paper describes the cold-adapted hemoglobin mutations), Rohland et al. (*PLoS Biology*, 2011, 8[12]: e1000564; this paper also describes mastodon DNA); Enk et al. (*Genome Biology*, 2011, 12: R51; this paper presents evidence for woolly mammoth and Columbian mammoth inbreeding).

Mammoth hair has been the subject of both descriptive and genetic work. In 2006, Römpler and colleagues identified a nuclear gene that indicated different hair colors (*Science*, 313: 62). Later, Claire Workman and her team surveyed forty-s even mammoths, sampled their DNA, and found that the genetic combination causing lighter hair was exceptionally rare (*Quaternary Science Reviews*, 2011, 30: 2304–08). Using a different tack in 2014 Silvana Tridico and colleagues microscopically examined over four hundred hairs from various mammoth mummies and described a kaleidoscope of color differences, including major color distinctions between the outer guard hairs and inner coat (*Quaternary Science Reviews*, 2014, 68–75).

Adrian Lister—mammoth expert extraordinaire at the Natural History Museum in London—has published a catalog of papers on woolly mammoth evolution and migrations. Two that were especially useful in writing this chapter were his coauthored 2005 review of mammoth evolution in Eurasia (*Quaternary International*, 126–128: 49–64), and his stirring 2015 *Science* paper on the multiple migrations of mammoths into North America (350: 805–9).

On the subject of mammoth herds and social lives, the Canadian tracksite discussed in the text was described by McNeill et al. (*Quaternary Science Reviews*, 2005, 24: 1253–59). On the subject of mammoth growth and nursing, Metcalfe et al. used isotopic studies of teeth and bone to show that mammoth mothers fed their babies milk for at least three years (*Palaeogeography, Palaeoclimatology, Palaeoecology*, 2010, 298: 257–70). Much of what we know about mammoth reproduction, childhood, and child-rearing comes from the spectacular one-month-old Siberian ice mummy, named Lyuba. The details of her discovery are told with gusto in Tom Mueller’s May 2009 *National Geographic* cover article. Key research papers on Lyuba include those by van Geel et al. on her diet and stomach contents (*Quaternary Science Reviews*, 2011, 30: 3935–46), Fisher et al. on her death and preservation (*Quaternary International*, 2012, 255: 94–105), and Rountrey et al. on her development and season of birth (*Quaternary International*, 2012, 255: 106–205).

Smilodon and other saber-toothed tigers are, like mammoths, an endless subject of fascination and research. Three of the best general overviews are Alan Turner and Mauricio Antón’s book *The Big Cats and Their Fossil Relatives* (Columbia University Press, 1997), Antón’s book *Sabertooth* (Indiana University Press, 2013), and *Smilodon: The Iconic Sabertooth* (Johns Hopkins University Press, 2018), a volume of technical papers edited by Lars Werdelin, Gregory McDonald, and Christopher Shaw. A nice summary of the Rancho La Brea deposits in Los Angeles can be found in the collection of papers edited by John Harris, *La Brea and Beyond: The Paleontology of Asphalt-Preserved Biotas* (*Natural History Museum of Los Angeles County Science Series*, 2015, 42: 1–174). My statistics on *Smilodon* body size were taken from Christiansen and Harris (*Journal of Morphology*, 2005, 266: 369–84).

Although the focus of my narrative is *Smilodon* itself, it is part of a broader saber-toothed family, Machairodontinae. The relationships of this family to modern cats has been clarified by genetic studies of *Smilodon* and other machairodontines, in a series of papers including those by Janczewski et al. (*Proceedings of the National Academy of Sciences [USA]*, 1992, 89: 9769–73), Paijmans et al. (*Current Biology*, 2017, 27: 3330–36), and two papers by Ross Barnett and colleagues (*Current Biology*, 2005, 15: R589–R590; *Current Biology*, 2020,

30: 1–8). Barnett wrote a fascinating book on the evolution and extinction of the megafauna in Britain: *The Missing Lynx* (Bloomsbury, 2019). The evolution and distribution of *Smilodon* in South America, after its double crossing, is explored by Manzuetti et al. (*Quaternary Science Reviews*, 2018, 180: 57–62).

How did saber-toothed tigers use their canines to hunt and kill? This question has fascinated paleontologists for generations and spawned an expansive literature. First things first, the Texas cave with mammoth bones in a saber-toothed lair was described by Marean and Ehrhardt (*Journal of Human Evolution*, 1995, 29: 515–47). More generally, Blaire Van Valkenburgh led an intriguing paper arguing that large Ice Age predators, like *Smilodon*, would have been able to feed on the juveniles of the largest megafauna, like mammoths (*Proceedings of the National Academy of Sciences [USA]*, 2016, 113: 862–67). Isotopic evidence that *Smilodon* preferred forest-dwelling species, and dire wolves grassland species, was presented by Larisa DeSantis and colleagues (*Current Biology*, 2019, 29: 2488–95). DeSantis is a leader in using isotopic analysis to study the diets and habitats of fossil vertebrates, and I’ve long admired her work in blending paleontology and chemistry.

Two scintillating papers have used computer modeling to study the *Smilodon* bite: a landmark study by McHenry et al. using techniques employed by engineers (*Proceedings of the National Academy of Sciences [USA]*, 2007, 104: 16010–15) and a more recent study by Figueirido et al. (*Current Biology*, 2018, 28: 3260–66). The two works differ in some detail; for instance, the former study argues for an exceptionally weak bite and skull in *Smilodon*, and the latter for a stronger skull that could withstand greater stresses. Regardless, both agree that a saber puncture (technically a “canine shear bite”) was the most likely way *Smilodon* killed. A paper by Julie Meachen-Samuels and Blaire Van Valkenburgh described evidence of particularly strong and robust forelimbs in *Smilodon*—evidence that the arms were used to wrestle prey before the saber bite delivered the coup de grâce (*PLoS ONE*, 2010, 5[7]: e11412).

The tough lives, pathologic bones, and broken teeth of *Smilodon* have been chronicled by Van Valkenburgh and Hertel (*Science*, 1993, 261: 456–59), Rothschild and Martin (in *The Other Saber-Tooths*, edited by Naples, Martin, and Babiarez, Johns Hopkins University Press, 2011), and Brown et al. (*Nature Ecology & Evolution*, 2017, 1: 0131). Chris Carbone and colleagues described evidence for *Smilodon* sociality in a 2009 paper (*Biology Letters*, 5: 81–85), which instigated a series of back-and-forth responses arguing whether the evidence was strong enough, or not. The information on *Smilodon* hyoids and roaring was gleaned from a *Scientific American* by John Pickrell, quoting in-progressing research by Christopher Shaw, presented at the 2018 Society of

Vertebrate Paleontology annual meeting and published in abstract form in the accompanying meeting volume.

The fossilized *Smilodon* family—mother and two offspring—was described by Ashley Reynolds, Kevin Seymour, and David Evans, who like me is nominally a dinosaur researcher, although dabbles in many things (*iScience*, 2021, 101916). The timing and pattern of *Smilodon* tooth growth were enumerated by Wysocki et al. (*PLoS ONE*, 2015, 10[7]: e0129847), and the robust skeletons of juvenile *Smilodon* were described by Long et al. (*PLoS ONE*, 2017, 12[9]: e0183175).

One of my greatest regrets in editing this book down to a digestible length was that I could not devote more attention to dire wolves—I conic and monstrous fossil dogs made famous by *Game of Thrones*. Yes, I can assure you, they were real. I briefly mention them in this chapter, as counterparts to saber-toothed tigers at La Brea. In fact, their bones outnumber *Smilodon* bones in the Los Angeles tar pits. Dire wolves were among the first successful pursuit predators, a subject touched on in the last chapter, and in papers by Blaire Van Valkenburgh and Borja Figueirido cited in the chapter 8 references above. As I was writing this chapter, a stunning new study on the genetics of dire wolves was published: it turns out they were an ancient group of homegrown North American wolves, not close relatives of today's North American gray wolves and coyotes, whose ancestors colonized the continent more recently (Perri et al., *Nature*, 2021, 591: 87–91).

The dwarf mammoths of Wrangel Island—the last and strangest of the extinct megafauna—and their bizarre, bottlenecked genomes have been studied by Nyström et al. (*Proceedings of the Royal Society, Series B*, 2010, 277: 2331–37), Rogers and Slatkin (*PLoS Genetics*, 2017, 13[3]: e1006601), and Arppe et al. (*Quaternary Science Reviews*, 2019, 222: 105884).

CHAPTER 10: HUMAN MAMMALS

The mammoth hunting story opening this chapter is not pure fiction, but based on two discoveries of mammoth skeletons near Kenosha, Wisconsin, at the Hebior and Schaefer sites. These mammoth skeletons are marked by cuts and wedges made by stone tools, some of which were found adjacent to the bones. The sites, their ages and environments, and the evidence for mammoth-human interaction have been described by Overstreet and Kolb (*Geoarchaeology*, 2003, 18: 91–114) and Joyce (*Quaternary International*, 2006, 142–143: 44–57).

Details of Leigh Van Valen's remarkable life and scientific achievements are summarized in a touching obituary by some of his former students, published in the journal *Evolution* (Liow et al., 2011, doi:10.1111/j.1558-5646

.2011.01242.x). I gathered other information from my own reminisces of him in Chicago, a chat with Christian Kammerer, and obituaries published in the *New York Times* (by Douglas Martin 2010) and by the University of Chicago.

Van Valen and Robert Sloan described and named *Purgatorius* in their 1965 *Science* paper (150: 743–45), and Van Valen much later monographed it (and other plesiadapiforms) in detail in another of his self-published journals, *Evolutionary Monographs* (15: 1–79). It is in this latter paper that he outlines why he identified *Purgatorius* and other plesiadapiforms as early primates, based on the shapes of their cusps; his rationale is not that clear in his shorter 1965 paper, at least to those (like me) uninitiated in 1960s terms for tooth cusps and ridges. Other important works on *Purgatorius* itself include papers on jaw and dental material by Bill Clemens (*Science*, 1974, 184: 903–5; *Bulletin of Carnegie Museum of Natural History*, 2004, 36: 3–13); studies of what were the oldest-known specimens when I started writing this chapter, from Saskatchewan, written by Richard Fox and Craig Scott (*Journal of Paleontology*, 2011, 85: 537–48; *Canadian Journal of Earth Sciences*, 2016, 53: 343–54); a study on what became the oldest-known specimen when I revised this chapter, from Montana, written by Greg Wilson, Stephen Chester, Bill Clemens, and colleagues (*Royal Society Open Science*, 2021, 8: 210050); and Stephen’s paper, with colleagues including Bill Clemens, describing ankle bones that show it was a capable climber (*Proceedings of the National Academy of Sciences [USA]*, 2015, 112: 1487–92).

Leigh’s great insight was that *Purgatorius*—which lived so soon after the end-Cretaceous extinction—was an early plesiadapiform, and thus an early primate. Earlier paleontologists had recognized the link between later-living plesiadapiforms and primates, including James Gidley (*Proceedings of the US National Museum*, 1923, 63: 1–38) and our recurring mammal phylogeneticist, George Gaylord Simpson (*American Museum Novitates*, 1935, 817: 1–28; *United States National Museum Bulletin*, 1937, 169: 1–287; *Bulletin of the American Museum of Natural History*, 1940, LXXVII: 185–212).

Mary Silcox has published widely on plesiadapiforms and early primates. Her 2001 PhD, at Johns Hopkins University, included a large phylogenetic analysis that corroborated Van Valen’s, Gidley’s, and Simpson’s earlier hypotheses that plesiadapiforms are primates. I do note here that some workers, including Christopher Beard and Xijun Ni, have argued that some plesiadapiforms might be more closely related to dermopterans (the “flying lemurs”) than primates. Mary and Sergi López-Torres review these debates in their masterful and enjoyable review of primate origins and early evolution, published in 2017 in *Annual Review of Earth and Planetary Sciences* (45: 113–37). She also collaborated with Gregg Gunnell to pen a more detailed review of plesiadapiform

taxonomy, anatomy, and evolution, published as a chapter in the 2008 book *Evolution of Tertiary Mammals of North America: Volume 2* (Cambridge University Press), and then a later review in 2017 (*Evolutionary Anthropology*, 26: 74–94). She published her work on plesiadapiform and early primate brain evolution in *Proceedings of the National Academy of Sciences (USA)* in 2009 (106: 10987–92). This was followed by another important study on plesiadapiform brains, by Maeva Orliac and colleagues (*Proceedings of the Royal Society, Series B*, 2014, 281: 20132792).

Other important plesiadapiform studies alluded to in the text are the descriptions of the *Torrejonia* skeleton, which was discovered by Tom Williamson and his sons Ryan and Taylor (Chester et al., *Royal Society Open Science*, 2017, 4: 170329); Jonathan Bloch and Doug Boyer's description of the Eocene-aged *Carpolestes* with long fingers and opposable toes (*Science*, 2002, 298: 1606–10); and Bloch's paper (with Mary, Doug Boyer, and Eric Sargis) on Paleocene plesiadapiform locomotion and phylogeny (*Proceedings of the National Academy of Sciences [USA]*, 2007, 104: 1159–64). While all bona fide plesiadapiforms are thus far Paleocene or younger, DNA-based phylogenies of primates imply a Cretaceous origin (see, for example, Springer et al., *PLoS ONE*, 2012, 7[11]: e49521).

The evolution, diversification, and dispersal of lemurs is fascinating. Gregg Gunnell and colleagues presented evidence for multiple dispersals to Madagascar (*Nature Communications*, 2018, 9: 3193), which Ali and Huber showed would have been possible on eastward-moving currents implied by ocean circulation models for that time (*Nature*, 2010, 463: 653–56).

Interesting sources on Oligocene primate evolution across the world include studies on Europe (Köhler and Moyà-Solà, *Proceedings of the National Academy of Sciences [USA]*, 1999, 96: 14664–67); Asia (Marivaux et al., *Science*, 2001, 294: 587–91; Marivaux et al., *Proceedings of the National Academy of Sciences [USA]*, 2005, 102: 8436–41; Ni et al., *Science*, 2016, 352: 673–77); Africa (Stevens et al. *Nature*, 2013, 497: 611–14); and the Middle East (Zalmout et al. *Nature*, 2010, 466: 360–64). The issue of New World monkeys and their lack of dispersal northward is discussed by Bloch et al. (*Nature*, 2016, 533: 243–46).

The early evolution of apes and close relatives has been reviewed by Williams et al. (*Proceedings of the National Academy of Sciences [USA]*, 2010, 107: 4797–4804). The divergence between chimps and humans, and its complex nature and timing, is discussed by Kumar et al. (*Proceedings of the National Academy of Sciences [USA]*, 2005, 102: 18842–47) and Patterson et al. (*Nature*, 2006, 441: 1103–08). The chimpanzee genome was fully sequenced in 2005 and is extremely similar to our genome (Mikkelsen et al., *Nature*, 431: 69–87).

The deeper origins of human's tyle bipedalism—or at least its first wobbly start—among apes is a subject of deep contention. I point readers in the direction of papers by Thorpe et al. (*Science*, 2007, 316: 1328–31) and Böhme et al. (*Nature*, 2019, 575: 489–93).

This is not a book about humans! It is a book about all mammals, including humans, which is why I give only a single chapter to us and our hominin kin. There is an *enormous* literature on early human evolution, so here I will keep this section to key books and papers that helped me shape my narrative.

To start, I will mention that there are several recent books on human evolution that are excellent, among them: *Fossil Men* by Kermit Pattison (William Morrow, 2020), which chronicles Tim White and Berhane Asfaw's work in Ethiopia, and from which I gleaned the story of Gadi and his *Ardipithecus* discovery; *Sediments of Time* by Meave Leakey (Houghton Mifflin Harcourt, 2020), an autobiography by the once's cion and now-matriarch of the great Leakey paleoanthropology dynasty; *The World Before Us* by Tom Higham (Viking, 2021), which is a meticulous outline of the timing of human origins and migrations and how we know these things based on DNA evidence and dating of rocks; *The Origin of Our Species* (Allen Lane, 2011) and *Lone Survivors* (Melia, 2012) by Chris Stringer of the Natural History Museum, a great popularizer of paleoanthropology; and *Almost Human* by Lee Berger and John Hawkes (National Geographic, 2017). *Nature* editor and fine writer Henry Gee provides a breezy and fun overview of human evolution in his book *A (Very) Short History of Life on Earth* (St. Martin's Press, 2021). For a slightly more iconoclastic take on the early evolution of apes and humans, check out Madeleine Böhme's *Ancient Bones* (Greystone Books, 2020). I also recommend anything written by Kate Wong of *Scientific American*, the leading journalistic sage on human origins, and one of my favorite editors.

The following is a breakdown of important references on early hominins mentioned in the text, their biology and evolution, and their world.

Ardipithecus: Kermit Pattison's book (cited above) is a magnificent work of journalism and explains the discovery and importance of *Ardipithecus* in detail. Tim White, Gen Suwa, and Berhane Asfaw named the species *ramidus*, based on Gadi's initial discovery of the teeth (which they credited as “found by Gada Hamed on Wednesday 29 December 1993”) in *Nature* in 1994 (371: 306–12). They initially placed *ramidus* in the genus *Australopithecus*, but the next year reassigned it to the new genus *Ardipithecus*, in a short follow-up in *Nature* (375: 88). The *Ardipithecus* skeleton—which was found near Gadi's original teeth, but belongs to a different individual—was described in detail in a special issue of *Science*, published on October 2, 2009 (vol. 326).

Australopithecus: The discovery of the Lucy skeleton is told with gusto in Donald Johanson's books of the Lucy series, the first of which was published in 1981. Johanson and Tim White scientifically described the Lucy skeleton in a 1979 paper in *Science* (203: 321–30). The footprints mentioned in the text are the famous Laetoli trackways, discovered by the eminent Mary Leakey in the mid 1970s. The brain of *Australopithecus* was studied by Phillip Gunz and colleagues in 2020 (*Science Advances*, 6: eaaz4729). Other important papers on *Australopithecus*, its age and origination, and the many species assigned to it include those by Leakey et al. (*Nature*, 1995, 376: 565–71; *Nature*, 1998, 393: 62–66), Asfaw et al. (*Science*, 1999, 284: 629–35), White et al. (*Nature*, 2006, 440: 883–89), Berger et al. (*Science*, 2010, 328: 195–204), Haile-Selassie et al. (*Nature*, 2015, 521: 483–88; *Nature*, 2019, 573: 214–19).

Other early hominins before *Homo*: A summary of the many human species coexisting in the Pliocene are provided by Haile-Selassie et al. (*Proceedings of the National Academy of Sciences [USA]*, 2016, 113: 6364–71) and a commentary piece by Fred Spoor in *Nature* accompanying the Haile-Selassie et al. (2015) paper cited above; both articles contain useful timelines showing which human species were living when. The environments that these early hominins lived in—and the issue of shrinking forests and growing grasslands—has been examined by Cerling et al. (*Nature*, 2011, 476: 51–56). The hard-object-feeding hominins mentioned in the text are the “robust australopithecines,” which are usually assigned to the genus *Paranthropus*. Meave Leakey and her team described the flat-faced *Kenyanthropus* in 2001 (*Nature*, 410: 433–40). The oldest stone tools are found in the vicinity of these hominins, although it is difficult to prove that they, and not another early human species, were the stonemasons (Harmand et al., *Nature*, 2015, 521: 310–15). The oldest tool cut marks on bone are slightly older and were described by McPherron et al. (*Nature*, 2010, 466: 857–860). I note here that distinguishing between human cut marks and animal bites can be difficult, leading to debate about the marks described by McPherron et al. and others (see, for example: Sahle et al., *Proceedings of the National Academy of Sciences [USA]*, 2017, 114: 13164–69). The origin of meat-eating, and how it was a game-changer for hominins, is elucidated by Zink and Lieberman (*Nature*, 2016, 531: 500–503). The diversity of African environments settled by early hominins is discussed by Mercader et al. (*Nature Communications*, 2021, 12:3).

Early *Homo*: The evolution of early *Homo* is reviewed by Antón et al. (*Science*, 2014, 345: 6192). Currently, the oldest-known fossils of our genus, *Homo*, are 2.8 million years old, come from Ethiopia, and were described by Brian Villmoare and colleagues (*Science*, 2015, 347: 1352–55). However,

the oldest-known fossils often underestimate the actual date of origin of a species. My PhD student Hans Püschel led a study—which also includes his brother Thomas, a noted human evolution expert, and my postdoc Ornella Bertrand—that used statistical techniques to predict that *Homo* most likely diverged around 3.3 million years ago, and perhaps as long as 4.3 million years ago (*Nature Ecology & Evolution*, 2021, 5, 808–19). The environments of the earliest *Homo* fossils were outlined by Erin DiMaggio and team (*Science*, 2015, 347: 1355–59), and later by Zeresenay Alemseged and colleagues (*Nature Communications*, 2020, 11: 2480).

Homo erectus: The violent nature of early humans is the subject of an interesting paper by Gomez et al. (*Nature*, 2016, 538: 233–37), which uses phylogenetic methods to put humans into the context of animals broadly, demonstrating that we come from a particularly violent part of the family tree. For information on how humans began to use fire, consult Gowlett (*Philosophical Transactions of the Royal Society, Series B*, 2016, 371: 20150164). The beautiful stone tools of *Homo erectus* are those of the Acheulian type. Information on locomotion and sociality in *Homo erectus* is covered by Hatala et al. (*Scientific Reports*, 2016, 6: 28766). Evidence for the mixing of *Homo erectus* and *Australopithecus* (and *Paranthropus* too!) in southern Africa is presented by Herries et al. (*Science*, 2020, 368: eaaw7293). The oldest Asian *Homo* fossils were described by Zhu et al. (*Nature*, 2018, 559: 608–12), and the circa 750,000-year-old age of the Peking Man fossils from Beijing were determined with clarity by Shen et al. (*Nature*, 2009, 458: 198–200). The oldest *Homo* fossils from the Philippines were described by Ingicco et al. (*Nature*, 2018, 557: 233–37); *Homo luzonensis* was described by Détroit et al. (*Nature*, 2019, 568: 181–86); and *Homo floresiensis* was described by Brown et al. (*Nature*, 2004, 431: 1055–61) and in many subsequent papers, and its age was accurately determined by Sutikna et al. (*Nature*, 2016, 532: 366–69), and earlier *floresiensis*-like fossils were described from about 700,000 years ago on Flores by van den Bergh et al. (*Nature*, 2016, 534: 245–48). Best indications are that both Flores and Luzon were far enough offshore from the Southeastern Asian mainland, and separated by deep enough water, that they would have required a cross-water journey even during times of low sea level in the Ice Age. While it seems most plausible to me that early *Homo* constructed watercraft, it is possible that they passively rafted on mats of vegetation after storms, like those New World monkeys that crossed the Atlantic.

I note here that, based on current evidence, it seems that *Homo erectus* was the first hominin to leave Africa. However, our fossil record is poor, and new discoveries are coming fast. It may be that earlier hominins ventured out

of Africa, and even deep into Asia. Who knows what the latest discoveries will be?

Homo sapiens: The currently oldest-known fossils of our species, *Homo sapiens*, come from Morocco and were described by Hublin et al. (*Nature*, 2017, 546: 289–92), and their age by Richter et al. (*Nature*, 2017, 546: 293–96). Our concept of *sapiens* origins is getting really complicated really fast, and older ideas about our species cleanly breaking from other *Homo* have been replaced by a pan-Africa network model, in which populations swapped genes and features until a modern-type *sapiens* body plan became fixed. It can be difficult to understand—for me, too, as I am used to thinking about anatomical features of fossils and not their genetic variation. For more information, please consult the excellent essays of Eleanor Scerri and colleagues (*Trends in Ecology & Evolution*, 2018, 33: 582–94; *Nature Ecology & Evolution*, 2019, 3: 1370–72), Chris Stringer (*Philosophical Transactions of the Royal Society, Series B*, 2016, 371: 20150237), two from Chris Stringer and Julia Galway-Witham in which they swapped first-authorship (*Nature*, 2017, 546: 212–14; *Science*, 2018, 360: 1296–98), a great review of *Homo* evolution over the last million years by Galway-Witham, Stringer, and James Cole (*Journal of Quaternary Science*, 2019, 34: 355–78), and a review of modern human origins published as I was writing this chapter (Bergström et al., 2021, *Nature* 590: 229–37).

Early *Homo sapiens*, and their close *Homo* relatives, migrated widely around Africa and the Mediterranean region (Middle East, Caucasus, parts of Europe). Timmermann and Friedrich explored how these migrations were likely driven by climate (*Nature*, 2016, 538: 92–95). The oldest reported European *Homo sapiens* fossils, from Greece, were described by Katerina Harvati and colleagues (*Nature*, 2019, 571: 500–504). As always, the relevance of these fossils comes down to the dating, as my colleague Huw Groucutt reminds me, and the quite old (ca. 210,000) dates for this Greek fossil need to be corroborated by other discoveries. It is undoubted, however, that by around 120,000 to 100,000 years ago some *Homo sapiens* were leaving Africa. Other important papers on early European *Homo sapiens*, and the close *Homo* relatives that were migrating around the same time, include those by Grun et al. (*Nature*, 2020, 580: 372–75) and Hublin et al. (*Nature*, 2020, 581: 299–302). Neanderthals, Denisovans, and *Homo sapiens* diverged from a common *Homo* ancestor, most likely between approximately 550,000 and 765,000 years ago (see: Prüfer et al., *Nature*, 2014, 505: 43–49; Meyer et al., *Nature*, 2016, 531: 504–7). This ancestor may have been a species like *Homo antecessor* or *Homo heidelbergensis*, or a very close relative; recently ancient proteins from *Homo antecessor*, *Homo*

erectus, *Homo sapiens*, Neanderthals, and Denisovans have been compared, to build a family tree (Welker et al., *Nature*, 2020, 580: 235–38). Although this part of our family tree is extremely convoluted, what is clear is that the various *Homo* species were moving and interacting.

The big, globular brain of *Homo sapiens* appears to not only be a key part of our signature species body plan, but perhaps it helped bring about advances in our toolmaking and cognition. Brain evolution in *Homo sapiens* has been chronicled by Simon Neubauer and colleagues (*Science Advances*, 2018, 4: eaoo5961). Information on human cognitive evolution was gleaned from an essay by the noted anthropologist Richard Klein (*Evolutionary Anthropology*, 2000, 28: 179–88) and a review by McBrearty and Brooks (*Journal of Human Evolution*, 2000, 39: 453–563). My paleoanthropology colleagues Huw Groucutt, Bob Patalano, and Eleanor Scerri explained to me how once-popular ideas about a sudden “cognitive revolution” are now outdated (and based largely on the European archaeological record), and instead the African record shows that different groups of early *Homo sapiens* developed advances in technology and brainpower in a mosaic fashion over many tens of thousands of years, and these coalesced as *sapiens* populations expanded, migrated, and mixed. One prime example of an African record of symbolic and technological advances, from Kenya, was presented by Shipton et al. (*Nature Communications*, 2018, 9: 1832).

For those interested in when and how *Homo sapiens* populated North and South America after traversing the Bering Land Bridge, the recent review essay by Michael Waters is an excellent read (*Science*, 2019, 365: eaat5447). Traditionally, a date of around 15,000 years ago has been widely considered as the time *sapiens* crossed the land bridge, but there have been several tantalizing clues of older humans in the Americas, both fossils and artifacts. Two prime candidates pushing the arrival of humans earlier, between 20,000 and 30,000 years ago, were published in 2020 (Ardelean et al., *Nature*, 584: 87–92; Becerra-Valdivia and Higham, *Nature*, 584: 93–97). This active debate has important implications for the question of whether humans caused the extinction of the megafauna mammals, as much of that debate comes down to timing of human migration and settlement (see below). One of the latest papers on when humans first reached Australia—perhaps by 65,000 years ago—is a study from Clarkson et al. (*Nature*, 2017, 547: 306–10). A review of *Homo sapiens* migrations to Asia—including evidence for meanderings prior to the large wave “out of Africa” 50,000–60,000 years ago—was penned by Bae et al. (*Science*, 2017, 358: eaai9067).

Neanderthals: As I was writing, a fantastic book about Neanderthals was

published by Rebecca Wragg Sykes, *Kindred* (Bloomsbury, 2020). It is a one-stop shop for everything you need to know about these close *Homo* cousins that we interbred with. Other references relevant to specifics mentioned in my text are papers on Neanderthal origins (Arsuaga et al., *Science*, 2014, 344: 1358–63), their cave constructions (Jaubert et al., *Nature*, 2016, 534: 111–14), and their cave art and use of pigments (Roebroeks et al., *Proceedings of the National Academy of Sciences [USA]*, 2012, 109: 1889–1984; Hoffmann et al., *Science*, 2018, 359: 912–15; Hoffmann et al., *Science Advances*, 2018, 4: eaar5255).

Denisovans: The very existence of these near-*sapiens* relatives was recognized in 2010, by David Reich, Svante Pääbo, and colleagues (*Nature*, 468: 1053–60). Reich, an eminent expert on the genetics of ancient *Homo* populations and how to extract this information from fossils and archaeological materials, wrote a book in 2018 on this subject (*Who We Are and How We Got Here*, Pantheon). Denny—the Denisovan and Neanderthal hybrid—was described in 2018 by Viviane Slon, Pääbo, and their team (*Nature*, 561: 113–16). The age of the Denisova Cave specimens was explained by Douka et al. (*Nature*, 2019, 565: 640–44). Other important papers on Denisovan DNA, their population structure, and how their genes have endured in Asian *Homo sapiens* populations today include studies by Meyer et al. (*Science*, 2012, 338: 222–26), Huerta-Sánchez et al. (*Nature*, 2014, 512: 194–97), Malaspinas et al. (*Nature*, 2016, 538: 207–14), Chen et al. (*Nature*, 2019, 569: 409–12), Massilani et al. (*Science*, 2020, 370: 579–83), and Zhang et al. (*Science*, 2020, 370: 584–87).

Landmark studies on the genetics of modern *Homo sapiens*, and how Neanderthal and Denisovan DNA remains in our genome, were published by the Simons Genome Diversity Project in 2016 (Mallick et al., *Nature*, 538: 201–6) and Pagani et al. (*Nature*, 2016, 538: 238–42). For a readable review of human migrations and interbreeding over time, and how these can be traced by ancient DNA analysis, check out the *Nature* essay by Rasmus Nielsen and colleagues (2017, 541: 302–10). When it comes to a readable and thought-provoking big history of *Homo sapiens*, I enjoyed Yuval Noah Harari’s *Sapiens* (Vintage, 2015), although I can’t vouch for how accurate and up-to-date its discussions of early human archaeology are, and I didn’t use it as source material for this chapter.

The extinction of the megafauna is expertly and tactfully tackled by Ross MacPhee in his book *End of the Megafauna* (W.W. Norton & Company, 2019), which cites all the most important literature on the subject. Excellent and digestible reviews on the subject are papers by Anthony Barnosky and colleagues (*Science*, 2004, 306: 70–75) and Paul Koch and Barnosky (*Annual Review of Ecology, Evolution, and Systematics*, 2006, 37: 215–50).

Paul Martin presented his idea of blitzkrieg in a 1973 paper in *Science* (179: 969–74), and fully fleshed it out in his popular book *Twilight of the Mammoths* (University of California Press, 2005). Some paleontologists and ecologists have pushed back and have targeted climate change as the cause of the extinctions. This is well articulated in a 2013 essay by Stephen Wroe and colleagues (including our old friend Michael Archer from chapter 8) published in *Proceedings of the National Academy of Sciences (USA)* (110: 8777–81), and a paper published after I wrote this chapter (Stewart et al., *Nature Communications*, 2021, 12: 965). For a balanced and critical review of the subject, check out the essay by David Meltzer (*Proceedings of the National Academy of Sciences [USA]*, 2020, 117: 28555–63).

The most recent studies, from a global perspective, present strong evidence that humans were the overriding cause of the extinctions, which in some cases were exacerbated by climate changes during the last glacial-interglacial transition (Sandom et al., *Proceedings of the Royal Society, Series B*, 2014, 281: 20133254; Bartlett et al., *Ecography*, 2016, 39: 152–61; Araujo et al., *Quaternary International*, 2017, 431: 216–22). More focused studies on particular landmasses also have identified humans as the main factor in the extinction, including those in Australia and adjoining lands (Rule et al., *Science*, 2012, 335: 1483–86; Johnson et al., *Proceedings of the Royal Society, Series B*, 2016, 283: 20152399; Saltré et al., *Nature Communications*, 2016, 7: 10511) and South America (Barnosky et al., *Quaternary International*, 2010, 217: 10–29; Metcalf et al., *Science Advances*, 2016, 2: e1501682; Polis et al., *Science Advances*, 2019, 5: eaau4546). The scintillating study of how humans may have coalesced extirpations started by warming shifts in the northern Holarctic was published by Cooper et al. (*Science*, 2015, 349: 602–6).

On the subject of domestication, scientist and ace science popularizer Alice Roberts wrote a book, *Tamed* (Hutchinson, 2017), that profiles ten major domesticated species, including dogs, cows, and horses, and key agricultural cultivars. Important works on the domestication of dogs include papers by Ní Leathlobhair et al. (*Science*, 2018, 361: 81–85) and Perri et al. (*Proceedings of the National Academy of Sciences [USA]*, 2021, 118: e2010083118). The numbers I cite for the percentage of domesticated mammal biomass on Earth today come from Bar-On et al. (*Proceedings of the National Academy of Sciences [USA]*, 2018, 115: 6506–11).

On the subject of mammoth cloning, I recommend Beth Shapiro's book *How to Clone a Mammoth* (Princeton University Press, 2015) and Helen Pilcher's book *Bring Back the King* (Bloomsbury, 2016), along with the section on cloning in Ross MacPhee's book (cited above).

EPILOGUE: FUTURE MAMMALS

The numbers on mammal extinctions over the last approximately 125,000 years, and predicted extinctions in the future, come from a study by Tobias Andermann and colleagues (*Science Advances*, 2020, 6: eabb2313). Figures for rates of background and current mammal extinction come from a study by Gerardo Ceballos and team (*Science Advances*, 2015, 1: e1400253). The prediction that if all currently threatened mammals go extinct then half the diversity from 125,000 years ago will be gone comes from a study by Felisa Smith and colleagues (*Science*, 2018, 360: 310–13). This study also explores body size trends in mammalian extinctions and makes the prediction that future mammal communities will be more homogenized and overrun with rodents, and that the largest mammals of the future might be domestic cows. Recovery rates for mammals, if the extinctions were to cease, are discussed by Davis et al. (*Proceedings of the National Academy of Sciences [USA]*, 2018, 115: 11262–67), and predictions for what mammal communities of the future will look like (hint: overrun with small, fast-living, fast-breeding, insect-eating generalists, like rodents) are given by Cooke et al. (*Nature Communications*, 2019, 10: 2279). Mammal migration patterns with climate change are detailed in a paper by Silvia Pineda-Munoz and team (*Proceedings of the National Academy of Sciences [USA]*, 2021, 118(2): e1922859118).

Other useful and interesting studies on how human activities have impacted mammalian communities and ecosystems are papers by Faurby and Svenning (*Diversity and Distributions*, 2015, 21: 1155–66), Boivin et al. (*Proceedings of the National Academy of Sciences [USA]*, 2016, 113: 6388–96), Lyons et al. (*Nature*, 2016, 529: 80–83), Smith et al. (*Quaternary Science Reviews*, 2019, 211: 1–16), Tóth et al. (*Science*, 2019, 365: 1305–08), and Enquist et al. (*Nature Communications*, 2020, 11: 699).

There is a huge literature on climate and temperature change, and how humans are causing it. In general, I point interested readers in the direction of the United Nations Intergovernmental Panel on Climate Change reports, which can be accessed at <https://www.ipcc.ch/>. The projections for temperature rise over the next few centuries, and comparisons with Pliocene and Eocene climates, come from papers by Burke et al. (*Proceedings of the National Academy of Sciences [USA]*, 2018, 115: 13288–93) and Westerhold et al. (*Science*, 2020, 369: 1383–87).

The Sixth Extinction is the subject of Elizabeth Kolbert's Pulitzer Prize-winning book of the same title (Henry Holt and Company, 2014), and an excellent review by Anthony Barnosky and colleagues (*Nature*, 2011, 471: 51–57). It is also covered in detail by Peter Brannen in his book *The Ends of*

the World (Ecco, 2017), from which I took the collapsing power grid analogy. You might note that I don't use the term *Anthropocene* in my narrative. This formal name has been proposed for the subdivision of the geological time scale during which humans have significantly impacted the planet. But when all is said and done, I don't think human activities will leave much of a mark in the rock record at all. It was one of Brannen's articles in the *Atlantic*, entitled "The Arrogance of the Anthropocene" (2019), that convinced me once and for all.

Finally, for accuracy's sake I must state that I do know why the Chicago Bears were thus named. It is because many early professional American football teams were named after baseball teams in the same city, so the Bears were named in reference to the Chicago Cubs. As a White Sox fan, who went to school on the South Side and comes from a long line of south suburban family, this pains me. For many years I thought our human species would go extinct before the Cubs won another World Series, but alas, 2016.