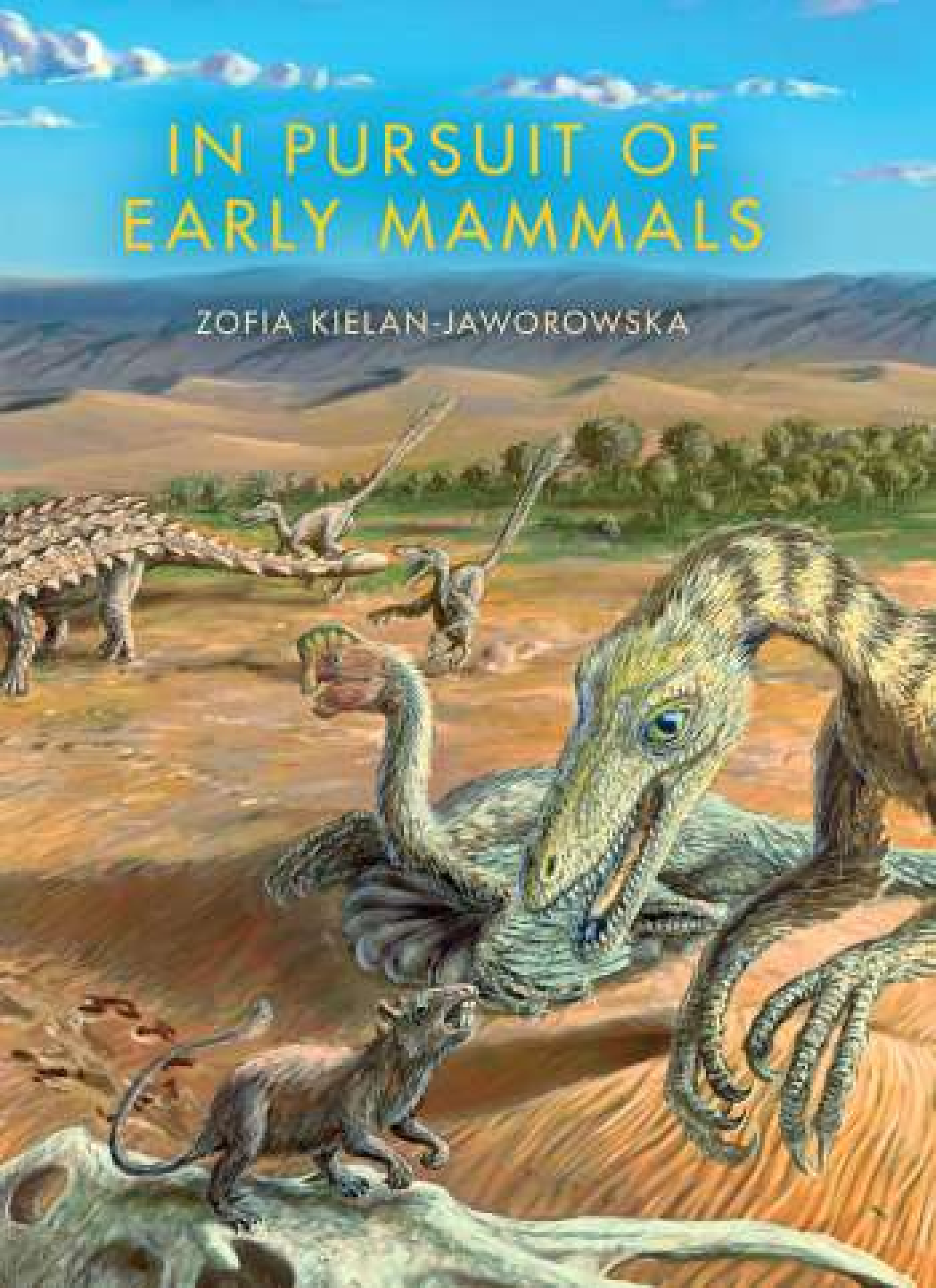
IN PURSUIT OF EARLY MAMMALS

ZOFIA KIELAN-JAWOROWSKA



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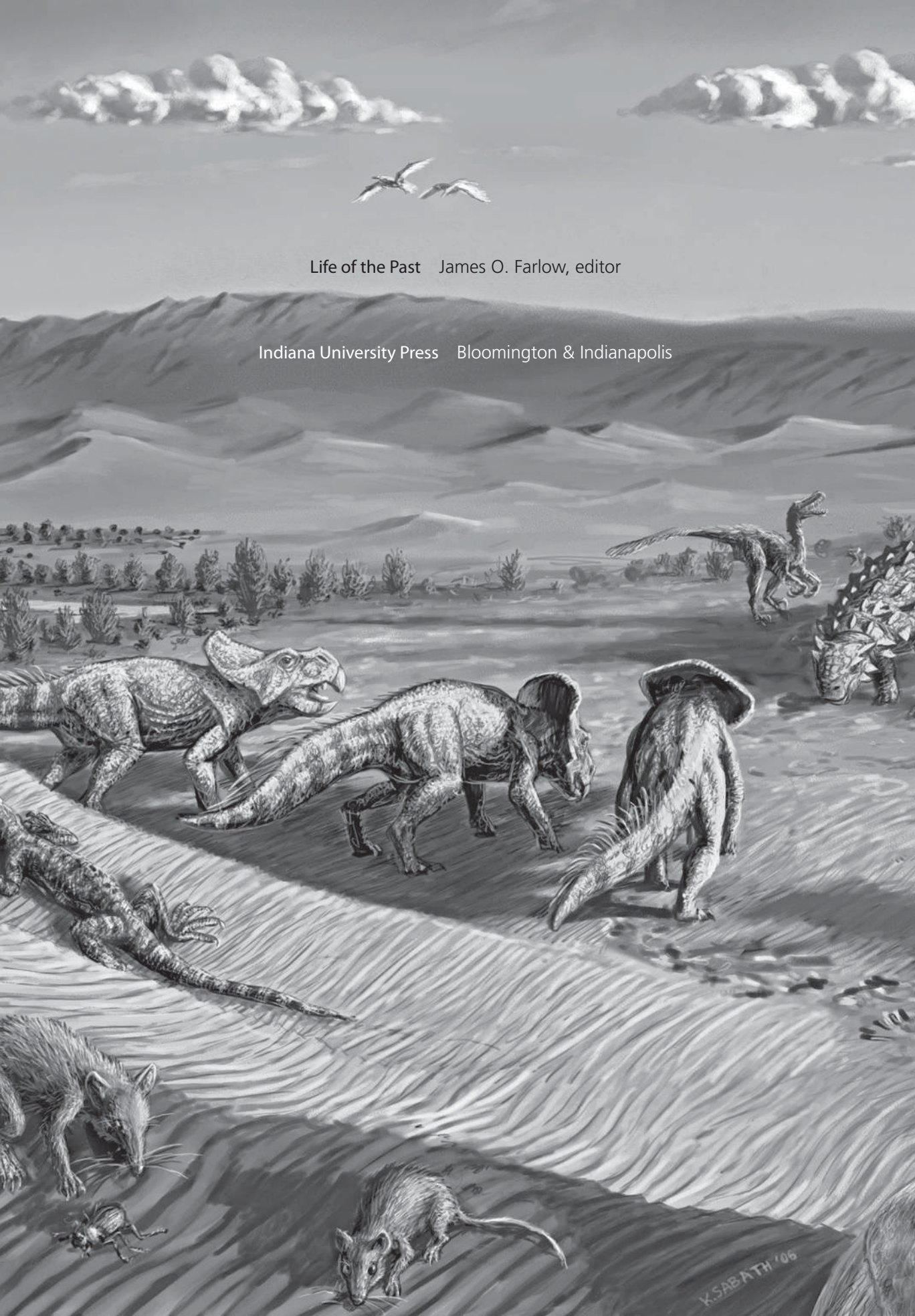

Life of the Past James O. Farlow, editor

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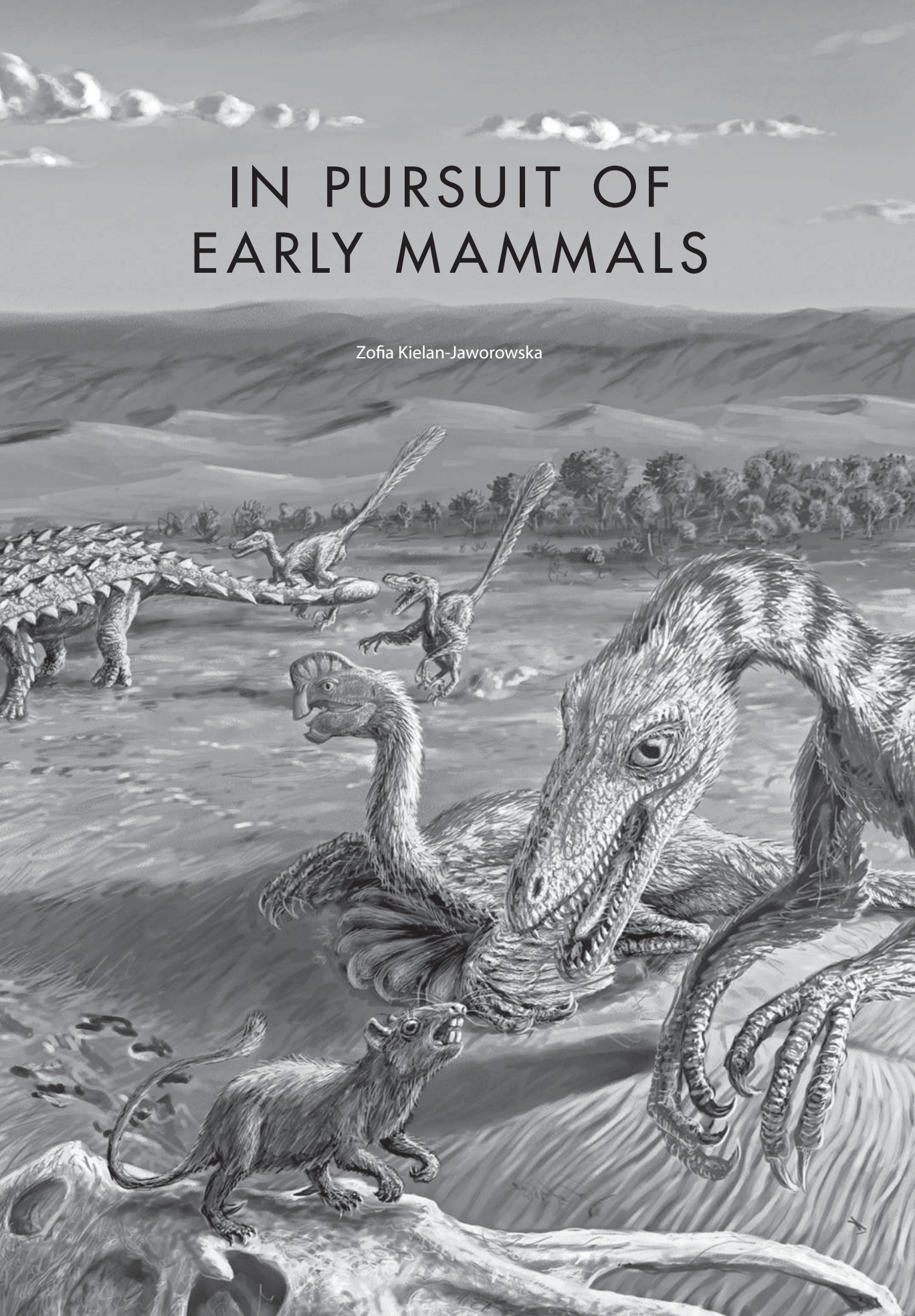

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I dedicate this book to the memory of my husband

ZBIGNIEW JAWOROWSKI

(17 October 1927–12 November 2011)

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Foreword

F

SINCE THE DEMISE OF NON-AVIAN DINOSAURS SOME 65 MILLION years ago, modern mammals—that is to say, marsupials, placentals, and monotremes—have become conspicuous, diverse elements of Earth's biota. But the family tree that includes mammals and their nearest relatives (mammaliaforms, in technical parlance) is far more deeply rooted in time, extending back to perhaps 220 million years ago. Clearly, then, the varieties known from the "age of mammals" that followed dinosaur extinctions represent only the uppermost boughs of what is increasingly being revealed as a bushy, complex tree.

Knowledge of early mammalian history—the lower part of that tree—has long been limited by a fossil record that is disappointingly sparse, even to those paleontologists who set a low bar when it comes to basic data. Fossils are generally tiny, fragmentary (most species are known by isolated teeth or jaw fragments), and incredibly hard to find. The dawn of discovery took place in the late nineteenth century. Synthetic study of these fossils, almost all from Britain and the western United States, was completed in the 1920s by the great evolutionary biologist G. G. Simpson. It was also at this time that the first mammalian skulls of Mesozoic age were discovered in Cretaceous rocks of Mongolia. Simpson recognized the existence of various now-extinct Mesozoic mammal lineages, as well as representatives (or, it now appears, relatives) of modern groups. But this early period of discovery and study raised fundamental questions that could not be addressed with the existing record. Did the egg-laying platypus and echidnas of Australia and New Guinea, for example, independently evolve from "reptilian" precursors? Meaningful biological interpretation also remained beyond reach: about all one could say is that early mammals were generally small, shrew-like creatures that probably preferred an insect-based diet. (The stereotype has persisted: as this book shows, it is erroneous.) Early mammal history had emerged from total darkness, but remained in the shadows.

The situation has changed profoundly in recent decades. A new period of fossil discovery began in the mid-twentieth century and its pace has quickened to a dizzying rate. A number of species are now known by breathtakingly complete specimens, some even preserving remnants of fur. Long-term, dedicated effort has resulted in the collection of large samples and comprehensive assemblages for some areas and time intervals. Informative fossils have been recovered from most major landmasses, and though substantial gaps in the record persist, much of the Mesozoic time scale has been sampled. And, of course, many

new species and some major groups have been discovered, revealing previously unimagined diversity among early mammals: some hopped; others climbed, burrowed, swam, and even glided; at least one species fed on young dinosaurs. Amazingly, a venom-delivery system (in the form of an ankle spur as seen in living monotremes) seems to have been widespread among early groups. This explosive growth in basic data—the fossils themselves—has been coupled with important conceptual, technological, and methodological advances. Ultrahigh-resolution X-ray computed tomography, for example, has made accessible a wealth of new anatomical information. Comparative studies of new fossils show that early mammals played a broad array of biological roles. Key evolutionary transformations, such as the appearance of the multi-function molar, expansion of the brain, and the development of the characteristic three-boned middle ear, are now relatively well understood. Notably, it appears that each of these transformations took place more than once in mammalian history. The fossil record now provides reasonable time constraints on the divergence of modern lineages—constraints that are consistent with estimates derived from molecular studies based on living species. Perhaps most significantly, new means of reconstructing genealogy have provided the outlines and many details of the mammalian tree mentioned earlier, and there is now general consensus about placement of many of the major branches on that tree.

Now, finally, we know enough about Mesozoic mammals that a general book on the subject is not only possible, but urgently needed. This volume serves that purpose. The author, Zofia Kielan-Jaworowska, has been at the vanguard of the field for half a century. In the following pages she recounts the origin, evolutionary history, relationships, and biology of early mammals—largely from firsthand experience in both field and lab. More than that, she tells us about the people who have discovered and studied the fossils unearthed during the modern era. No field program has contributed more to—or symbolizes better—this modern era of discovery than the now-legendary Polish-Mongolian Expeditions (1963–1971), which Kielan-Jaworowska herself led. Here she gives us a compelling personal account of those remarkable journeys—the logistics, hazards, setbacks, and successes, together with a behind-the-scenes tour of subsequent research that shed important new light on early mammals.

Where do we go from here? We now have a rough outline of mammalian history during the Mesozoic. That outline is still very much a work in progress. Simple logic tells us that "state-of-the-art" is, after all, just a state; and the history of science provides us with ample evidence that states of understanding are ephemeral. Despite all that we have learned in the past half-century, the data remain scant: significant as they are, the advances reported on these pages represent approximately charted islands of a barely explored sea. The study of Mesozoic mammals is ripe with opportunity. Single new specimens can overturn decades of established wisdom. Fundamental new interpretation and understanding will

depend on the discovery of new fossils and the adoption of new perspectives. May this book inspire the next generation of paleontologists to set out in pursuit of early mammals!

Richard L. Cifelli

Preface

P

THIS BOOK PRESENTS A HISTORY OF MESOZOIC MAMMALS AS SEEN through the eyes of people studying them, including myself and the colleagues with whom I had a chance to work over the years. The Mesozoic Era was the time when dinosaurs ruled the earth. Mammals living with them were mostly small, and it seemed for a long time that they did not play an important role in Mesozoic faunas. But in recent decades our view has changed. Thanks to new methods of searching for them, and new expeditions organized to countries from which they previously were unknown, or hardly known, new collections of Mesozoic mammals have been gathered and studied.

In contrast to my earlier book *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*, which I wrote in collaboration with Richard L. Cifelli and Zhe-Xi Luo (2004), in which we used the traditional definition of Mammalia including extinct groups outside the crown group, in the present book I follow the high-rank systematics of Rowe (1988) and McKenna and Bell (1997). The crown group, as defined by Jeffries (1989), consists of the living members of a monophyletic group, their latest living ancestor, and all descendants of that ancestor. Mammalia are thus restricted to the three crown groups living today (placentals, marsupials, and monotremes), their common ancestor, and all the intermediate forms.

I do not explain anatomical terms in this book, referring readers instead to the *Nomina Anatomica Veterinaria* (International Committee on Veterinary Gross Anatomical Nomenclature 2012) and to the very useful books by Schaller (1992) and Evans (1995). In a few cases I have included drawings that display specialized terminology (for example, figures 5.2 and 14.2) in order to demonstrate the extent to which paleontologists are sometimes obliged to study the details of anatomy of various fossil mammals in order to understand the relationships among fossil and extant mammals.

For characters of the skull that do not occur in extant mammals I follow Kielan-Jaworowska et al. (1986, 2004); for the postcranial skeleton I use as guides Kielan-Jaworowska and Gambaryan (1994) and Hurum and Kielan-Jaworowska (2008). For the description of muscle reconstructions I follow the terminology of Kielan-Jaworowska and Gambaryan (1994).

I have also not explained the terms of phylogenetic systematics, referring readers to the original book by Hennig (1966), the book by Wiley (1981), a very useful article by Carlson (2001), and numerous articles published in such journals as *Systematic Zoology* and other specialist journals

not cited here. As a rule I do not provide museum catalog numbers of the discussed specimens, but there are a few exceptions concerning, in particular, the holotypes.

Transcription of Mongolian names follows that suggested by Benton (2000), and hence I use, for example, Hermiin Tsav locality and beds, rather than Khermeen Tsav, which was used in previous papers. I have tried to avoid using anatomical abbreviations in figures and in the text, except for the teeth, and I use I, C, P, M, for upper incisors, canines, premolars, and molars, respectively, and i, c, p, m for corresponding lower teeth. Other anatomical abbreviations that I use are for metacarpal bones, for example, Mc I–V, and for metatarsals Mt I–V. I cite paraphyletic taxa in quotation marks.

Most of the photographs of persons studying early mammals have been kindly provided by the individuals in the photographs, and in such cases I do not credit these photos. There are few exceptions in which the photos have been provided by someone else, and in such cases I acknowledge the names of persons providing the photographs.

Acknowledgments

A

DURING THE MORE THAN SIXTY YEARS OF MY SCIENTIFIC LIFE, I have had the opportunity to collaborate with numerous eminent scientists, many of whom have now passed away. From my late colleagues, friends, and teachers, I learned much and enjoyed our cooperation. They are (in alphabetic order): Demberlyin Dashzeveg, Antoni Bolesław Dobrowolski, Beverly Halstead, Karen Hiiemae, Farish A. Jenkins, Anna Jerzmańska, Doris M. Kermack, Kenneth A. Kermack, Kazimierz Kowalski, my dear teacher and supervisor of my earlier work Roman Kozłowski, Walter G. Kühne, Henryk Makowski, Malcolm C. McKenna, Vincent L. Morgan, Lev A. Nessov, Halszka Osmólska, Pamela Robinson, Karol Sabath, Jan Samsonowicz, and Wojciech Siciński.

Among my younger colleagues I wish to express my special gratitude to Richard L. Cifelli and Zhe-Xi Luo. During their numerous visits at our home, I often had an opportunity to discuss with them various issues related to early mammalian evolution. Other colleagues who helped me in various ways are Alexander Averianov, Demchig Badamgarav, Rinchen Barsbold, José Bonaparte, Magdalena Borsuk-Białynicka, David Bruton, Percy M. Butler, William A. Clemens, Alfred W. Crompton, Philip Currie and his wife Eva Koppelhus, Margerita Erbajeva, Dick Fox, Ryszard Gradziński, Yamila Gurovich, Natascha Heintz, Jim Hopson, Jørn H. Hurum, Tom Jerzykiewicz, Jerzy Lefeld, Jason A. Lillegraven, Alexey Lopatin (figure 7.1F), Hans-Arne Nakrem, Michael J. Novacek, Kenneth Rose, Guillermo Rougier, Timothy Rowe, Barbara Rzebik-Kowalska, Denise Sigogneau-Russell and her husband Donald Russell, Wojciech Skarżyński, Hans-Dieter Sues, Hubert Szaniawski, Philip Taquet, and John Wible.

Three persons provided essays about late colleagues, which I publish in this book: Priscilla McKenna on her late husband Malcolm C. McKenna, Alexander Averianov on his teacher and friend Lev A. Nessov, and Vincent Morgan on his granduncle Walter W. Granger, the field leader of the Central Asiatic Expeditions organized in the 1920s by the American Museum of Natural History in New York.

Several colleagues occasionally corrected parts of my English. These were Rich Cifelli, Philip Currie, Brian Davis, and Priscilla McKenna. The greatest help in this respect I received from my American-Australian friends Thomas Rich and his wife Patricia Vickers-Rich, who corrected the English of the whole version completed during the summer of 2010. They and Alexander Averianov from the Zoological Institute of the Russian Academy of Sciences, Magdalena Borsuk-Białynicka from the

Institute of Paleobiology in Warsaw, and Zhe-Xi Luo from the Carnegie Museum in Pittsburgh did enormous service to me in reading almost the whole book, and I am extremely thankful for the time they spent reading, correcting, and discussing some problems with me. I am very grateful to Zhe-Xi Luo, who shared with me his knowledge of the history of paleontology in China.

I am also thankful to the two artists who made the illustrations for the book. Oscar Sanisidro, a Spanish artist, made reconstructions of several early mammals. Oscar generously offered the drawings made by him as a gift to me. I appreciate his kindness very much. Aleksandra Hołda-Michalska prepared scanned versions of several drawings and prepared final digital files of the illustrations. She also made several reconstructions of early mammals. My friend Jerzy Dzik kindly devoted his time to preparing the first project of figure 16.1. Aleksandra Hołda-Michalska, Agnieszka Kapuścińska, Jolanta Kobylinska, and Aleksandra Szmielew, helped me in technical editing of the book.

The SEM micrographs published here were taken by Jørn H. Hurum from the University of Oslo, Christiane Weber-Chancogne from the Institute de Paléontologie, Museum Natural d'Histoire Naturelle in Paris, and Wojciech Skarżyński from the Institute of Paleobiology in Warsaw. Most of the photographs published in the book are housed in the archive of the Institute of Paleobiology in Warsaw and were taken by Ryszard Gradziński, Wojciech Skarżyński, and Marian Dziewiński. The remaining photos were taken by various photographers in numerous institutions in which I had an opportunity to work or by journalists visiting our institute, and as a rule they are acknowledged in the photograph's captions. I deeply apologize if I have omitted some names or mixed them, the possibility of which cannot be excluded.

My granddaughter Zofia Jaworowska (Zosia), a student of philosophy and of social anthropology, and Jolanta Kobylinska kindly helped me check the references.

Finally, I wish to acknowledge the enormous help received from my late husband Zbigniew Jaworowski, who has always been willing to assist me in various possible ways. His knowledge, experience in different sciences, sense of humor, and friendship created an atmosphere in our home that helped me complete this book. Unfortunately, he passed away on 12 November 2011, two months before the submission of the final version of the book.

To all these persons and institutions I wish to express my most sincere thanks and gratitude.

Institutional Abbreviations

AMNH	American Museum of Natural History, New York, United States
BMNH	Natural History Museum, previously British Museum (Natural History), London, Great Britain
CAE	Central Asiatic Expeditions of the American Museum of Natural History
CUP	Catholic University of Peking, China
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, China
MAE	Mongolian Academy–American Museum Expeditions (the collections are for the time being housed at the American Museum of Natural History in New York)
PIN	Paleontological Institute, Russian Academy of Sciences, Moscow, Russia
PM	Paleontological Center of the Mongolian Academy of Sciences, Ulaanbaatar, Mongolia
ZIN	Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia
ZPAL	Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland

In Pursuit of Early Mammals

1.0. Geological time scale of the Mesozoic.

Modified from Palmer and Geissman (1999).

PERIOD	EPOCH	AGE	Ma
CRETACEOUS	LATE	MAASTRICHTIAN	65
		CAMPANIAN	71.3
		SANTONIAN	83.5
		CONIACIAN	85.8
		TURONIAN	89.0
		CENOMANIAN	93.5
	EARLY	ALBIAN	99.0
		APTIAN	112
	NEOCOMIAN	BARREMIAN	121
		HAUTERIVIAN	127
		VALANGINIAN	132
		BERRIASIAN	137
JURASSIC	LATE	TITHONIAN	144
		KIMMERIDGIAN	151
		OXFORDIAN	154
	MIDDLE	CALLOVIAN	159
		BATHONIAN	164
		BAJOCIAN	169
		AALENIAN	176
	EARLY	TOARCIAN	180
		PLIENSBACHIAN	190
		SINEMURIAN	195
		HETTANGIAN	202
TRIASSIC	LATE	RHAETIAN	206
		NORIAN	210
		CARNIAN	221
	MIDDLE	LADINIAN	227
		ANISIAN	234
	EARLY	OLENEKIAN	242
		INDUAN	245 248

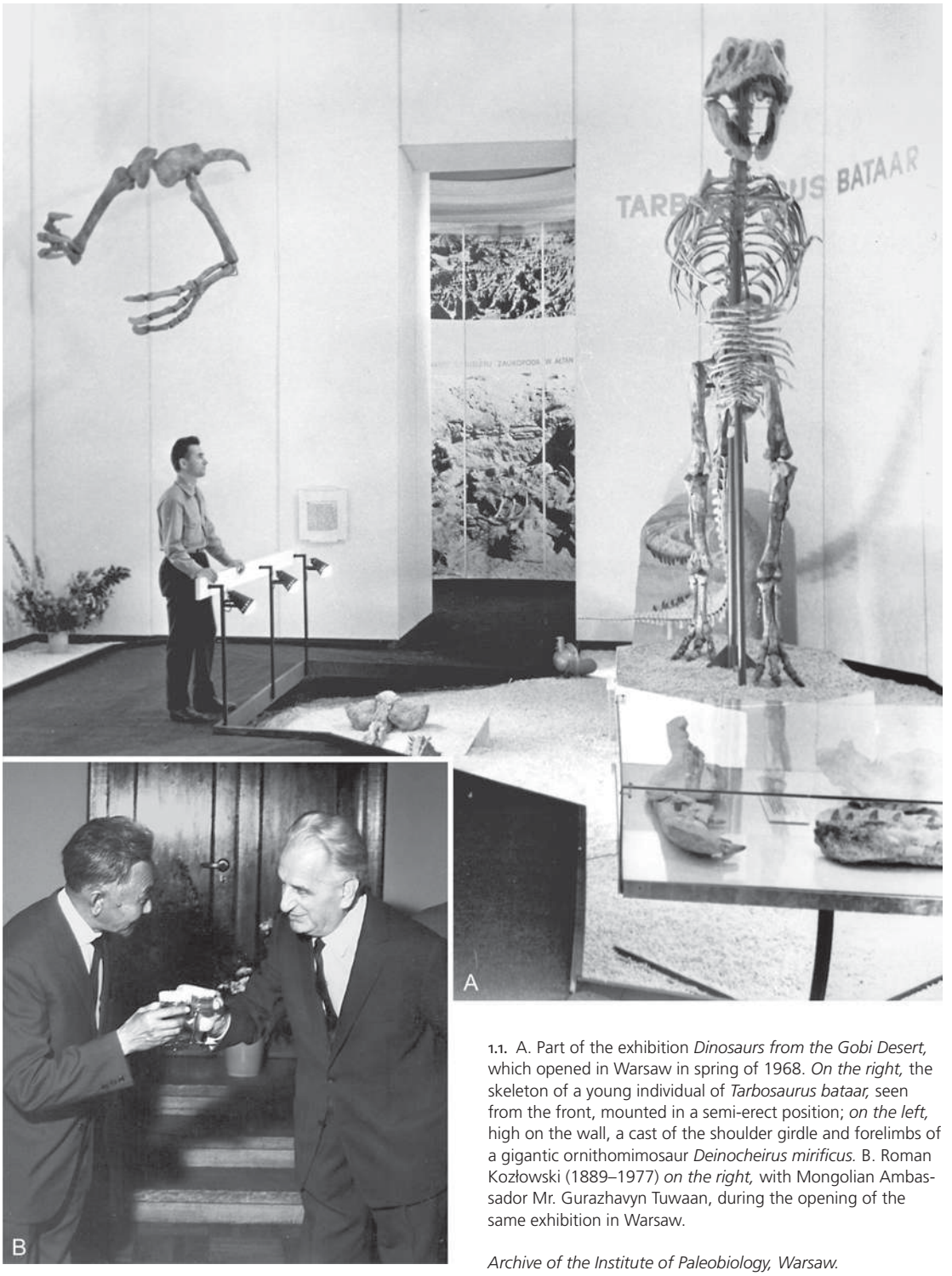
Introduction

1

THE EVOLUTION OF MAMMALS DURING THE AGE OF DINOSAURS (IN the Mesozoic era; see figure 1.0), which encompasses 160 million years (Ma), or more than two-thirds of all mammalian history, was for a long time poorly known, with intriguing mysteries surrounding their origins and the relations among the different groups. Among the first to sort through this history was George Gaylord Simpson. In his first monograph on Mesozoic mammals (Simpson 1928a), he re-described most of the British Mesozoic mammals that had been collected since the middle of the nineteenth century and that are housed in the British Museum (Natural History) in London (now the Natural History Museum). His book also contained descriptions of some cynodonts (tritylodontids), which were at the time regarded as mammals. A year later, he published a second large monograph devoted to the Mesozoic mammals of North America (Simpson 1929). It was valuable work, but new discoveries were already beginning to alter our view of early mammals.

Simpson's work contained no account of the significant material being uncovered in the deserts of Mongolia by the American Museum of Natural History's Central Asiatic Expeditions (see chapter 3). Between 1922 and 1930, five expeditions to Mongolia brought back numerous dinosaur and mammal skeletons, as well as the first Cretaceous mammal skulls ever found. In addition to hundreds of articles and books on the scientific results of the paleontological expeditions to Mongolia, a number of popular or semi-popular books and articles were published in various languages, beginning with the great work of Roy Chapman Andrews, *The New Conquest of Central Asia (1932)*.

In 1930, and again after the Second World War, the Mongolian People's Republic was closed to Western scientists, but paleontologists from Poland (a member of the Eastern Bloc) were allowed to work there. In 1963, I organized for the Institute of Paleobiology of the Polish Academy of Sciences the first Polish-Mongolian Paleontological Expedition to Mongolia. From 1963 until 1971 a total of eight expeditions were at work in Mongolia (see chapter 4). When the collections assembled by the first few expeditions arrived in Warsaw and were in large part prepared, the institute decided to show some of the prepared specimens to the public, and in 1968 opened the first exhibition in the Palace of Culture in Warsaw under the title *Dinosaurs from the Gobi Desert* (figure 1.1). Then in the summer of 1975 a permanent dinosaur exhibit opened in the Park of Culture in Chorzów (an industrial center in Silesia; figure 1.2). Subsequently,



1.1. A. Part of the exhibition *Dinosaurs from the Gobi Desert,* which opened in Warsaw in spring of 1968. *On the right,* the skeleton of a young individual of *Tarbosaurus bataar,* seen from the front, mounted in a semi-erect position; *on the left,* high on the wall, a cast of the shoulder girdle and forelimbs of a gigantic ornithomimosaur *Deinocheirus mirificus.* B. Roman Kozłowski (1889–1977) *on the right,* with Mongolian Ambassador Mr. Gurazhavyn Tuwaan, during the opening of the same exhibition in Warsaw.

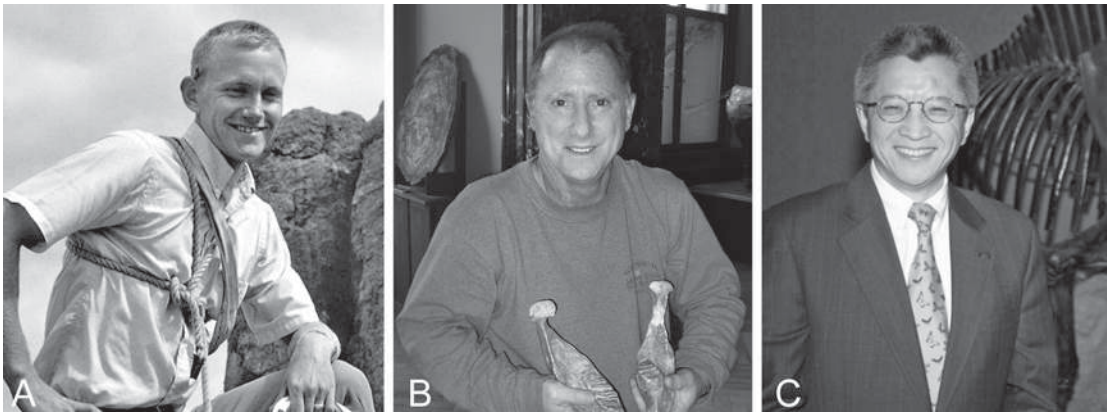
Archive of the Institute of Paleobiology, Warsaw.

1.2. A. The first Dinosaur Park, open in Poland, at Chorzów in Silesia (southwestern Poland) in 1975. The models of dinosaurs were made at the Institute of Paleobiology in Warsaw, at the scale 1:10 by Wojciech Skarżyński and then enlarged to natural size by professional sculptors, on the spot. B. Reconstruction of a running *Gallimimus bullatus* in Chorzów Park.

Archive of the Institute of Paleobiology, Warsaw. Photographs by W. Skarżyński.

our institute opened in 1978 a permanent exhibit in the Palace of Culture in Warsaw entitled *Evolution on Land*.

The Polish-Mongolian expeditions were of great importance for my work on the Late Cretaceous mammalian fauna, and I established many contacts with other workers in the field. One of these contacts proved to be particularly fortuitous. Beginning in 1965, I was in touch with Jason Lillegraven (figure 1.3A), who was working on his dissertation on the mammal fauna from the upper part of the Edmonton Formation in Canada (now referred to as the Scollard Formation). Since I had been working on Late Cretaceous mammalian faunas from Mongolia, we closely cooperated at that time. In a letter dated 1 March 1976, Jay announced that he and Bill Clemens thought the time was ripe for a new book on Mesozoic mammals and asked whether I would be interested in contributing a chapter on Asiatic Mesozoic mammals. I agreed with enthusiasm! During the next months our correspondence concerned



1.3. A. Jason A. Lillegraven as a student in 1964. B. Richard L. Cifelli. C. Zhe-Xi Luo.

mostly the details of the book and its chapters. I then accepted an invitation from the University of Wyoming to visit for six weeks in November and the beginning of December 1976 to work on editing our book. I spent the summer of 1976 in Poland in the cottage my husband and I shared in the small village of Zdziarka on the Vistula River some 60 km northwest of Warsaw hammering out on a typewriter (there were no personal computers at that time!) the chapters assigned to me.

During the autumn of 1976, typescript in hand, I arrived in Laramie, Wyoming, where Lillegraven had just settled into a new, large family house with his first wife, Bernie, and two small, charming children, Brita and Turi. And we began our work. In the preface to the book (Lillegraven et al. 1979), we described our rationale for the project: "The idea of this book developed through a course on the subject of Mesozoic mammals offered in the spring of 1976 in the Department of Geology of the University of Wyoming. Recognition by the students of: (1) the scattered nature of the literature; (2) the lack of recent general reviews; and (3) the fact that knowledge on Mesozoic mammals is expanding rapidly, led to the conclusion that it was opportune to provide a summary of the 'state of art' as of the late 1970's."

From correspondence with Jay, I had been led to understand that some of his students would provide descriptions of some groups of Mesozoic mammals. However, not much had been accomplished when I arrived in Laramie. It was evident that writing such summaries had been just too difficult for some students, and these chapters were not going to be written without contributions from paleontologists currently studying Mesozoic mammals. So we invited our Harvard colleagues Alfred W. Crompton and Farish A. Jenkins – specialists on early mammals – to write chapters on the "Origin of Mammals" and on the "Triconodonta." In addition, William A. Clemens, one of the book's editors, discussed with me the chapter on Multituberculata, which we decided to write together. He also agreed to correct the chapter on Symmetrodonta and become a co-author along with Michael L. Cassiliano, who originally had written this chapter (Cassiliano and Clemens 1979).

By the time I was ready to leave Laramie in December 1976, we had a more or less clear picture of how the book should be subdivided into chapters, whom we should contact as potential authors, and what more should be done. It was evident that we would need to meet at least once more. I invited Jay and Bill to Poland, and they arrived in Warsaw in the early spring of 1977. We packed all the literature we had on Mesozoic mammals and left for the cottage at Zdziarka to work for three solid weeks on our book. Beginning in 1977 Jay Lillegraven worked hard on the final editing of the book, *Mesozoic Mammals: The First Two-Thirds of Mammalian History*, which appeared in 1979.

In June 1981, the eminent Italian paleontologist Eugenia Montanaro Gallitelli (1906–1997), a specialist on fossil corals and micropaleontology, invited numerous invertebrate and vertebrate paleontologists from around the world to an international paleontological meeting in Venice, at which they presented papers on crucial problems of paleontology. I provided a lecture on "Marsupial-Placental Dichotomy and Paleogeography of Cretaceous Theria," which, together with other lectures read at the symposium, was subsequently published in the book edited by Montanaro Gallitelli (1982).

In 1982 my husband Zbigniew Jaworowski, at that time professor of radiobiology at the Central Laboratory for Radiological Protection in Warsaw, received an invitation from the Centre d'Etudes Nucléaires in Fontenay-aux-Roses near Paris to come for a year to study the history of the contamination of the French population with heavy metals and radioactive elements. I took a one-year leave from the Institute of Paleobiology and joined him. Our stay in Paris was prolonged until August 1984 (see chapter 10 for a description of my work during our stay in Paris).

In the summer of 1985 I chanced to read in *Nature* an announcement from the University of Oslo calling for applications for the position of professor of paleontology. The situation of Polish science was at that time very difficult – there was no money for equipment and no funding for scientific literature or for traveling abroad. After a short discussion with my husband we decided that I should apply. In September, I sent my application with five boxes containing all of my publications, copies of my diplomas, and other necessary documents. The University of Oslo (figure 1.4) appointed a five-member international committee to assess ten candidates who applied from Norway, Sweden, Denmark, Germany, Great Britain, and Poland. The committee completed its work in December 1986 and informed me that I won the competition. The nomination, in distinguished and beautiful regal style, signed by King Olav VI himself, was sent to me in January 1987. I was expected to take my position at the university by 1 June 1987.

My husband and I spent eight years and four months (1987–1995) in Norway (figure 1.4), where I received several grants from the Norwegian Science Foundation, which enabled my cooperation with colleagues from abroad, in particular with Russian paleontologists – the late

Lev A. Nessov (1947–1995) and the Armenian Russian zoologist Petr P. Gambaryan (working in the Zoological Institute in St. Petersburg).

During this time, the riches of the Gobi Desert were opened to scientists from the West when the political situation in European and Asiatic countries changed, beginning in 1989 with the Solidarity movement in Poland. The new political openness also resulted in invitations being extended to Mongolian paleontologists to exhibit Mongolian dinosaurs in the West.

As a consequence of one of these invitations, an exhibit entitled *Dinosaurs et Mammifères du Désert de Gobi* was set to open in Paris in

1992 (Muséum National d'Histoire Naturelle 1992). My friend Philippe Taquet, at that time director of the Paleontological Institute of the Museum of Natural History in Paris, decided that the dinosaur displays would be more interesting if the dinosaurs were shown in association with the mammals that lived at that time. Two eminent French specialists on early mammals from the institute in Paris, Denise Sigogneau-Russell and her husband Donald Russell, visited me in Oslo at the beginning of February 1992. It was during that visit that Don, also a world-renowned specialist in preparing casts of minute fossils, produced copies of the Late Cretaceous mammals collected by members of the Polish-Mongolian Paleontological Expeditions. These casts were subsequently displayed alongside the dinosaur skeletons at the Paris exhibition. For the book released in connection with the exhibit, written by the staff of the museum in Paris in cooperation with Mongolian paleontologists based in Ulaanbaatar, Philippe Taquet contributed the section on dinosaurs (Taquet 1992), while Denise Sigogneau-Russell (1992) described the Mesozoic mammals.

A cooperative endeavor between the Mongolian Academy and the American Museum of Natural History led by American paleontologist Michael Novacek, a specialist on the evolution of eutherian mammals, and the late Demberlyin Dashzeveg, from Mongolia, began its work in 1990. In addition to numerous papers on the scientific results of the expeditions, Novacek published a charming popular book, *Dinosaurs from the Flaming Cliffs* (1996), describing the work of the expeditions.

In 1995, just before my husband and I were to leave Norway and return to Poland, David M. Unwin contacted me on behalf of the editors (M. J. Benton, M. A. Shishkin, D. M. Unwin, and E. N. Kurochkin) of the book *The Age of Dinosaurs in Russia and Mongolia* and proposed that I contribute a chapter on "Mammals from the Mesozoic of Mongolia." I accepted but suggested that three other scientists, who in the last few years had contributed to the knowledge of Mesozoic mammals from Mongolia, join me as co-authors – M. J. Novacek, B. A. Trofimov, and D. Dashzeveg. My proposal was accepted, and I submitted our chapter in 1997. In 2000 the book was published by Cambridge University Press (Kielan-Jaworowska et al. 2000).

The last quarter of the twentieth century saw a remarkable accumulation of knowledge about early mammals. Mesozoic mammals have been discovered on all the continents (except Antarctica) and in regions where they had been unknown previously, for example, Australia and Madagascar. These discoveries include excellently preserved teeth, jaws, and parts of skeletons belonging to the groups that were formerly poorly known or unknown. In 1998, Richard L. Cifelli (figure 1.3B), from the University of Oklahoma, and I decided to write a new book on Mesozoic mammals. However, as both of us had been working mostly on Cretaceous mammals, it soon became evident that we needed a specialist on the earliest mammals and mammalian origins. We invited our colleague and friend Zhe-Xi Luo to join us.

1.4. A. The building of the Mineralogical-Geological and Paleontological Museum in the Botanical Garden in Oslo. B. The cast of *Tyrannosaurus rex* mounted in a horizontal position of the lumbar and thoracic vertebrae. C–E. Part of the staff of the Museum. C. Jørn H. Hurum. D. Hans-Arne Nakrem. E. *Standing from left,* Natascha Heintz, Kjell Bjørklund, and David Bruton; *sitting,* Bogdan Bocianowski.

A and B. Courtesy of Per Aas, Paleontologisk Museum, Oslo; E. Courtesy of Zbigniew Jaworowski.

Cifelli and Luo are both eminent specialists on Mesozoic mammals. Rich Cifelli, born in 1954 in Centralia (Washington, United States) is the son of Richard Cifelli, a micropaleontologist. He received his Ph.D. in vertebrate paleontology in 1983 at Columbia University under Malcolm C. McKenna. In 1986 he came to the University of Oklahoma as a professor of zoology and as the curator of vertebrate paleontology at the Oklahoma Museum of Natural History. His main scientific interests concern early mammals and their origins, relationships, and paleoecology. Being a hard worker and a talented writer, and owing to his ability to synthesize information, his deep knowledge, and impressive field experience, he is one of the leading authorities on Mesozoic mammals in the United States.

Zhe-Xi Luo (figure 1.3C), born in 1958 in Beijing, was one of the first Chinese students allowed to study abroad as a consequence of Deng Xiaoping's reforms. He arrived in the United States in 1982 as a 24-year-old student of paleontology. He received his Ph.D. from the University of California at Berkeley and his postdoctoral training at Harvard. In 1986 he joined the Carnegie Museum of Natural History, where he was curator of vertebrate paleontology and associate director of the museum. In 2011 he became professor of vertebrate paleontology at the University of Chicago. I met him in 1983 when I visited William Clemens, who had supervised Luo's doctoral dissertation, at Berkeley. Like me, Luo studied the mammals of the Mesozoic era, and our paths often crossed. According to international agreement, Chinese students were supposed to return to their homeland after completing their studies. However, in April 1990, several months after the Tiananmen massacre, the U.S. government, with approval of President George Bush, decided that about 80,000 Chinese students could stay in the United States. Luo and his wife, a doctor of chemistry, were in this group. Now Luo often visits China and cooperates with Chinese colleagues on descriptions of new Mesozoic mammals found there.

In 2004, after five years of intensive cooperation, during which my co-authors (figures 1.3B and C) came to Konstancin, Poland, once or twice a year to work with me, the comprehensive volume *Mammals from the Age of Dinosaurs* was published by Columbia University Press (Kielan-Jaworowska, Cifelli, and Luo 2004). The early mammals have also been treated in three more recent books: *The Origin and Evolution of Mammals* by Tom S. Kemp (2005), *The Rise of Placental Mammals*, edited by Kenneth D. Rose and J. David Archibald (2005), and *The Beginning of the Age of Mammals* by Kenneth D. Rose (2006). In 2010 José F. Bonaparte and Laura A. Migale published a book (in Spanish) on the Mesozoic mammals of South America.

In addition to hundreds of articles and books on the scientific results of the paleontological expeditions to Mongolia, a number of popular or semi-popular books and articles have been also published in various languages. Soviet expeditions to Mongolia working in 1946, 1948, and 1949 were reported in two articles written by their leader Ivan Efremov

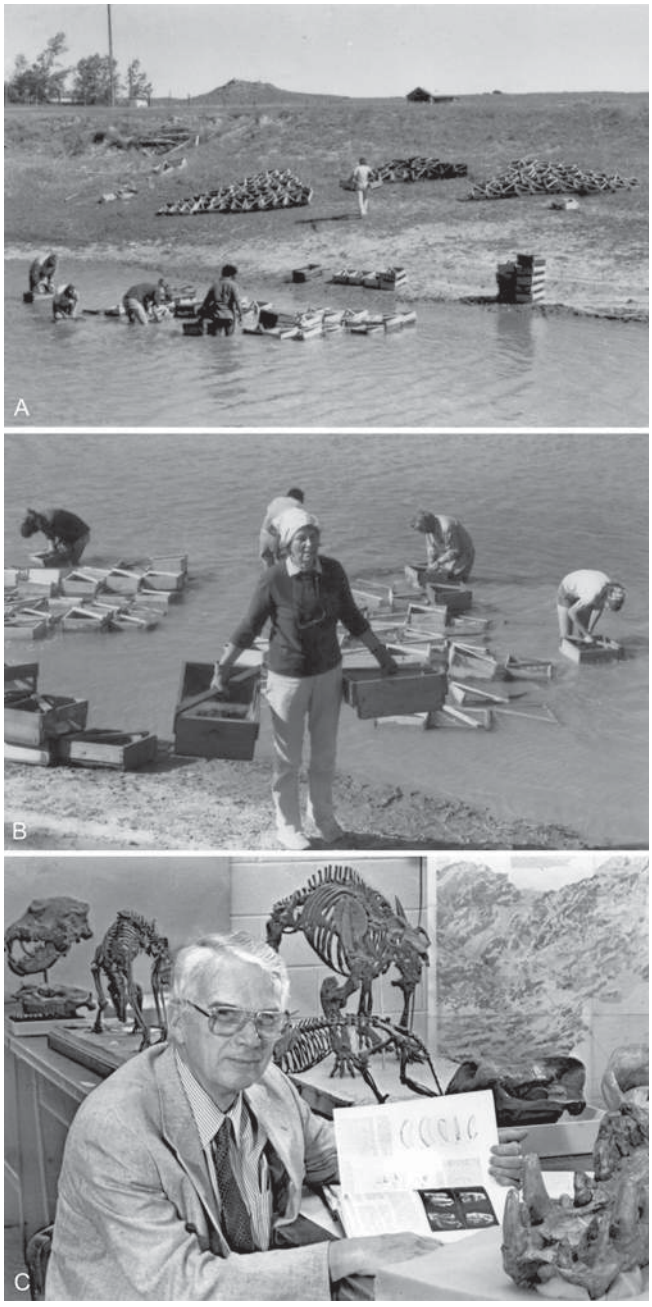
(1949, 1954, both in Russian) and in the book by Anatolii Rozhdestvenskii (1969), published in Russian and also translated into Japanese (see also chapter 3). I wrote two popular books, describing the Polish-Mongolian Paleontological Expeditions (published in Polish in 1969 and 1972 but not cited here). The first of these books was translated into English (as *Hunting for Dinosaurs*) and published in 1969 by MIT Press (Kielan-Jaworowska 1969b).

An interesting book describing the work of paleontologists in the Gobi Desert was published in 1993 in New Zealand by J. R. Lavas, who never has been in Mongolia. He graduated in zoology from the University of Auckland and is an illustrator as well as a zoologist. While writing the book, he contacted paleontologists and members of the Gobi expeditions in various countries and managed to collect an enormous number of photographs, notes, and information. His book describes very competently the stories of the paleontological work in the Gobi Desert, which brings me to the present volume.

In the pages that follow, I review the current state of our knowledge about Mesozoic mammals, their origins, anatomy, systematics, paleobiology, and distribution, based mostly on my personal experience. I recount the difficulties and pleasures encountered in seeking out these rare fossils and the effort involved in organizing fieldwork (including major expeditions), using new methods, and removing the fossils from the rock once they have been discovered. The book also explores the special techniques employed to obtain as much information as possible about the fossils, the changing views on the origin and relationships among early mammals, the discoveries and reassessments that result from paleontologists' endless discussions with colleagues, and a range of related issues. In the first place, I describe my own experiences and those of my close friends, whose work I was able to observe directly. There are, however, groups of early mammals that I know mostly from the literature or from contacts with specialists who work on them. In such cases I discuss these groups based on the information I have gathered on the history of research on those mammals and the persons involved in the relevant studies. As my working experience has focused largely on my own studies of Cretaceous mammals from Mongolia, I recapitulate in chapter 4 my fieldwork during the Polish-Mongolian Paleontological Expeditions to the Gobi Desert.

2.1. A, B. Fieldwork in Hell Creek, Wyoming, organized by Malcolm C. McKenna in the summer of 1983. A. Soft sediment was placed in wooden crates with bottoms made of metal netting. Members of the crew moved the crates in water and then placed the crates for drying the residue on the surrounding hills. B. *In the foreground,* Zofia Kielan-Jaworowska, carrying two boxes with residue to be placed on the hill for drying. C. Malcolm C. McKenna (1930–2008) in his study at the Natural History Museum in New York in 1998.

All figures courtesy of Priscilla McKenna.



Methods: Collecting Materials and Establishing Relationships

2

UNTIL ABOUT THE MIDDLE OF THE TWENTIETH CENTURY, PALEONtologists thought that Mesozoic mammals were small, rare, and poorly differentiated creatures represented by primitive groups. Intensification of search for Mesozoic mammals all around the world, however, changed this opinion. The great impact on this increase of specimens and studies on fossil vertebrates in the second half of the twentieth century was related to development of new methods and organization of expeditions to areas not exploited or hardly exploited earlier.

In 1928, the American paleontologist Claude W. Hibbard (1905–1973) started to collect small vertebrate fossils by screen washing and drying soft sediments (Hibbard 1949). Hibbard's method was then developed for Mesozoic mammals by McKenna (1962, 1965), McKenna et al. (1994), and Clemens (1965). Their screening techniques were further improved by Jason A. Lillegraven, who in the early 1960s collected small vertebrate fossils from the Late Cretaceous upper Edmonton Formation (now known as the Scollard Formation) at outcrops along the Red Deer River in Alberta, Canada. Jay Lillegraven described his method in his Ph.D. thesis, published in 1969. For washing the soft sediments yielding small vertebrates, Jay used the Red Deer River's current, with a fluctuating water level. He and Tom Rich (at that time a graduate student) constructed several floating "rafts," which they aligned perpendicular to the river current. Each "raft" had an empty bottom divided by smaller boards into 24 compartments; Lillegraven placed into each compartment two washing boxes, with bases made of bronze netting. He used two types of washing boxes: one coarse-screened with openings of 1.5–2 mm in diameter, and a second type with openings with diameters 0.6 mm. After one night of washing using the three rafts agitated by the river current, a "super-concentrate" was collected, dried, and transported to the laboratory (Lillegraven 1969: figures 3 and 4). Lillegraven was lucky in having access to the current of the Red Deer River. More often, in the field there is only a small pond (reservoir) or stream that is available for washing sediment.

By 1983 the technique had become quite sophisticated, as I discovered that summer when at the invitation of Malcolm C. McKenna I joined him and his crew at Lance Creek in Wyoming where they were collecting mammals from outcrops of Late Cretaceous age in the Lance Formation. Malcolm brought 300 boxes with a base made of metal and a bulldozer to excavate sediment. He transported the sediments to a reservoir, where the ten of us in his crew stood in water up to our knees and

washed the sediment by shaking the boxes in pond water (figure 2.1A, B). The washed sediment, still in boxes, was left to dry in the sun, and a new cycle of washing with new boxes started.

The crew washed about one metric ton of sediment a day. Malcolm was a man of great enterprise, who contributed enormously to the improvement of the screen-washing method introduced by Hibbard. At the beginning, he visited Claude Hibbard in the field and discussed methods with him. While Hibbard used 12 washing boxes during typical fieldwork, McKenna increased this number to 300, which allowed him to collect fossils at a much greater rate. In 1983 at Lance Creek, several long tables covered with canvas were set up on the hills, near the washing boxes, and the dry concentrated sediment was dumped on these tables in very thin layers. Crew members sat around the tables and, sometimes using hand lenses, hand picked through the concentrated sediment, putting the small vertebrate fossils they picked out into plastic boxes.

By using such water-screening techniques in the United States and Canada, and later on in Europe, Asia, and South America, the number of Mesozoic mammals in paleontological collections of museums around the world increased several-fold, helping to advance our understanding of the structure and evolution of these previously rarely found animals.

An important new methodology for determining how species are phylogenetically related was introduced in the twentieth century by the German entomologist Willy Hennig (1913–1976). Beginning in 1950, Hennig put forward the idea of phylogenetic analysis, known also as cladistic analysis. Hennig first published in German, and his new method was little known outside Germany until the 1966 publication of his book *Phylogenetic Systematics* in the United States. The main difference between Hennig's cladistic method and the traditional phylogenetic method is that traditional phylogenetics is based on all anatomical knowledge without necessarily giving some morphological characters more importance than others. Hennig's phylogenetic analysis is based on the recognition that only "derived characters" can be used to work out relationships.

With the advent of the computer era, cladistics flourished enormously as specialized programs enabled rapid analyses of vast numbers of characters. This resulted in a cornucopia of "equally parsimonious trees," which mercifully leaves some room for further exploration by the human mind in figuring out how taxa are related.

The third phylogenetic method, introduced by Sokal and Sneath (1963), called numerical taxonomy, or phenetics, has also been used. It differs from cladistic systematics in that all characters used for analysis have the same value.

In contrast to Sokal and Sneath, Hennig recognized two types of characters:

1) Plesiomorphic characters, which occur in the primitive members of the studied group, and which should not be used in cladistic studies.

2) Apomorphic (or derived) characters, which made their appearance in the studied group and occur in all its members. According to Hennig, phylogenetic analysis should be based on apomorphic characters.

Cladistic analysis with respect to early mammals was used for the first time by Timothy Rowe in his Ph.D. dissertation at the University of California, Berkeley, supervised by Kevin Padian. Rowe subsequently published the main ideas of his thesis in 1988 in the *Journal of Vertebrate Paleontology*. Rowe (1988: 241) defined Mammalia as "a taxon originating with the most recent common ancestor of the extant Monotremata and Theria." To diagnose Mammalia as so defined, 176 characters in the skull and postcranial skeleton, distributed among Placentalia, Marsupialia, Multituberculata, Monotremata, Morganucodontidae, Tritylodontidae, and *Exaeretodon*, were designated as primitive (plesiomorphic) or advanced (apomorphic) and analyzed by Swofford's (2000) PAUP program.

Rowe subsequently published another paper on a similar subject, which he presented at a conference on mammals in New York organized by F. S. Szalay, M. J. Novacek, and M. C. McKenna at the end of May 1990 (and which was published in 1993). In addition to the paper by Rowe, there are several articles on the systematics of particular groups of Mesozoic mammals, published in the same volume, some of which I discuss in chapters related to the relevant groups.

Malcolm C. McKenna – Mammalian Paleontologist (1930–2008)

After the death of Malcolm C. McKenna in 2008, I corresponded with his wife and my friend, Priscilla. She provided this biographical sketch of her husband and his fascination with Mongolia.

Malcolm McKenna (figure 2.1C) grew up in Claremont, California, at that time a community surrounded by orange groves in the eastern part of the Los Angeles Basin. It was a small town whose distinction was that it contained Pomona, Scripps, and Claremont Men's Colleges and the Webb School for Boys.

At the age of 13, Malcolm was enrolled in the Webb School, where he came under the influence of Raymond Alf, a dramatic and charismatic teacher of life sciences. During weekends and school vacations Ray took the boys on fossil collecting trips – to the Mojave Desert of California, the big Badlands of South Dakota, the famous fossil localities along the Niobrara River in Nebraska, the Green River Basin of Wyoming, and especially to Arizona and the Grand Canyon. The fossils collected on those trips are now in the Raymond M. Alf Museum of Paleontology at the Webb School.

During his lifetime, Malcolm made 13 or 14 hikes down various trails into the Grand Canyon and also four boat trips through the canyon of Colorado River. There is no way that a person like Malcolm could have had that kind of intimate contact with the Grand Canyon and its

surroundings and not develop a deep fascination with understanding the forces that created the earth's crust.

The home where Malcolm lived was at the foot of the San Gabriel Mountains, the steepest and most active mountain range in the continental United States. As he grew up, he spent his spare time wandering the foothills and mountains behind his home, where he studied rocks and life forms and collected all kinds of creatures. He was an indefatigable hiker, a characteristic well remembered by his graduate students, who often had to run to keep up with him!

In his early teens, his love of exploration was captured by the real-life stories of the Central Asiatic Expeditions of the American Museum of Natural History under the leadership of Roy Chapman Andrews and Walter Granger. He began to read everything he could find on the history and geology of Central Asia and conceived a strong ambition to travel there to study and collect. He made a significant collection of pertinent publications and became expert on the subject. Little did he know then that, one day, he would become curator of the fossil mammals collected in the Gobi by the very same Central Asiatic Expeditions.

And so, even before he finished high school, he had established the three most important elements that would define his career as a vertebrate paleontologist: a fascination with the history of the earth's crust and the forces that formed it; a love of animals and a desire to collect them; and a taste for exploration and a deep ambition to explore for fossils in Mongolia.

After a year studying under Chester Stock at the California Institute of Technology, Malcolm transferred to the University of California at Berkeley and began work on his doctoral project on the Eocene mammals of the eastern Washakie Basin in northwest Colorado. In 1950, at the end of his sophomore year at UC Berkeley, Malcolm successfully persuaded George Gaylord Simpson, one of the best-known vertebrate paleontologists in the world and curator of fossil mammals at the American Museum of Natural History in New York City, to take him on as a member of his field crew working with him and his colleagues in the San Juan Basin in New Mexico.

After spending a year in a sanatorium being cured of tuberculosis – during which he studied the great treatises of western science – Malcolm received his Ph.D. from Berkeley in 1958, and in 1960 he became the Frick Curator of Fossil Mammals at the American Museum in New York, replacing George Gaylord Simpson, who had moved to Harvard. At that time Malcolm became curator of the collections of fossil mammals from Mongolia made in the early 1920s by the museum's Central Asiatic Expeditions.

Studying those fossils only strengthened Malcolm's desire to work in the Gobi, and, in preparation for that possibility, he and his wife, Priscilla, learned Russian. In the summer of 1964, Malcolm traveled to Mongolia with one of the first groups of Western tourists allowed into that

country, hoping to meet someone with whom to negotiate the return of the American Museum to do field work in the Gobi.

Unfortunately, because of the political situation at that time, they were prevented from meeting with either Mongolian paleontologists or with the Polish expedition that was working in the Mongolian Gobi that summer, organized by Dr. Zofia Kielan-Jaworowska. However, both McKennas fell in love with the country, and Malcolm in no way abandoned his ambition eventually to work there. During the long years of political estrangement between the United States and Mongolia, Malcolm kept in touch, whenever it was possible, with his Mongolian colleagues by mail.

His Mongolian plans were sidelined for the ensuing 26 years until 1990, when the political situation in Mongolia changed and the Mongolian ambassador to the United Nations came to the American Museum and invited its paleontologists to resume paleontological field work in his country. Of course the invitation was enthusiastically accepted, and the American Museum–Mongolian Academy of Sciences Paleontological Expeditions were organized and carried out.

The McKennas were part of that effort, doing paleontological work in the Gobi for most of the summers in the 1990s, thereby finally realizing Malcolm's lifelong ambition. That joint expedition is still collecting in the Gobi, a place of great paleontological richness, and the specimens found by the museum's scientists are prepared, studied, and replicated at the museum in New York; they will then be returned to the Mongolian Academy of Sciences in Ulaanbaatar.

Priscilla McKenna

Since the publication of the English version of Hennig's *Phylogenetic Systematics* over 40 years ago, his ideas have been considerably developed in the United States and Canada and gradually developed in Europe, Asia, and South America. Many enthusiasts of cladistic systematics around the world have contributed to improvement in the method, for example, Wiley (1981), Carlson (2001), and many others. Phylogenetic systematics as now employed differs in many respects from the original system, but it is beyond the scope of this book to summarize it.

About the same time, developments in molecular genetics (see Hedges and Kumar [2010] for a summary) have had a great impact on the understanding of early mammalian diversification. Molecular genetics is of value in paleontological studies, as it allows one to compare results, which often differ considerably, that have been obtained by two kinds of methods. Those differences in results may well have been due to the incompleteness of the fossil record. However, one should remember that in the case of extinct groups without living relatives, the molecular genetics methodology cannot be used.

3.1. Roy Chapman Andrews (*on the right*) and a Danish member of the Central Asiatic Expedition, George Olsen, admiring the nest of dinosaur eggs found by Olsen. Bayan Zag (Shabarkh Usu), Gobi Desert, Mongolia, 1925.

Courtesy of Vin Morgan, Granger Papers Project.

Paleontological Exploration of Mongolia by American, Japanese, Soviet, and Russian Expeditions, including the Mongolian Academy/American Museum and Mongolia/Japan Joint Expeditions

3

Central Asiatic Expeditions of the American Museum of Natural History (1922–1930)

AT THE END OF THE NINETEENTH CENTURY, PALEONTOLOGICAL investigations had become fairly advanced in the United States and in various parts of Europe. At that time the problem of the place of origin of placental mammals was widely discussed. Rich placental faunas were known from Paleocene deposits, but no single placental mammal had been recovered from the underlying Late Cretaceous formations. The diversity of placental mammals in the Paleocene indicated that they must have had a long history during the Cretaceous, perhaps outside of North America and Europe to where they migrated at the beginning of the Paleocene. Around 1900, the eminent American paleontologist Henry Fairfield Osborn (1857–1935), director of the American Museum of Natural History in New York, suggested that the pre-Paleocene development of placental mammals could have taken place in Central Asia. Twenty years later, the issue of the place of origin of placental mammals was under discussion again at the American Museum of Natural History. It was suggested that the Gobi Desert might reveal such terrestrial Cretaceous fossils.

After two years of preparations, in April 1922 the first of a series of expeditions of the American Museum of Natural History, known from 1926 on as the Central Asiatic Expeditions, left Peking (Beijing) for Mongolia under the leadership of well-known explorer Roy Chapman Andrews (figure 3.1). Between 1922 and 1930, five successive expeditions explored the southern region of today's Mongolian People's Republic, as well as Inner Mongolia territory, which now is a part of China. Expeditions were organized on a grand scale, the largest made up of forty members. The main purpose of the expeditions was paleontological, but topographers, geographers, geologists, archeologists, zoologists, and botanists also took part. The main base of the expedition was in Peking.

The leader of the paleontological part of the expeditions was a paleontologist from the American Museum of Natural History—Walter W. Granger (figure 3.2). Much about the life and work of Walter Granger is known because of his grandnephew Vincent L. Morgan, who established the Granger Papers Project in 1993 and later wrote a monograph devoted

to his life (Morgan and Lucas 2002). In 2000 he established the Walter Granger Memorial Award.

Walter W. Granger (1872–1941)

Walter Willis Granger (figure 3.2) was born at Middletown Springs, Vermont, on 7 November 1872 to the family of Charles H. and Ada Haynes Granger. His father Charles was an agent for Mutual Life Insurance and a distinguished member of the Rutland School Board in Vermont. After finishing primary school and the first year of high school, Walter, just 17, left home in September 1890 and found a job at the American Museum of Natural History in New York. From early childhood Walter had shown an interest in biology, collecting fossil and living animals, and had become a skillful taxidermist. In fact, Granger spent his first six years in the Taxidermy Department of the museum. Beginning in 1896 Granger moved to the Vertebrate Paleontology Department during its heyday under Henry Fairfield Osborn, collecting dinosaur and mammal fossils. He carried out much of this period's best collecting and research on Paleocene and Eocene mammals from the American Western Interior, frequently collaborating with fellow mammal paleontologists William King Gregory, William Diller Matthew, and George Gaylord Simpson.

Granger possessed the keen eye, steady hand, and infinite patience needed for finding and collecting even the most delicate fossils. While his primary localities were the basins and ranges in Wyoming, New Mexico, and South Dakota, he also participated in two major AMNH foreign field campaigns: the Fayum of Egypt expedition in 1907 and the famous Central Asiatic Expeditions (CAE) to China and Mongolia from 1921 to 1930, which resulted in so many key dinosaur and mammal discoveries.

In the spring of 1921, Granger sailed out of San Francisco with his wife Anna, bound for China. He was one of the first of a stream of CAE scientists to follow over the next decade to pursue systematic scientific explorations in China and Mongolia. The Central Asiatic Expeditions, so termed by Henry Fairfield Osborn in 1926, captured the fascination of scientists, adventurers, and enthusiasts all over the world. The paleontological accomplishments alone are heralded even today.

Granger was the CAE's chief paleontologist and second in command and, during five summers in Inner and Outer Mongolia (as they were then known), he and his assistants collected a series of faunas ranging in age from Jurassic to Pleistocene. The Mongolian fossil hunts yielded a wealth of unprecedented mammal and dinosaur discoveries. From new dinosaur finds, such as *Protoceratops*, *Velociraptor*, and *Oviraptor* and the first ever found nests of dinosaur eggs, to finds of rare Mesozoic mammals and more common post-Mesozoic mammals, from a tiny multituberculate to the giant *Paraceratherium*, the expedition's abundant collections enabled scientists to expand their understanding of evolution and the circumstances of prehistoric life.

3.2. Walter W. Granger with his parents, brothers, and sisters. Walter stands in the middle of the upper row; on his right is his older sister Daisy, on his left his younger sister Mary. His parents, Charles and Ada, sit in the middle of the lower row. On both sides of the parents sit two of his brothers.

Courtesy of Vin Morgan, Granger Papers Project.

Granger's arrival in China a full year ahead of the CAE's 1922 Mongolian undertaking was for another purpose. Once established at headquarters in Peking, he embarked on a lesser-known aspect of the CAE's Asian exploit—the hunt for fossils in the remote areas of south China. Granger's search ultimately took him to a tiny, remote mountain village in the western highlands named Yenchingkuo (Yanjinggou) in Szechuan (Sichuan) Province. It was situated 1,000 feet above sea level about 20 miles past Wanhsien (Wanxian) on the south side of the River Yenchingkuo ("salt well gully"), just below a limestone ridge that would yield an unprecedented collection of Pleistocene fossils.

Granger's successful first trip to Szechuan Province lasted from August 1921 to March 1922. He returned there for two more winters, and then to Yunnan Province for yet another. Throughout this period, Granger and his party were in constant danger from warlord battles, banditry, and often-harrowing river travel. He also, of course, participated in all five Mongolian summer explorations.

Before making his first trip to Szechuan Province, Granger agreed to accompany a Swedish geologist stationed in China, Johan Gunnar Andersson, to Choukoutien (Zhoukoudian) just west of Peking. Having allotted just a few days to inspect and assess the area for evidence of hominid presence, they were delighted to find it on the very first day.

With Otto Zdansky, a young Austrian paleontologist assisting Andersson that season, they promptly opened the excavation that became known as Locality #1 and eventually produced Peking Man, or *Sinanthropus pekinensis* (currently *Homo erectus pekinensis*).

For much of the early Mongolian work, Granger was assisted by his longtime field hand, George Olsen, who was originally from Denmark. Olsen, discoverer of the first dinosaur eggs and nest in Mongolia in 1923, had worked with Granger at various sites in the American West and had accompanied him to the Fayum of Egypt in 1907. We get a taste of Olsen and Mongolia from a letter he wrote in 1924: "Mongolia is a great deal like the Laramie Plains long stretches of flat country but no Trees, and at times I almost forgot at I was in Mongolia." Olsen did not write often, but another of Granger's longtime field hands, Albert "Bill" Thomson, who succeeded Olsen, did.

While still prepping at the American Museum's lab in New York, Thomson wrote, "I wish you could see some of these Mongolian fossils – I am working on a *Protoceratops* skeleton and it is a 'hum-dinger', every bone in position – but delicate – oh boy." About a close call in Mongolia in 1930, he wrote, "Just 24 hours after we had passed a given point, there were nearly 400 bandits put in their appearance for the sole purpose of capturing our 4 cars on our way out of the Gobi. Had they caught up with us and attacked, I am sure they would have known they had been in some scrap or other as we had quantities of ammunition for long distance [rifles] and at close range we had 3 No. 12 [gauge shotguns] and a couple of No. 10 [gauge] shotguns and backed by good shoulders. However, I am wondering what the results would have been."

The Olsen and Thomson correspondence supplements Granger's own, along with his CAE diary and that of his wife Anna, which are now held by the Granger Papers Project. There are no other diaries in the archive and, with much of the CAE's original motion picture film destroyed through editing and acid deterioration and scant written documentation elsewhere, the Granger material is all that remains to provide firsthand narration of the CAE.

On the evening of 5 August 1922, at Lake Camp, Granger noted that he had taken "a much needed bath in the lake before teatime" that afternoon. Shallow for several hundred yards out, the lake, he wrote, had a sandy bottom and a temperature of around 70°F [21°C]. The Chinese bathe every day, he continued, and seine for the small fish which abound in the fall season. The Mongols did not venture into the water, however. Granger's Chinese assistant "Buckshot" had said that if "Mongol take bath pretty soon make die."

A few weeks later, on 27 August 1922, Granger noted that "our well water is splendid for washing but not good for drinking – not bad but the kind one doesn't linger over. Has something like washing soda in it. The Mongol, Bato, says that camels like this kind of water. . . . These are very quiet, peaceful days – excellent for collecting." On 15 September 1922,

after he and Andrews left the convoy to make a hasty prospect of nearby outcrop, they found "a fine pair of jaws (?Titanothere). Other cars had gone on and we had only a short time to work in. Decided to take a section of one jaw with the cheek teeth. Had no wrapping material – it being ahead in No. 2 car – so we appropriated our pocket handkerchiefs and hats and managed to get the sections to camp without serious damage. Jaw found 238 paces north of road."

In addition to recording the quality of the well water, the doings of the locals, the weather, the mileage, the status of food and gasoline and collecting fossils and sundry other details, Granger also listed each season's party, often including primary native assistants and occasional pets. The expedition's Westerners, he noted, practically lived on antelope, supplemented by sheep once a fortnight or so, just to keep them from tiring of the game.

On 9 July 1923, a trio of soldiers approached camp to check passports. One, "who seemed to be No. 1, and who arrived later than the other two, was inclined to argue our right to excavate fossils in this kingdom. After establishing our right to [do] this by our passports the soldiers resorted to the superstition about excavating in the ground and said that sickness among the natives would be soon to follow our work. Andrews finally talked him into submission."

Some observations were less pleasant or humorous. Just two days before, Granger had recorded, "Wonderful sunset. Day's run 111 miles. . . . Camped on grass tonight. In P.M. passed several dead horses & 2 [dead] men. Chinese soldiers killed many Mongols two years ago." Several days later, he wrote that two Mongols came into "our clinic today – one for sore eyes – a common disease hereabouts – and one for the treatment of sores on the head, possibly syphilis." On 7 August 1923, with the camel caravan long overdue and food supplies nearly exhausted, he wrote, "We now have a half sack or more of Mongol flour (whole wheat) and about ¼ sack of white flour and less than a half sack of buckwheat. Further use of flour for pasting is to be prohibited and only such skulls, etc, as can be taken out with the paste already mixed will be taken up. We have tea (fine Chinese) in plenty and there are still two tins of Anna's 'S.S. Washington' coffee left and there is a small quantity of rice and spaghetti, also a few tinned beets." Breakfast had been reduced to "thin rice gruel and pancakes."

Ultimately a vertebrate paleontologist, paleoanthropologist, primatologist, and functional and comparative morphologist, Walter Granger, along with William Gregory and George Simpson, was a Darwinian in a time when American paleontology was dominated by orthogeneticists like their own employer, Henry Fairfield Osborn. [Orthogenesis is a theory of evolution, popular at that time, according to which variations follow a particular direction but are not result of natural selection or other external factors – Z. K-J].

Granger deserves the honor of having been the greatest collector of fossil vertebrates that ever lived. If you could handle the thousands of specimens that he collected, you would begin to get some idea of the magnitude of his achievement.

Vincent L. Morgan

The scientific achievements of the Central Asiatic Expeditions were great. They assembled numerous dinosaur skeletons at Bayan Zag and other localities, discovered some of the first dinosaur eggs found in the world, the first skulls of Cretaceous mammals ever found, and numerous skeletons of younger Tertiary mammals. These collections were brought to the American Museum in New York, substantially increasing the paleontological collections housed and displayed there. They brought many new visitors to the museum and led to a significant increase in the American public's interest in paleontology. The scientific results of the Central Asiatic Expeditions were published in large quarto volumes in the Natural History of Central Asia series (Berkey and Morris 1927; Andrews 1932) and in numerous articles published in both *American Museum Novitates* and the *Bulletin of the American Museum of Natural History*.

The Mongolian Paleontological Expeditions of the Academy of Sciences of the Soviet Union and the Expeditions of Lev A. Nessov

A new series of paleontological expeditions to Mongolia was organized by the Paleontological Institute of the Soviet Academy of Sciences in Moscow between 1946 and 1949. In 1946 the institute mounted the first exploratory expedition to Mongolia, led by I. A. Efremov (1908–1972; see figure 3.3A and also Efremov [1949, 1954]), a well-known paleontologist who became subsequently famous in Russia for his science fiction books. Professor Yuri A. Orlov, the director of the Paleontological Institute in Moscow, also participated in this first expedition (his popular book *In the World of Ancient Animals* was published in 1989 in Russian). There were also six other scientists and technicians. Although they spent only two months in Mongolia, they managed to organize two trips, one exploring the southeastern Gobi, the other the southern Gobi. During the second trip they discovered a large "cemetery" of big Late Cretaceous dinosaurs in the Nemegt Valley. The American expeditions had not reached this area, so paleontologically speaking, this was still virgin soil. Two subsequent expeditions were organized in 1948 and 1949, with the aim of carrying out large-scale excavations. Both expeditions were headed by Efremov. Anatolii Rozhdestvenskii (figure 3.3B), despite his young age, was second in command. Rozhdestvenskii participated in both the 1948 and 1949 expeditions to Mongolia (see Rozhdestvenskii 1957, 1969). In 1948, the Soviet group included 15 scientists and 14 laborers. They conducted excavations in southeastern Mongolia, at the area of Sayn Shand,

in southern Mongolia, in Nemegt Basin and Bayan Zag, and lastly more to the west around the Lake Oron Nur.

The 1949 expedition was of a similarly large scale, including 33 persons (both Russian and Mongolian). The work began first in western Mongolia, in the area of Kobdo, in a valley of large lakes. The group discovered there a rich deposit of Pliocene mammals, which was investigated subsequently by the Polish-Mongolian Expedition of 1964 (see Borsuk-Białynicka 1970). In 1949, the Soviet Expeditions continued work begun in the previous year in the Nemegt Valley and in southeastern Gobi. There the Late Cretaceous outcrops at Nemegt, Tsagaan Khushuu, and Altan Uul yielded ten complete skeletons of the carnivorous *Tarbosaurus*, the duckbilled *Saurolophus*, and ankylosaurid dinosaurs, as well as younger Cenozoic mammals (see the list of papers by Efremov, Maleev, Rozhdestvenskii, and Trofimov, cited by Kielan-Jaworowska and Dovchin [1969]). After 1949, Rozhdestvenskii led more Soviet expeditions working in Mongolia and in 1958–1962 led the Chinese-Soviet Expeditions working in China.

The Soviet collections had great scientific value and served as a focus for future exhibitions. Rozhdestvenskii participated in the organizing of the new paleontological museum in Moscow, in particular the very important part concerned with dinosaurs. When the political situation in the Eastern Bloc countries started to change, the Paleontological Institute in Moscow sent an exhibit of dinosaurs to Japan. In 1973–1974, Rozhdestvenskii took part in the organization of the exhibit in Japan, and his popular book on the first Soviet expeditions to Mongolia was translated into Japanese and published in Japan. I remember Rozhdestvenskii as a very competent dinosaur specialist and a hard worker and, at the same time, a very kind and modest person.

The Soviet expeditions were engaged in excavating dinosaurs, which was a major logistic enterprise, and at the beginning did not emphasize the search for Cretaceous mammals. However, in 1969 during fieldwork at the Höövör locality in Guchin Depression, south of Arvayheer, deposits of soft sediments of Early Cretaceous age were discovered by the Soviet Expedition (see Shuvalov 2000: figure 14.4, note 5). The beds yielded Early Cretaceous dinosaurs of the species *Psittacosaurus mongoliensis* and other vertebrates, indicating an Aptian-Albian age of the sediments. The sediments were screen washed and dried during the three successive expeditions (until 1971), yielding hundreds of isolated mammalian teeth, dentaries, and maxillae. The late Russian paleontologist Boris A. Trofimov (1920–1966) published the first reports on triconodonts, symmetrodonts and multituberculates found there (Trofimov 1978, 1980).

Mongolian paleontologist Demberlyin Dashzeveg also collected fossils at Höövör on his own. He approached me and Trofimov with a proposal of describing together the multituberculate mammals found here, which we did. (See chapter 10 for a description of our work. Other fossil mammals from Höövör are discussed in the relevant systematic chapters below.)

3.3. A. Ivan A. Efremov (1908–1972), the leader of the Mongolian–Soviet Union Academy of Sciences Expeditions, in Altan Teli (western Mongolia) in 1949. B. Anatoli K. Rozhdestvenskii (1920–1983), the second in command during the Mongolian–Soviet Union Academy of Sciences Expeditions in 1948.

Courtesy of E. Kurzanov.

The Joint Soviet-Mongolian Paleontological Expeditions (later renamed the Russian-Mongolian Expeditions) began in 1970 and continued until recently. Their work was organized on a large scale, covering the whole area of Mongolia. Over 50 volumes of the expeditions' findings have been published, many of them dealing with invertebrates.

We owe our knowledge of Mesozoic mammals from the so-called Srednaja Asia to the late Lev A. Nessov (1947–1995; figure 3.4), who beginning in the 1970s started to organize the paleontological expeditions to the countries of the former Soviet Union (Uzbekistan, Kazakhstan, Kyrgyzstan, and Tajikistan). Nessov had an enormous influence in developing the interests of Soviet and later Russian paleontologists in searching for early mammals.

Lev Alexandrovitch Nessov (1947–1995)

Born in Tallinn, Estonia, Lev Alexandrovitch Nessov graduated from Leningrad State University in 1969, where he studied paleontology. After university, he worked as an assistant, first in the Zoological Institute of the Russian Academy of Sciences and then in the Department of Vertebrate Zoology at Leningrad University, where he wrote his dissertation, "The phylogeny and systematics of the Mesozoic turtles of the USSR *and their relationships to the modern groups," under the supervision of Lev Issakievich Khozatsky. In his dissertation Nessov set up seven families of turtles in*

the Cretaceous of the Soviet Union, whereas before only two families had been recognized (Trionychidae and Dermatemydidae).

The scientific interests of Lev Nessov were remarkably diverse. In his relatively short, 25-year scientific career, he published more than 170 scientific papers and two monographs (one appearing posthumously). He described more than 350 new taxa of fossil organisms, mainly from the Jurassic, Cretaceous, and Paleogene deposits of Kyrgyzstan, Uzbekistan, Kazakhstan, and various parts of Russia. He worked predominantly on Mesozoic vertebrates but also described some Precambrian invertebrates, plants, and trace fossils.

Important to Nessov's research were his expeditions to Middle Asia. As a young man he participated in extended geological expeditions to the Fergana Depression, Kyrgyzstan, in 1967 and 1971, led by N. N. Verzilin, during which the important locality of Early Cretaceous vertebrates, Kylodzhun, was found and excavated. The abundant and diverse turtle material from this locality was the basis of his dissertation.

In 1973 Nessov received a collection of fossil turtles from the Late Cretaceous of southwestern Kyzylkum Desert in Karakalpakistan (west Uzbekistan) collected by geologist S. S. Schultz. In 1974–1975 he visited this area and sampled a diverse assemblage of vertebrates, including the carettochelyid turtle *Kizylkumemys* and the ceratopsian dinosaur *Asiaceratops* (both being first occurrences for the Soviet Union). Moving to the east into the central Kyzylkum Desert of Uzbekistan in 1977, Nessov reached the Late Cretaceous outcrops in the Itemir-Dzharakuduk Depression. This area had been known since 1914 as a locality for dinosaurs and other vertebrates; the most notable find was a complete shell of the turtle *Lindholmemys*, described by A. N. Riabinin in 1935. This locality had been explored by A. K. Rozhdestvenskii in 1958 but was thought not to be a good prospect for future work because of the lack of articulated dinosaur specimens, despite the fact that Lev Alexandrovitch had found a theropod braincase, later described as *Itemirus medullarris*, and the best preserved such specimen known at that time.

A major turning point in Nessov's career occurred at the field season of 1977 in Dzharakuduk. In the twilight of the last day he found a fossil bone of a frog. Before this, no one had discovered a Mesozoic lissamphibian in the Soviet Union. In darkness, Nessov and two students dry screened several bags of matrix, which were transported to Leningrad and picked over during long winter evenings. As a result, a diverse assemblage of microvertebrates was found, including fishes, amphibians, lizards, turtles, pterosaurs, and dinosaurs – including birds. This complex was remarkably similar to the assemblage known from the late Maastrichtian Lance Formation in Wyoming in the United States, described by R. Estes. Nessov surmised at the time that, as in North America, mammals should occur in such assemblages. With this idea in mind, he and two students returned to Dzharakuduk in 1978, finding the jaw of what was later described as *Daulestes kulbeckensis*, only the second Mesozoic mammal

found in the Soviet Union. Altogether Nessov undertook 11 expeditions to Karakalpakistan and 10 to the central Kyzylkum. He discovered several localities with Mesozoic mammals in the Cenomanian Khodzhakul Formation (Karakalpakistan), the Turonian Bissekty Formation (central Uzbekistan), and the Santonian Yalovach Formation (Tajikistan). These mammal assemblages covered an important interval of mammalian evolution, extremely poorly known in other regions (early Late Cretaceous). In contrast to the geologically younger localities of Mesozoic mammals in Mongolia (Campanian), in Uzbekistan and adjacent countries the assemblages were dominated by diverse eutherians with very rare symmetrodontans, multituberculates, and metatherians.

A brilliant lecturer, Nessov never missed a chance while in the field to inform local shepherds, militiamen, well diggers, or even passengers on a bus how interesting paleontology is and what remarkable animals had lived millions years ago in their country. These lectures were always a striking success. Lev Nessov was a brilliant man uncommonly devoted to science. He never complained of the deprivations that he and scientific colleagues faced following the dissolution of the Soviet Union. For Nessov, science came first. Toward the end of his career he made a concerted effort to reach out to colleagues beyond the Soviet Union, eager to share everything that he and his students had discovered. Although his work had begun somewhat in isolation, his influence became global to such an extent that international expeditions to his discovery sites are his legacy.

A. O. Averianov

Mongolian Academy–American Museum Expeditions

From his childhood, Malcolm C. McKenna (figure 2.1C) dreamed of going to Mongolia (see page 15 and below). His desire was so great that together with his wife Priscilla they learned Russian to facilitate contact with Mongolian colleagues. In 1964 McKenna participated in one of the first tourist trips organized to Mongolia, but the country was still closed to Western scientists, and McKenna was unable to meet with any Mongolian paleontologists or with the Polish group working at that time in the Gobi Desert.

As we have seen, with the collapse of the Soviet Union, cooperative projects with Mongolian paleontologists became possible. One such initiative was the Mongolian Academy–American Museum Expeditions led by Demberlyin Dashzeveg (figure 3.5D) of Mongolia and Michael J. Novacek (figure 3.5E) from the American Museum of Natural History in New York. They began paleontological exploration of the Gobi Desert in 1990. Joining them was Malcolm McKenna, finally able to realize his dream.

Beginning in 1992, the Mongolian Academy–American Museum Expeditions worked in two separate groups. One of them, led by McKenna,

3.4. Lev A. Nessov.

Courtesy of A. Averianov.

focused on investigating Paleocene outcrops in the Nemegt Basin. The other group, led by Novacek and Dashzeveg, searched for new localities. In addition to these, other scientists also were involved in studying the materials collected by the Mongolian Academy–American Museum Expeditions, including James Hopson (figure 5.1F), Altangerel Perle (figure 4.4G), Guillermo Rougier (figure 3.5G), and occasionally other Mongolian and American paleontologists (see figure 3.5).

I met Malcolm McKenna for the first time in 1963, when I attended the International Zoological Congress in Washington. I knew that he was especially interested in Mongolian mammals. In 1964 we collected the first Late Cretaceous mammals in Mongolia, and I informed Malcolm about our findings. In April 1965, he arrived in Warsaw for the first time to see our – modest at that time – collection of Mongolian mammals. From that time forward, our roads often crossed, and we became good friends. Malcolm helped Polish paleontologists in various ways. Among others, he sent us the casts of Cretaceous and Tertiary mammals collected by the Central Asiatic Expeditions in Mongolia and a number of papers reporting the results of their work in Mongolia. This was a great help to our studies. He also often corrected the English of

our papers. In May 1991 he was elected a foreign member of the Polish Academy of Sciences.

In 1969 I published a preliminary report on the eutherian fauna from Bayan Zag (Kielan-Jaworowska 1969b), in which I erected a new genus and species, *Kennalestes gobiensis* (the generic name erected in honor of Malcolm McKenna). In the same paper I figured two beautifully preserved specimens of *Zalambdalestes*. In addition to these two taxa, I mentioned the presence of a relatively large, incomplete dentary, which I subsequently recognized as belonging to *Deltatheroides*. The most intriguing specimen in the collection was a tiny skull of a eutherian mammal, associated with two dentaries in occlusion (discussed in chapter 14).

In the summer of 1966, Malcolm arrived in Warsaw with his wife, Priscilla, and two older children, Douglas and Katharine. All the family stayed with us, and I went with them to the Białowieża forest reservation to see the breeding of the European bison. From Warsaw the McKenna family went to Portugal and then on a trip all around the world.

The first three years of the Mongolian Academy–American Museum Expeditions did not bring spectacular discoveries of Cretaceous mammals or dinosaurs. The situation changed in 1993, when the party under the leadership of Michael Novacek and Demberlyin Dashzeveg discovered the fossil locality known as Ukhaa Tolgod in the southeastern part of the Nemegt Basin (Dashzeveg et al. 1995). This site has produced the richest collection of Mesozoic mammals and small dinosaurs in the world. The age of the productive Ukhaa Tolgod beds is regarded by the American paleontologists as an equivalent of the Djadokhta Formation of Bayan Zag. However, it is possible that the beds might be a bit younger, perhaps intermediate in age between the Djadokhta and Baruungoyot Formations. The enormous collection of early mammals and mammaliaforms, exceeding five hundred specimens, is temporarily housed at the American Museum of Natural History in New York.

Not all of the specimens collected have been as yet prepared from the rock. Papers based on this collection continue to be published, increasing our knowledge about the evolution of mammals during the time of dinosaurs.

Mongolia-Japan Joint Paleontological Expeditions

The Mongolia-Japan Joint Paleontological Expeditions (organized from the Japanese side by the Hayashibara Museum of Natural Sciences) explored paleontological sites throughout the Gobi Desert, beginning in 1993 (Watabe 2000; Suzuki and Tsubamoto 2010). Paleontologists from other institutions in Austria, China, France, Italy, Japan, Korea, and the United States have also worked with Mongolian scientists in the Gobi.

In 2002, after arriving in Ulanbaatar with the Nomadic Expedition (see chapter 4), I spent two days, mostly with Jørn Hurum (a Norwegian, my former student from the University of Oslo, also a participant in the expedition; see figure 1.4C), at the Paleontological Center of the

3.5. A. The new building of the Paleontological Center of the Mongolian Academy of Sciences in Ulanbaatar, built as a gift by the Japanese government and the Hayashibara Museum of Natural Sciences. The building was finished in 2000. B–G. Selected Mongolian, Japanese, and American paleontologists who participated in studies on materials collected by the Mongolian Academy–American Museum of Natural History Expeditions and by other expeditions. B. Mahito Watabe. C. Nao Kusuhashi. D. Demberlyin Dashzeveg (photo taken in 2002). E. Michael J. Novacek in his laboratory in AMNH. F. John Wible. G. Guillermo Rougier.

A. Courtesy of Mahito Watabe. D. Courtesy of Jørn H. Hurum.

Mongolian Academy of Sciences, examining the collections. Thirty-one years ago, the center was housed in wooden barracks that were divided into several rooms. To my astonishment, the barracks had been partially demolished to make way for a nice-looking building for the Paleontological Center (Figure 3.5A). The building included a number of roomy offices for the scientists, ample space on the first floor for a small paleontological exhibit with several mounted skeletons of dinosaurs, a large preparation laboratory, and a huge storage area for fossils in the basement. We learned that the new center was a gift from the Japanese sponsors of the Mongolia-Japan Joint Paleontological Expeditions. Part of the building was reserved for the Japanese paleontologists to work in during their visits in Ulaanbaatar and for the storage of their equipment during the rest of the year.

In 2000, Japanese paleontologists (see Figure 3.5B, C) began to publish reports of the expeditions in book form, as part of the *Research Bulletin* of the Hayashibara Museum of Natural Sciences. Three volumes have appeared so far. The first two included almost exclusively the reports of the consecutive expeditions and some logistic issues. In the second volume, Watabe, Sonda, and Tsogtbataar (2004) published a short article containing the list of presentations and publications on the joint expeditions of 2000–2002. A similar list, covering the years 2003–2009, was published by Suzuki and Tsubamoto (2010) as volume 3 of the *Research Bulletin*.

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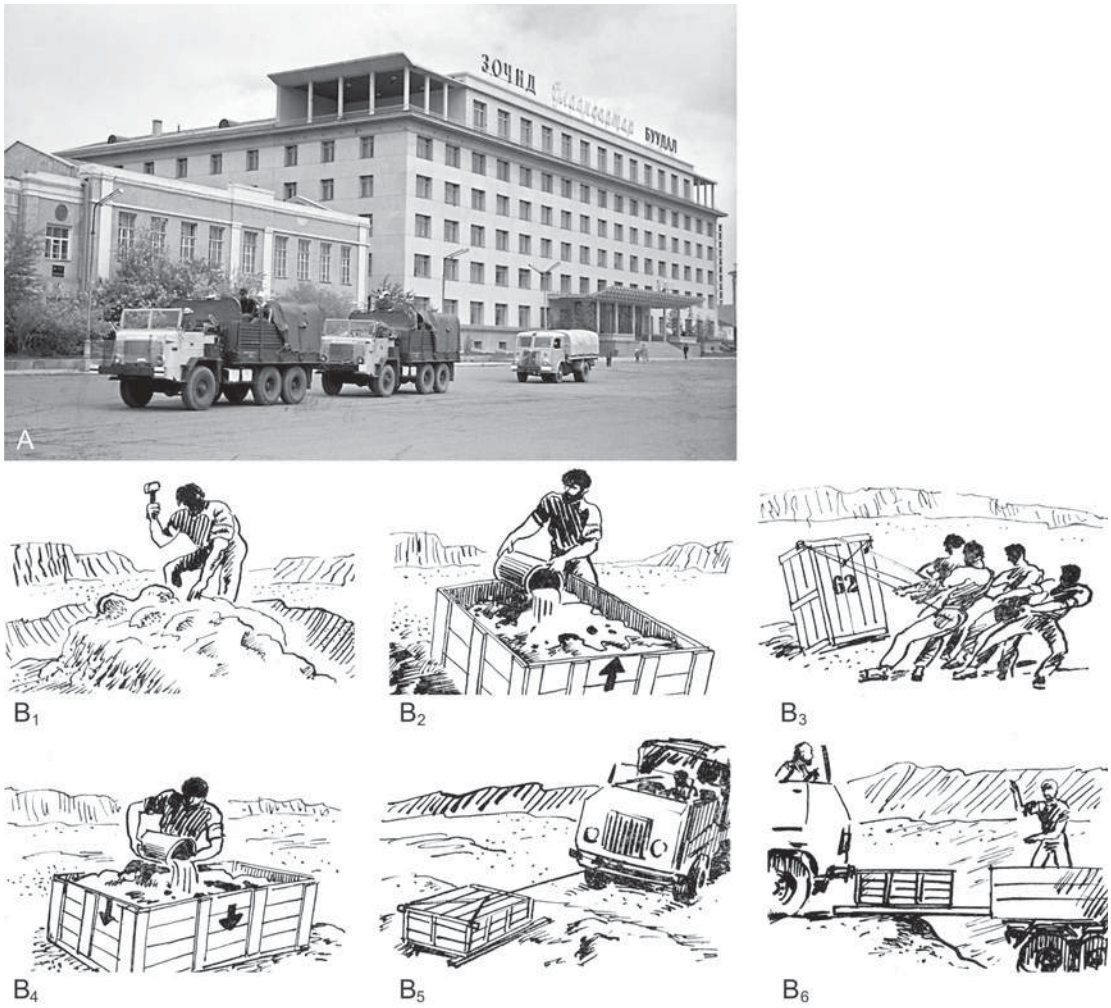


4.1. A. Three trucks used in the Polish-Mongolian Paleontological Expedition in 1965, leaving Ulanbaatar from the hotel, on the way to the Gobi Desert. B. Drawings illustrating consecutive stages of making a monolith. B_1. Excavating bones from the rock. B_2. Placing the wooden frame around a block of the rock with the bones and immobilizing it with plaster of paris. B_3. Turning over the monolith. B_4. Filling the lower side of the monolith with plaster of paris. B_5. Moving the monolith with a truck windlass from its original position to a launching ramp. B_6. A truck pushes the monolith from a ramp onto the other truck.

A. Archive of the Institute of Paleobiology in Warsaw. Photograph by R. Gradziński. B. Artwork by Maciej Kuczyński, slightly emended by Aleksandra Hołda-Michalska.

The Polish-Mongolian Paleontological Expeditions, 1963–1971, and the Nomadic Expedition, 2002

4

Introduction

ALTHOUGH THIS IS NOT A BOOK ABOUT DINOSAURS, DURING THE course of the Polish-Mongolian Paleontological Expeditions we collected skeletons of dinosaurs that were coeval with early mammals, and we spent a lot of time and effort in their excavation and later on in their study. These giant skeletons are obviously much more spectacular than those of minute mammals, the Lilliputians of the Mesozoic world. Accordingly, the illustrations in this chapter are mostly of the skeletons of dinosaurs excavated by us. Although the discovery of fossil mammals was our goal during these expeditions, they are discussed mostly in later chapters of the book, which are devoted to particular groups of mammals. But let me "begin with the beginning."

During the Second World War, the Germans occupied Poland for more than five years. The official aim announced by Adolph Hitler and his accomplices was extermination of most Poles, with the rest (those who could "count to 500, sign their name, and not necessarily be able to read") turned into German slaves. However, at the risk of the death penalty, Poles organized a clandestine countrywide system of education at all levels. High school teachers and university professors continued to give lessons and lectures in private homes. Gradually, a secret network of instruction was established, constituting part of the Polish resistance. At the University of Warsaw in 1944, approximately 300 members of the academic staff and 3,500 students participated in these studies. The majority of students served as underground soldiers at the same time. I attended the clandestine high school; lessons were conducted in the private homes of the pupils, in groups of six to eight persons. In 1943/1944 I attended the clandestine University of Warsaw, studying zoology. These classes were suspended after the Germans put down the Warsaw Uprising of August–September 1944 (in which I took part as a medic). Systematically, block by block, and in cold blood, the Germans blew up and burned down my city. Intense evil guided this job. The result was more than 200,000 murdered civilians, the total destruction of 85 percent of Warsaw, and the expulsion of all the surviving inhabitants. The ruined and burned down city was left empty: "annihilated forever," according to Hitler's order.

But in December 1945 the university reopened. That was when I met Professor Roman Kozłowski (1889–1977; figure 1.1B, on the right), the great Polish paleontologist, my dear teacher and supervisor (see Kielan-Jaworowska and Urbanek 1978).

Due to Professor Kozłowski's influence, I decided to study paleontology, being especially interested in the evolution of vertebrates, including humans. However, as the majority of Phanerozoic sediments in Poland are of marine origin, and until recently only a few fossil land vertebrates had been found here, Professor Kozłowski suggested that I study trilobites, the extinct marine Paleozoic arthropods. Later on, I carried out my research on Paleozoic polychaete jaw apparatuses, preserved in Ordovician and Silurian limestones.

I spent some 14 years or so of my early scientific life collecting and describing marine invertebrates, mostly in the Holy Cross Mountains (Góry Świętokrzyskie) in central Poland. Most important from my work on Paleozoic invertebrates were my two monographs on trilobites and one on polychaete jaw apparatuses, all published as separate volumes of *Palaeontologia Polonica*, and not cited herein. I almost never had time to go on vacation in the summer, as I used to spend the three summer months in the mountains carrying out fieldwork. I made one exception in 1950, when my colleagues from the Mountaineering Club invited me to join them in a trip to a lake, Morskie Oko (Sea Eye) in the Tatra Mountains, to try high mountain climbing. Despite my interest in sports, I did not enjoy the climbing. But this trip was quite worthwhile. This was when I met Zbigniew Jaworowski (Zbyszek), at that time a student of medicine at Jagiellonian University in Kracow, and we became close friends. Eight years later, in 1958, we were married.

The pre-war building of the Department of Geology and Paleontology, in the central part of Warsaw University on Krakowskie Przedmieście Street, close to the old town, burned down during the first days of the war in September 1939. When the university reopened in 1945, Professor Kozłowski began his first lectures on paleontology in a small room in his private apartment in the middle of the town, miraculously spared from the Teutonic barbarism. It was there that I heard for the first time about the Central Asiatic Expeditions of the American Museum of Natural History.

In Warsaw in 1946 we had no contact with Soviet paleontologists, but we learned eventually that the Paleontological Institute of the Academy of Sciences of the Soviet Union in Moscow sent the first of three expeditions to Mongolia in 1946. (There were subsequent expeditions in 1948 and 1949.) In my most audacious dreams I did not think that one day I would also go there or that 14 years later I would organize and lead a new series of the expeditions to the Gobi Desert. But it happened.

Roman Kozłowski, the organizer and first director of the Institute of Paleobiology (originally called Department of Paleozoology) of the Polish Academy of Sciences in Warsaw retired at the end of 1960. Beginning in January 1961, I replaced him. About that time, the Academy of Sciences of the Mongolian People's Republic was established in Ulaanbaatar. In 1962, a delegation of the Presidium of the Polish Academy of Sciences traveled to Mongolia to sign an agreement on scientific cooperation between the two academies for a period of three years (1963–1965). I

prepared a proposal with plans for three years of the Polish-Mongolian Paleontological Expeditions, to be included in the agreement, and Professor Kozłowski (figure 1.1B), as a member of the delegation, took my proposal with him. The proposal was well received by the authorities of both academies, and upon the return of the delegation to Poland, I was appointed by the authorities of the Polish Academy of Sciences to organize the expeditions and take on their scientific leadership.

Organization and Methods of the Expeditions

My colleagues and I conducted fieldwork in Mongolia over eight seasons between 1963 and 1971. Our first expedition in 1963 was simply a reconnaissance. The most important expeditions took place in 1964, 1965, 1970, and 1971. There were also three "mini-expeditions" in 1967, 1968, and 1969, during which small groups of paleontologists collected fossils on the surface of outcrops, without carrying out excavations (Kielan-Jaworowska and Dovchin 1969; Kielan-Jaworowska and Barsbold 1972).

Organization of large expeditions is logistically difficult, involving coordinating the efforts of many persons. In each of the four large expeditions there were upward of 15 persons from the Polish side and several from the Mongolian. In addition, we also hired Mongolian workers on the spot. Thus, the expeditions could involve as many as 30 members each. Preparations for the expeditions were carried out in winter. Since we had to work in isolated desert territory, sometimes hundreds of kilometers from the nearest settlements, we had to be completely self-sufficient. That is why the list of equipment taken was more than 20 pages long.

At the institute in Warsaw we collected everything we might need in the field – all sorts of tools for excavating, glues and brushes, tons of plaster of paris for wrapping and protecting the specimens during transportation as well as materials for packing, boards for making crates, tools for writing and producing technical drawings in the field, a carpenter's shop, and hundreds of other items. We also had a vast quantity of camping equipment – tents, sleeping bags, air mattresses, canvas roofs to be put over tables, field kitchens, table settings, food for 20 persons for three to four months, flashlights and candles, a medicine chest for all possible situations, heavy six-wheel drive trucks (Star 66s), which we borrowed from the state factory of trucks at Starachowice, as well as smaller field vehicles which the institute bought outright. We also had to take petrol for the big trucks in 200 liter gasoline drums. All this equipment was sent from Warsaw by February or March to Ulaanbaatar by rail, where it was received by our Mongolian colleagues. The members of expeditions arrived in Ulaanbaatar by plane in May or June.

We usually spent at least the first two weeks in Ulaanbaatar arranging the formalities and preparing for the road (figure 4.1A). As a rule we also hired additional trucks with Mongolian drivers in order to send immediately as much equipment as possible to the capital of the Southern Gobi province (*ajmak* in Mongolian) – Dalanzadgad, where we hired a fenced place or a shed for storage. At the beginning of each expedition, when we

were staying in Ulaanbaatar, several trips by truck were needed to transport the equipment for a distance of about 600 km to Dalanzadgad, where we had the intermediate storage area – then for some additional 300 km over a nearly roadless terrain to the outcrops of the Nemegt Valley.

The logistics were daunting. A single sauropod skeleton excavated by us in 1965 at Altan Uul IV (also known as Altan Ula), together with surrounding rock, weighed 12 tons. To transport it back to Ulaanbaatar from Altan Uul, a distance of almost 1000 km, required at least four round trips using a three ton truck.

We needed trucks not only for transporting members of the expeditions, equipment, and fossils but also for continuously bringing water from the wells to our camps, often over a distance of some 80 km, and for collecting fuel wood of *saksauul* (genus *Haloxylon*), a shrub that grew in profusion in this semi-desert. We used this in our field kitchens for boiling drinking water and cooking our food. With these trucks, we drove Mongolian workers from their home villages to our camps and back, and we sent reconnaissance teams to various places. At the end of expeditions, we used the trucks to wind up camps and transport people, equipment, and fossils back to Ulaanbaatar. Maciej (Maciek) Kuczyński (figure 4.8), our technical organizer, who had extensive experience in organizing speleological and scientific expeditions to different countries, was in charge of this transportation puzzle. In the evenings sitting together, we discussed these complex organizational issues. Often Teresa Maryańska joined us.

Teresa Maryańska (figure 4.4E) was born in 1937 in Warsaw. She obtained a master's degree in geology at the University of Warsaw in 1960 and a Ph.D. in paleontology in 1967 on the basis of a paper on Tertiary bryozoans. Beginning in 1961, she worked at the Museum of Earth in Warsaw, becoming deputy director of the museum in 1976. She retired in 2006. Teresa participated in four big expeditions to Mongolia organized by the Institute of Paleobiology in 1964, 1965, 1970, and 1971, being one of the most active members. Her main scientific interest concerned ankylosaurid dinosaurs, about which she published several papers (see, for example, Maryańska 1977). She also collaborated with Halszka Osmólska, with whom she published jointly many papers on pachycephalosaurid dinosaurs, protoceratopsids, hadrosaurians, and other groups.

During our expeditions we also faced the problem of protecting large specimens during transportation. We decided to use a method applied by the Mongolian Expeditions of the Academy of Sciences of the Soviet Union in 1946–1949. We called it "making monoliths." Our method, shown in figure 4.1B, which is also the method described by Japanese and Mongolian colleagues (see Watabe, Sonda, and Tsogtbataar 2004), differs from that commonly used in the United States of making irregular plaster jackets on completely excavated specimens. In our method, when a skeleton, or a part of it, was exposed, we took exact measurements in order to build a wooden frame around it. The frame was put over the bones in the rock, and the skeleton was covered with plastic foil and cellucotton; then we poured in plaster to fill the empty spaces in the frame.

In order to make the monolith lighter, we put pieces of wood, dry *Haloxylon* branches, and empty food cans into it. When the frame was filled with plaster, we let it set overnight, and the next day we nailed the wooden lid over the frame. Then we dug a trench around the base of the frame and as much as possible below the specimen, put a rope around the bottom corners, and turned the crate over. Often, all male members of the expedition took part in turning a monolith over, half of them pulling the ropes on one side, the others pushing the crate from the other side. When the monolith broke loose from the underlying sediment and was overturned, we filled the empty spaces with plaster, let it set, and nailed the lid from the other side. We painted the symbol of the locality and a number on the resulting crate, and only then was the monolith ready for transportation. The monoliths were heavier than the plaster jackets, but the bones inside were better protected to survive the 1000 km journey back to Ulaanbaatar along the bumpy roads. An advantage of monoliths, too, was that their rectangular shape allowed a more economic packing on truck platforms. In addition, people could put inflatable mattresses on the monoliths so they could sit or even sleep on them during the long journeys back.

When preparing the first proposal for the expeditions to Mongolia, I was aware that in the Cretaceous deposits of the Gobi Desert one might find rare skeletons of mammals that lived during the time when dinosaurs ruled the Earth. Before our expeditions, only 11 poorly preserved skulls of Cretaceous mammals or their fragments, found by members of the Central Asiatic Expeditions, were known. The members of the Mongolian Expeditions of the Academy of Sciences of the Soviet Union (1946–1949) had focused their efforts on finding big dinosaurs and did not search in particular for Cretaceous mammals. Because the dinosaurs were already well known when we began our expeditions, our project focused on the search for tiny Cretaceous mammals. Each year we discovered and excavated several nearly complete dinosaur skeletons and a number of their fragments. Children and adults all around the world were fascinated with these extinct giants, and obviously we all were fascinated with dinosaurs, too. But Cretaceous mammals were our priority, and while the greatest difficulty in excavating the skeletons of dinosaurs was related to their enormous size, the issue in searching for Cretaceous mammals was their small size.

The first skulls of Cretaceous mammals found by members of the Central Asiatic Expeditions at Bayan Zag had been relatively large by Mesozoic standards, with skull lengths of 4–5 cm (see Simpson 1925a, 1928a, 1929; and Gregory and Simpson 1926). These skeletons apparently had been exposed for a long time on the surface of the sandstone of the Djadokhta Formation, which crops out there, exposed to wind, rare rainfall, and snow. The bone surfaces of these mammals had been strongly weathered, and the state of preservation was generally poor. Plate 6, shows a reconstruction of the Gobi in the time of the deposition of the Djadokhta Formation, with artwork by the late Karol Sabath. I suspect that

members of the Central Asiatic Expeditions did not search intensively for these Cretaceous mammals – rather, they collected the skulls on the surface, when passing by, concentrating on dinosaurs instead.

As commonly happens when paleontologists arrive at a locality never before searched by specialists, they first find an abundance of fossils accumulated on the surface of outcrops over thousands or even millions of years by weathering. Such was the case when members of the Central Asiatic Expeditions first arrived in Bayan Zag. It was also our good fortune in 1970 when we were looking for fossils at the outcrops of the Baruungoyot Formation at Khulsan, and again in 1971 at Hermiin Tsav, as the localities had never before been searched by paleontologists. The members of the Mongolian Academy–American Museum Expeditions (see chapter 3) were in a similarly lucky situation when in 1993 they began collecting at the Ukhaa Tolgod locality, which was unusually rich in fossils. In all these places, successive expeditions working at the same outcrops had much less success.

In the case of Cretaceous localities that are "rich in fossil mammals," the rocks are not littered with mammal bones. That is why, when searching for them and other small fossils at Bayan Zag in 1964 and 1965, we adopted a method that I described in 1969 in a paper with Naydin Dovchin: "The Cretaceous mammals and lizards at Bayn Dzak, the finding of which was a special interest to our expeditions, occur in a horizontal layer, exposed over a wide area. The weathered sandstone forms an area covered with nodules, that is, concretions of strongly cemented rock, resistant to weathering. Because of the small size of fossils that were being looked for, and their great scarcity, it was necessary to search for them on hands and knees, examining the nodules of strongly cemented sandstone with a magnifying glass" (Kielan-Jaworowska and Dovchin 1969: 11).

In the 1960s, American paleontologists (see chapter 2) began using the method of washing and screening the sediments for collecting Mesozoic mammals and so assembled large collections of isolated teeth, jaws, skull, and postcranial fragments. This method could not be used for the Upper Cretaceous sandstones of the Gobi Desert, as these were too strongly cemented and would not dissolve in water. Additionally, in many parts of the Gobi Desert there was a problem with availability of water. However, the Soviet-Mongolian Expeditions, which began their work in 1969 and continue through the present (renamed Russian-Mongolian), employed this method for collecting mammal fragments from soft sediments of Early Cretaceous (Aptian or Albian) age at the locality of Höövör in Guchinus County (also called Khovboor, Khoobur, and Guchin Us) in the Gobi Desert.

The 1964 Expedition

In 1964 we conducted large-scale excavations in the Gobi Desert. In that year I could not leave Warsaw for a period of three months, and I asked my friend, the late Kazimierz ("Kazik" to his friends) Kowalski, at that time the director of the Kraków Branch of the Institute of Zoology of the

Polish Academy of Sciences, to lead the expedition. Kazik accepted my proposal with enthusiasm.

Kazimierz Kowalski (1925–2007; see figure 4.4A) was an outstanding Polish paleontologist, zoologist, and speleologist. He was the head of the Institute of Systematics and Evolution of Animals of the Polish Academy of Sciences in Kraków from 1960 to 1987, except for five years (1978–1983), which he spent with his family in Algeria as a professor at Oran University. He was the organizer and leader of many expeditions to caves in various European and South American countries. Kowalski published 12 monographs and more than 500 scientific papers. Among other topics, he described Tertiary mammals collected by our expeditions (see, for example, Kowalski 1969, 1974). He is the author of three comprehensive volumes devoted to Polish caves. From 1971 on, he was a member of the Polish Academy of Sciences, and he organized the scientific Station of the Polish Academy in New York. He was also a member of the Polish Academy of Arts and Sciences and in 1996–2000 was its president. In 2005 Professor Kowalski was awarded the title of "Super Colossus" for his achievements in speleology by the Polish Society of Travelers, Alpinists, and Sailors.

In 1964, I traveled to Mongolia for several weeks after the expedition was already working in the Nemegt Valley, some 900 km southwest of Ulaanbaatar. All of the successive expeditions worked under my leadership. Staff of the 1964 expedition included 11 Polish and 4 Mongolian members. When I arrived in June 1964 in Ulaanbaatar, the Mongolian Academy provided me a small Soviet-made field car, a GAZ 69, and a Mongolian driver. I was also accompanied by an employee of the foreign office of the Mongolian Academy, who had spent a year and a half in Poland and spoke Polish. We left Ulaanbaatar driving southward. Immediately after we left town the asphalt road ended and we had to drive off-road, following old tracks left by passing cars. We were driving through practically uninhabited steppe, save for lonely nomad tents (*yurts*) tens of kilometers apart, with rare settlements. The journey to the Nemegt Valley took three days. The first night we spent in a small hotel in Mandal Gob, capital of the Central Gobi *ajmak*.

The next day we arrived in Dalanzadgad, the capital of the Southern Gobi *ajmak*, from which our road turned westward to the Nemegt Valley. We passed the Gurvan Saichan mountain range and stopped for a night at the village of Bayan Dalay, in a hotel set up in two yurt tents. It was my first night in a yurt.

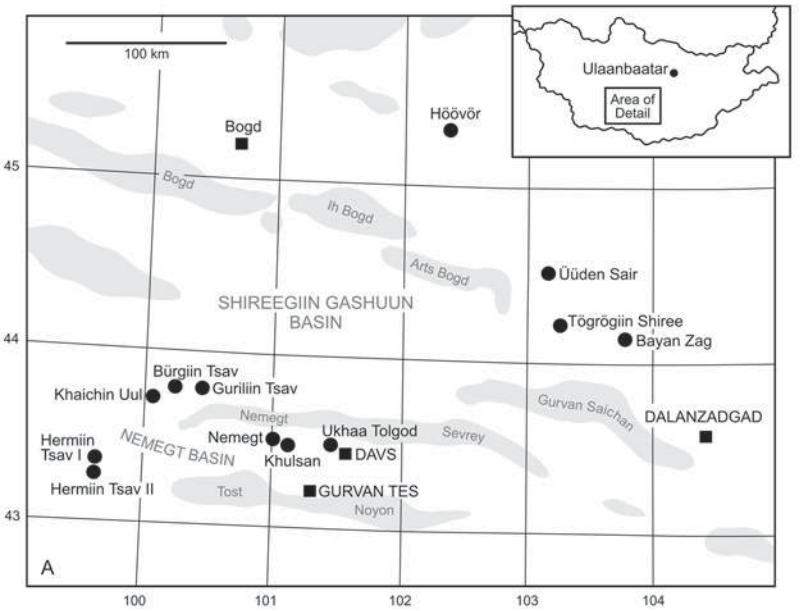
A yurt is a round dome-like tent, with a low vertical wall about 1.6 m tall, all supported on a wooden skeleton (figure 4.2A, B). Yurts come in various sizes. The one in which I spent my first night was some 7 m in diameter. In the middle of the yurt there is a strong, tall supporting pole, surrounded at the top by a round frame. Between the round frame and the top of the latticed vertical wall there extend wooden rafters, which support the sloping roof. This wooden scaffolding is first covered with felt, on which a cover of canvas is placed. The round frame at the top is open,

4.2. A. The structure of the yurt showing its scaffolding. B. Visiting in the yurt, in 1968. *From the left,* Zofia Kielan-Jaworowska, a Mongolian girl, and Halszka Osmólska.

Archive of the Institute of Paleobiology in Warsaw. A. Photograph by R. Gradziński. B. Photograph by W. Skarżyński.

but it can be sealed in case of rain or frost. The wooden floor is covered with camel-hair rugs. In the vertical wall there is a low wooden door, but the middle of the yurt is high and spacious. On hot days, the felt and canvas can be rolled up, exposing the bottom part of the wooden vertical lattice, so allowing wind to pass through and cool the inside of the yurt. I was told that in winter a small iron stove is placed in the center of the yurt to allow this structure to stay warm and cozy. The yurts in which the Mongol nomads live in the southern Gobi are usually smaller than those used for hotels, more like 4–5 m in diameter. As a rule, a family owns two yurts, one used for living, the other for the storage of tools, camel wool, dried meat, cheese, and other necessities.

In the north, the Nemegt Valley is bordered by four mountain ranges composed of Precambrian and Paleozoic rocks, which in the south contact the Upper Cretaceous badlands (figure 4.3A). The sandstone sediments of the badlands were deposited in great rivers and lakes, which



4.3. A. Map of the Cretaceous deposits of the Gobi Desert, yielding dinosaurs and mammals. B. Outcrops of the Nemegt Formation in Nemegt, Nemegt Valley.

A. From Kielan-Jaworowska (1974), emended. B. Archive of the Institute of Paleobiology in Warsaw. Photograph by R. Gradziński.

some 70 Ma flooded the area of what is now the Gobi Desert. Today the sandy, soft Cretaceous sediments are slowly being eroded by wind and occasional rainfall, forming picturesque gullies with nearly vertical walls (figure 4.3B). In the Nemegt Valley, younger rocks of Paleocene age (some 65–60 Ma old) crop out, as, for example, do those in Naran Bulag and Tsagaan Khushuu in the southern part of the valley.

4.4. Selected members of the Polish-Mongolian Paleontological Expeditions, in 1944 and 1945: A. Kazimierz Kowalski (1925–2007). B. Halszka Osmólska (1937–2008). C. Ryszard Gradziński. D. Rinchen Barsbold. E. Teresa Maryańska. F. Ongoj (*on the left*) and Wojciech Skarżyński. G. Altengerel Perle. H. Zofia Kielan-Jaworowska and Demberlyin Dashzeveg (1937–2010), after the 1965 expedition, at the airport waiting for a plane. I. Members of the "mini expedition" at Bayan Zag in 1968. *From the left,* Halszka Osmólska, Naidin Dovchin, Zofia Kielan-Jaworowska, Urigdżiibu (the driver), and Wojciech Skarżyński.

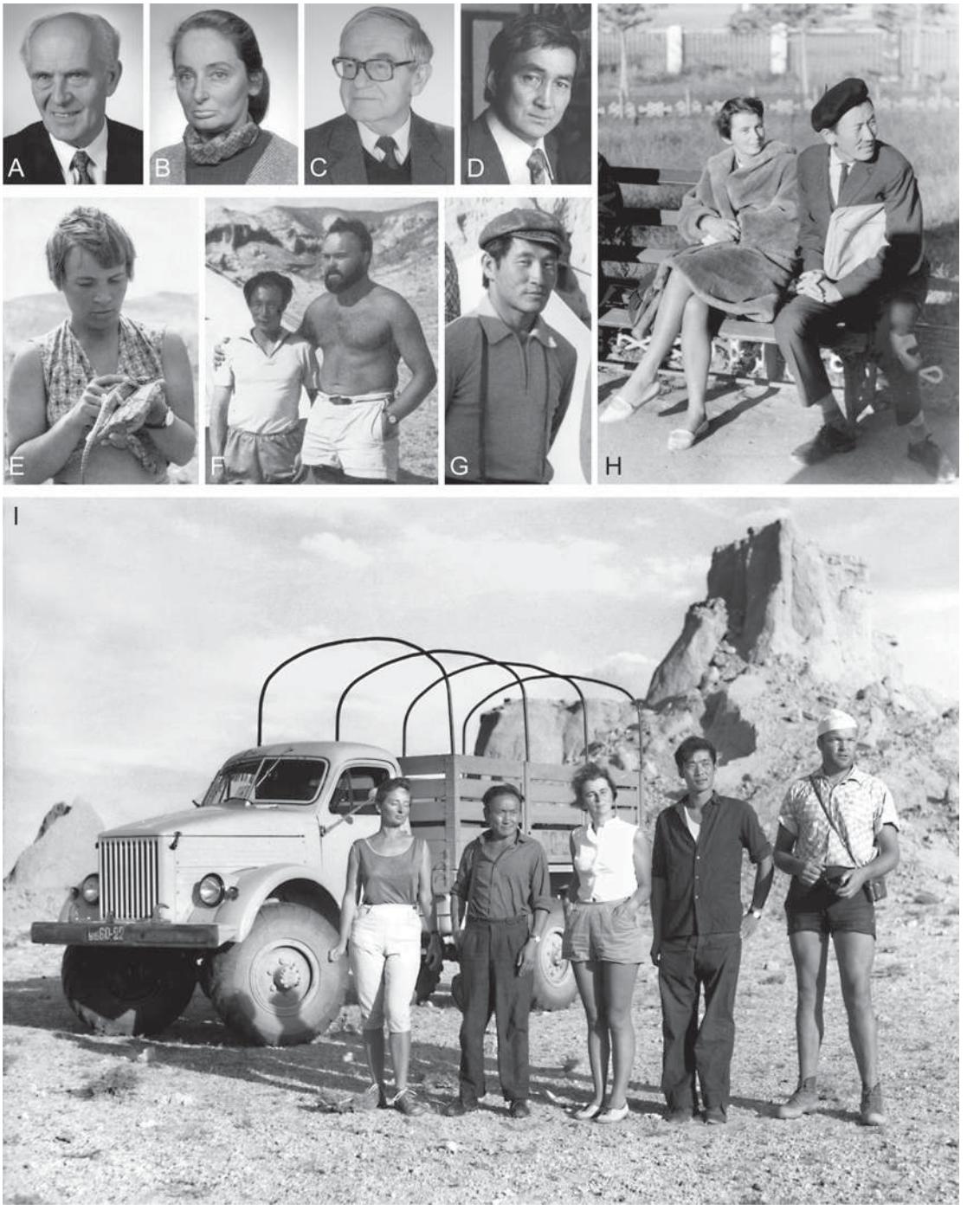
A. Courtesy of Barbara Rzebik-Kowalska. B. Courtesy of Agata Osmólska. C–I. Archive of the Institute of Paleobiology in Warsaw. E. Photograph by R. Gradziński. I. Photograph by W. Skarżyński.

Although numerous paleontological and geological expeditions from various countries had worked before us in Mongolia, some parts of the Gobi Desert remained, as far as general topographical and geological recognition is concerned, completely blank. Fortunately, our chief geologist Ryszard Gradziński ("Bryś" to his colleagues), hard worker that he is, decided to prepare a topographical map of parts of the Nemegt Valley as well as geological profiles of the main outcrops.

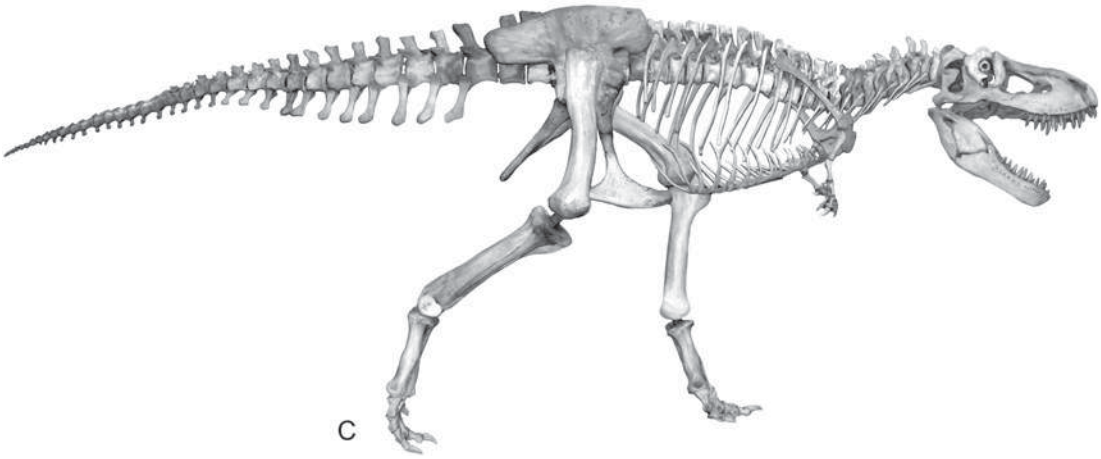
Ryszard Gradziński (figure 4.4C) was born in Kraków in 1929. He received his Ph.D. from Jagiellonian University in 1962. For 20 years he taught geology at Jagiellonian University, and in 1970 he took up a post at the Kraków Branch of the Institute of Geological Sciences of the Polish Academy of Sciences. Gradziński published over 170 scientific papers and seven books and participated in three Polish-Mongolian Paleontological Expeditions (in 1964, 1965, and 1970). As early as in the first part of the series Results of the Polish-Mongolian Paleontological Expeditions, published in 1969, Gradziński, in collaboration with geologist Jerzy Lefeld and geologist-paleontologist Józef Kaźmierczak, published a 52-page paper, entitled "Geographical and Geological Data from the Polish-Mongolian Paleontological Expeditions," containing 35 figures and three photographic plates (Gradziński et al. 1969). In part II of the Results, which appeared in 1970, he published his *doctor habilitatus* monograph, entitled "Sedimentation of the Dinosaur-Bearing Upper Cretaceous Deposits of the Nemegt Basin, Gobi Desert." When I participated in the Nomadic Expedition in 2002 (see below), numerous members of this expedition had GPS sets, but they seldom used them in the Nemegt Basin, saying that the maps and profiles in Gradziński et al. (1969) were so accurate that GPS was not necessary.

When I arrived in the Gobi Desert in 1964, the expedition had already been working at Tsagaan Khushuu, in the southern part of the Nemegt Valley. I met there the late Demberlyin Dashzeveg (1936–2010), a Mongolian paleontologist (figure 4.4H) and a specialist on Tertiary mammals, who in the winter of 1964/1965 spent a month at our institute in Warsaw. Dashzeveg was a very efficient prospector for small mammals and a competent paleontologist. He later visited Warsaw several times, as did other Mongolian paleontologists, and I published a number of papers on Cretaceous mammals in collaboration with him.

Dashzeveg was born in Eroo in Mongolia in 1937. In 1961 he graduated from the Geo-Exploratory University in Moscow with a bachelor of science, and in 1971 received from the same university the degree of a candidate of sciences (corresponding to a Ph.D. in Western countries). Throughout his scientific life he worked at the Geological Institute of the Mongolian Academy of Sciences in Ulanbaatar. When the political situation in the so-called Eastern Bloc countries changed around 1989, Dashzeveg (with approval of the authorities of the Mongolian Academy of Sciences) suggested to Michael Novacek, deputy director of the American Museum of Natural History in New York, that they organize joint Mongolian Academy–American Museum Expeditions to Mongolia. The



expeditions started in 1990. Their greatest achievement was the discovery in 1993 of the locality Ukhaa Tolgod in the Nemegt Basin, which yielded several hundreds of specimens of Cretaceous mammals and usually well preserved skeletons of dinosaurs, which are now temporarily housed at the American Museum of Natural History in New York.



My fondest memory from my stay at Tsagaan Khushuu in 1964 is the excavation of the exquisitely preserved skeleton of a young individual of a tyrannosaurid dinosaur *Tarbosaurus bataar*, (figure 4.5A) found by Gwidon Jakubowski, a paleontologist from the Museum of Earth in Warsaw. The skeleton was nearly complete, lying on its side with its head thrown back and hind legs drawn up. We had often observed dead camels in a similar position in the desert. The forelimbs, as typical for

tyrannosaurid dinosaurs, were so short that the animal could not even reach its mouth with them. Paleontologists suggest that the short forelimbs of these giant carnivorous dinosaurs (e.g., the North American *Tyrannosaurus rex*, which is similar in general appearance to the Asiatic *Tarbosaurus bataar*) served to anchor the front part of the body against the ground, when the animal was rising from a resting position.

The largest skeletons of *Tarbosaurus* collected by our expeditions were almost 13 m in length, similar to those of *Tyrannosaurus*. Before the anatomy of the Asiatic *Tarbosaurus* had been studied in detail, several paleontologists suggested that North American and Asiatic tyrannosaurids might belong to the same genus. However, a detailed comparative study of the skull structure of the Asiatic and North American tyrannosaurids published in 2003 by Canadian, Norwegian, and Polish paleontologists demonstrated that *Tarbosaurus* and *Tyrannosaurus* are separate genera and are likely not even sister taxa (Currie 2003; Currie, Hurum, and Sabath 2003; Hurum and Sabath 2003).

In the nineteenth and twentieth centuries, up to the late 1970s, bipedal dinosaurs such as large carnivores and numerous herbivores of the order Ornithischia had been posed in a semi-erect, sometimes almost vertical posture. The Gobi Desert skeletons of these dinosaurs recovered by the Soviet paleontologists in the 1940s were first exhibited in this position at the Paleontological Museum in Moscow (e.g., *Tarbosaurus bataar* and *Saurolophus angustirostris*). Such was the posture of a *Tarbosaurus* skeleton in the Municipal Museum in Ulaanbaatar and of many skeletons of bipedal dinosaurs in other paleontological museums around the world. Likewise, in our first exhibition, *Dinosaurs from the Gobi Desert*, which opened in Warsaw in 1968, we exhibited the skeletons of *Tarbosaurus* and *Gallimimus* in this semi-erect position, as accepted at that time (figure 4.5B). Similarly, the reconstructions of all the bipedal dinosaurs mounted in Chorzów's Park of Culture in Silesia (in southeastern Poland) stand very tall, in the semi-erect position (see figures 1.1A and 1.2A).

Such a posture was inherited from the nineteenth-century idea that dinosaurs were clumsy, slow-moving creatures. The late American paleontologist, Professor John H. Ostrom, from Yale University in New Haven, Connecticut, a dinosaur specialist and an expert on the origin of birds, published several papers in the 1960s and 1970s on a variety of small carnivorous and other dinosaurs. Ostrom had been a friend of Polish paleontologists and visited our institute in Warsaw many times, discussing the structure and relationships between the various groups of dinosaurs with our specialists. His meticulous work on the anatomy of dinosaurs indicated that some dinosaurs were likely "warm-blooded" rather than all being "cold-blooded," as thought before. In one of his popular articles, Ostrom published a reconstruction of a running *Deinonychus* drawn by the eccentric student of paleontology, Robert T. Bakker, an extremely talented artist. In 1986, Bakker published his well-known book *The Dinosaur Heresies*, in which he argued for high activity and endothermy

4.5. A. Excavation of a young individual of *Tarbosaurus bataar* (Maleyev, 1955) at Tsagan Khushu during the 1964 Polish-Mongolian Expedition. B. The same skeleton after being prepared from the rock, mounted in a semi-erect position, in the exhibit *Dinosaurs from the Gobi Desert,* in Warsaw in 1968. C. Another skeleton of *Tarbosaurus,* mounted in a horizontal position of the lumbar and thoracic vertebrae, at the Institute of Paleobiology in Warsaw.

Archive of the Institute of Paleobiology, Warsaw. A. Photograph by R. Gradziński. B. Photograph by W. Skarżyński. C Photograph by M. Dziewiński.

in dinosaurs and published several beautiful reconstructions of running dinosaurs.

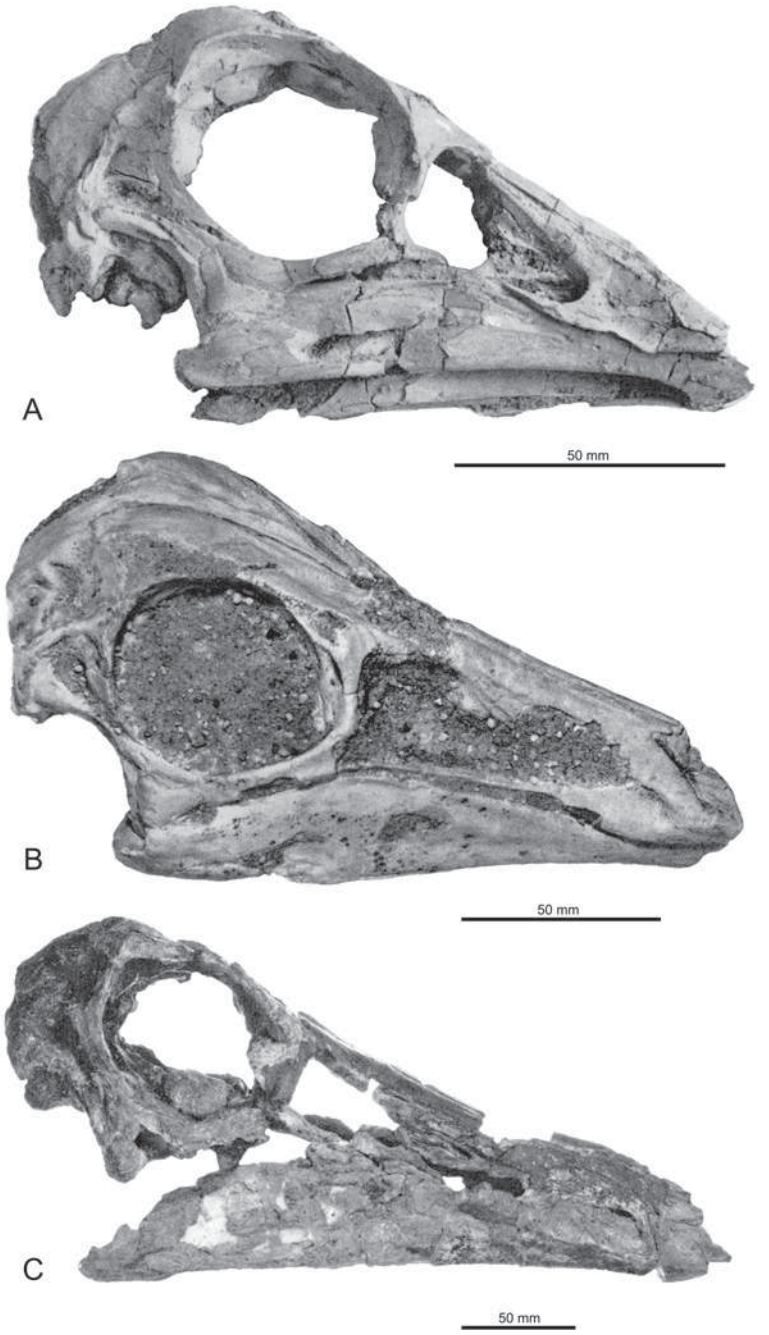
Another source of evidence for activity and endothermy in dinosaurs were the studies of the French anatomist and paleontologist, Professor Armand de Ricqlès (see chapter 10 and plate 5D) from the University of Paris VII, who studied the histology of the bones of ancient vertebrates. He demonstrated that dinosaur bone microstructure and the details of the Haversian canal system more closely resemble the bone histology of birds and mammals than that of modern reptiles. Another talented person who painted reconstructions of running dinosaurs is an American artist from Baltimore, Gregory S. Paul. Greg received training as an artist and is an amateur paleontologist of unusually high qualifications. He has written a number of books with reconstructions of dinosaurs.

Once the notion of sluggish dinosaurs had been put to rest, many museums all around the world faced the problem of re-mounting their dinosaur skeletons. This was recently done at the Museum of Evolution of the Institute of Paleobiology in Warsaw. My colleague Jerzy Dzik (now director of the Institute of Paleobiology) supervised the mounting of a cast of the skeleton of an adult specimen of *Tarbosaurus* from the Nemegt Formation, using bones from several specimens of approximately the same size, and displayed with the dorsal vertebrae in a horizontal position (see figure 4.5C).

In 1964, after my departure from the field, the Polish-Mongolian Expedition moved to another locality in the northern part of the Nemegt Basin, where they were able to collect another skeleton of *Tarbosaurus*, along with several isolated dinosaur bones. At different localities in the Nemegt Basin, in sediments of the Nemegt Formation, skeletons of *Tarbosaurus* are among the most common dinosaurs found. This seems contrary to the wisdom of ecology because, in any recent ecological community, the number of carnivores is far lower than the number of herbivores. A possible explanation for this anomaly might be that the Cretaceous sandstone of the Nemegt Formation was deposited during floods, which were more dangerous for the purely terrestrial tyrannosaurids than for herbivorous dinosaurs, which, according to their anatomy, appear to have been semi-aquatic.

At Tsagaan Khushuu, 2 days after my arrival, Wojciech (Wojtek) Skarżyński, the technical assistant of our institute, found an incomplete skeleton of a small dinosaur and began excavating. Next day he uncovered a beautifully preserved skull with large eye sockets and a narrow toothless snout, apparently covered in life with a horny beak (figure 4.6). The skull convinced us that the specimen was an ornithomimid (ostrich-like dinosaur).

Skarżyński (figure 4.4F, on the right), because of his skill and dedication, contributed enormously to the success of our work. Beginning in 1964, he participated in almost all of the expeditions, found several dinosaur skeletons, actively worked on the excavations, and subsequently prepared and mounted the skeletons at the institute. He is descended from



4.6. Three skulls of an ornithomimid dinosaur *Gallimimus bullatus,* all in lateral view. A. Skull of the smallest specimen, found at Bugeen Tsav, GI DPS, 100/10. B. Plaster cast of the skull with the mandible of a young individual from Tsagaan Khushuu, before preparation, ZPAL Mg-D-I/2. C. Incomplete, poorly preserved skull of an adult individual from Tsagaan Khushuu, GI, DPS 100/11.

All photographs originally published by Osmólska, Roniewicz, and Barsbold (1972: pl. XXIX). Archive of the Institute of Paleobiology in Warsaw. Photograph by W. Skarżyński.

the family of the famous Polish painters Juliusz Kossak and Wojciech Kossak, and with this heritage, he is also a gifted sculptor. He produced several restorations of the dinosaurs as they might have appeared in life. His models of the Gobi Desert dinosaurs formed the basis for the construction of a life-size display of dinosaurs, produced in concrete, which we opened in 1975 in the Chorzów Park of Culture in southeastern Poland (see figure 1.2).

Ornithomimid dinosaurs had previously been known from the Late Cretaceous of North America, but only small fragments had been found in the Gobi Desert by the Central Asiatic Expeditions and the Mongolian Expeditions of the Soviet Academy of Sciences in 1946–1949. The skull of a small ornithomimid that we discovered at Tsaagan Khushuu was the first ornithomimid skull ever found in Asia. A few days after this find, I happened upon a much larger, nearly complete skeleton of another ornithomimid. The specimen was preserved lying on its back, with only the neck vertebrae missing. Further excavation revealed, at the very bottom of the specimen, the skull, preserved underneath the pelvis. This is one of the largest ornithomimid dinosaur skeletons known, with an estimated length of 4.5 m, a dinosaur with long forelimbs, armed with claws.

Late in 1966, I took two or three dinosaur bones to our house to examine them more closely over a weekend. I laid them on my desk, which was separated from the office of my husband, Zbigniew Jaworowski, by a thin brick wall. It so happened that, at that time, he had a problem with his low-level beta radiation counter, where the background counts suddenly jumped from about one pulse per minute (probably a world record at that time) to more than ten. He suspected that this was due to an increased emission of radioactivity from a nuclear reactor at his institute, and so he took the counter home to check it in a cleaner environment. But when he switched it on at home, the counts skyrocketed to thousands per minute. Soon we discovered that the dinosaur bones on my desk were the source of this enormous radiation. The next day, his technicians discovered that the concentration of radon in the preparation rooms at our institute where we kept the fossils from Gobi was above the permissible level. So we were forced to place extra ventilation in those rooms.

I gave my husband 32 bones of dinosaurs, turtles, crocodiles, and mammals from the Nemegt Basin, Bayan Zag, and four other localities. Together with his colleague, he soon found that the bones contained natural uranium in equilibrium with most of its daughters: radium-226, polonium-210, and other nuclides. The 75–80 million-year-old (Late Cretaceous) bones from the Nemegt Valley were highly radioactive – nearly twice as radioactive as the Polish uranium ore used by the Soviets to make nuclear weapons. The Paleocene bones (65–55 million years old) from the Nemegt Valley were seven times less radioactive than those from the Cretaceous. Late Cretaceous, Paleocene, Oligocene, Miocene, and Pliocene specimens from all other localities (400–1200 km from the Nemegt Valley) contained practically no radioactivity. Radioactivity of sandstones from the Nemegt Valley was also low. This indicated that uranium had accumulated in the Nemegt Basin bone from percolating ground water in quantities depending on duration of that accumulation. Tiny concentrations of uranium over millions of years had been transported in solution from a distant source, likely granite rocks of mountain ranges a few tens of kilometers away. In their paper published in *Nature*, Jaworowski and Peńsko (1967) outlined the details of the study of these bones and their

radioactive content, together with an autoradiograph of beautiful tracks of alpha particles crossing the Haversian channels of a *Gallimimus* rib from Tsagaan Khushuu.

During the same expeditions where these radioactive samples were collected and in later expeditions, we recovered several skeletons of ornithomimids, unfortunately preserved without skulls. The ornithomimid dinosaurs were described by Halszka Osmólska, Ewa Roniewicz, and Rinchen Barsbold in 1972 and assigned to a new genus and species named *Gallimimus bullatus*. *Gallimimus* was made into a film star by Steven Spielberg's 1993 film *Jurassic Park* (where, by the way, most of the dinosaurs were from the Cretaceous Period, rather than from the Jurassic Period). In this film there is a beautiful scene showing a herd of our *Gallimimus* gracefully and swiftly running with a *Tyrannosaurus* in hot pursuit.

In 1964, our expedition also conducted fieldwork in Bayan Zag, where members of the field team excavated several dinosaur skeletons. They continued to concentrate on searching for Cretaceous mammals and discovered the first nine skulls of these small mammals. The expedition ended in the middle of September. Among the paleontologists taking part was Kazik Kowalski, mentioned earlier, who led the expedition; Magdalena Borsuk-Białynicka; and Gwidon Jakubowski, who did not join our expeditions again. Kazik Kowalski (and his co-workers) and Magdalena Borsuk-Białynicka participated in the scientific description of many of the collected fossils, with Magdalena describing various fossils, including rhinoceroses, dinosaurs, and lizards, which are discussed in different parts of the Results of the Polish-Mongolian Paleontological Expeditions series. Later, she started to search for small vertebrates in Early Triassic fissure fillings in southern Poland. She found there, among others, a stem-frog named *Czatkobatrachus*, which she described in cooperation with Susan Evans (see Evans and Borsuk-Białynicka 1998, 2009).

The 1965 Expedition

In 1965 we were joined in the field by several new members. Among these, in addition to Teresa Maryańska, was also another "dinosaur lady," Halszka Osmólska. Osmólska (1930–2008, see figure 4.4B) was born in Poznań. She first studied biology at Poznań University and then moved to Warsaw, where she continued her studies. Beginning in 1955, she worked for more than 50 years at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, progressing from assistant professor to professor. In 1974–1983 she was deputy director of the institute, and in 1984–1989, the director. From 1975 until 1992, she was the editor of *Acta Palaeontologica Polonica* and a member of various scientific societies and committees. At the beginning of her career, Halszka was engaged in studies of the Devonian and Carboniferous trilobites of Eurasia, becoming a well-known specialist. In 1969, she started to study Cretaceous dinosaurs and other reptiles from the Gobi Desert and soon became an authority in this field. She is co-editor (with David B. Weishampel and Peter

4.7. A. Excavation of a large sauropod dinosaur *Opisthocoelicaudia skarzynskii* at Altan Uul in the Nemegt Basin, from the rocks of the Nemegt Formation, during the 1965 Polish-Mongolian Paleontological Expedition. B. Reconstruction of *Opisthocoelicaudia.*

A. Archive of the Institute of Paleobiology in Warsaw. Photograph by R. Gradziński. B. From Borsuk-Białynicka (1977), emended.

Dodson) of the widely acclaimed volume, *The Dinosauria* (Weishampel et al. 2004).

Halszka never studied mammals, but by taking part in numerous Polish-Mongolian Paleontological Expeditions to Mongolia, she made significant contributions to the assembled collection of Cretaceous mammals. She worked with great purpose, entirely devoted to science. She had a serene character and was well known for her sense of humor and modesty. She was my close friend and one of the kindest persons I ever met. She had a happy family life with her late husband Tadeusz – a geologist – and left behind a son, a daughter-in-law, and three grandchildren. Halszka made substantial contributions to paleontology that will stand as an enduring legacy.

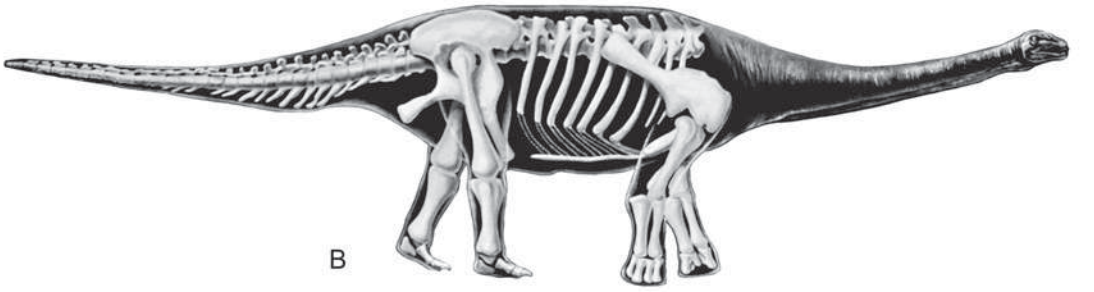
The 1965 expedition was by far the largest, with 15 members making up the Polish team and 6 on the Mongolian side. In addition, during our stay in the Nemegt Valley, we hired 10 Mongolian workers. We spent four months in Mongolia, carrying out excavations in the Nemegt Valley and in Bayan Zag. Some expedition members also travelled to western Mongolia. As we were such a large group, we often divided into smaller teams in order to carry excavations into two different regions at the same time. At the beginning, I joined the group headed for the Nemegt Valley. In 1965 our plan was to start working in the most westerly part of the valley, called Altan Uul IV, where we established our first camp.

One of our greatest problems was water supply. In this hot climate, where the temperature at noon could reach 40° Celsius in the shade, we needed about 4–5 liters of drinking water per person per day. In addition to water for drinking and washing, we needed a great supply of water for plaster, used for making our monoliths, or plaster jackets, protecting the fossils during transportation. Once, every few days, one truck had to make a difficult 40 km trip to a well, bringing back several 70 liter barrels of drinking water, as well as 200 liter barrels with water for plaster.

The area around Altan Uul covers some 100 km^2 of badlands, informally divided from east to west as Altan Uul I, II, III, and IV. Inspecting this region during the first few days yielded some isolated dinosaur bones. On the fifth day our geologist Ryszard Gradziński was lucky to find a concentration of huge, well preserved bones, high up on a wide ledge. We expected that these bones might be from one skeleton, fairly complete, and the next day we started excavating.

The bones near the surface were well preserved and easy to remove from the rock, but bones lying deeper were embedded in hard, heavily cemented sandstone (figure 4.7). After recovering some bones, we knew that we were dealing with a nearly complete skeleton of a sauropod, but the neck and the skull were missing. Sauropods were the biggest quadrupedal dinosaurs, with long necks and tails and relatively small heads.

As the excavations began, I left Altan Uul and travelled to Bayan Zag to join the group searching there for mammals, lizards, and other fossils. When I returned to Altan Uul four weeks later, the sauropod skeleton was already packed. Our team had a serious problem with transporting



this skeleton, as it had been found in an area inaccessible to trucks. The nearest place the trucks could reach was situated some 600 m from the skeleton. The team had to transport by hand a 12 ton skeleton (the estimated weight of the sauropod embedded in rock) over this distance. Workers carried the smaller pieces on their backs. But the larger pieces still enclosed in the rock weighed up to 700 kg. My colleagues improvised a kind of a sledge from a sheet of metal fashioned from a petrol drum, to which they attached strong ropes. The largest pieces were put on the

sledge and pulled by hand to the trucks. At this point a carpenter's shop was constructed, where big crates were crafted, and into those crates the bones were packed.

During the 1965 expedition we finally found the skull of a sauropod in Nemegt, in beds of the same age as those from which the postcranial skeleton had been extracted. During the expeditions, before this material was described, we thought that there was only one species of sauropod that had survived during the latest Cretaceous in the Gobi Desert region. The skull was described by Aleksander Nowiński in 1971, who named a new genus and species, *Nemegtosaurus mongoliensis* (figure 4.8), placing it in the subfamily Dicraeosaurinae, family Diplodocidae.

Magdalena Borsuk-Białynicka (1977) named the large sauropod skeleton preserved without the skull *Opistocoelicaudia skarznskii* (figure 4.7B). She placed it in the family Camarasauridae. In 1983 Soviet paleontologists reported another sauropod genus from the Late Cretaceous (but from the Baruungoyot Formation, which is older than the Nemegt Formation, yielding *Nemegtosaurus* and *Opisthocoelicaudia*) based on an incomplete skull and dubbed it *Quaesitosaurus orientalis*. It seemed almost certain that the two skulls and the postcranial skeleton belonged to three different groups. In the second edition of *The Dinosauria* (Weishampel, Dodson, and Osmólska 2004), *Nemegtosaurus* is assigned to the Nememegtosauridae, superfamily Diplodocoidea, while *Opistocoelicaudia* is assigned to a distant family, Saltasauridae. The minority view that both genera belong to the same family, or are even congeneric (belonging to the same genus), has not been supported. Until associated postcranial and cranial skeletons are discovered, the problem must remain unresolved.

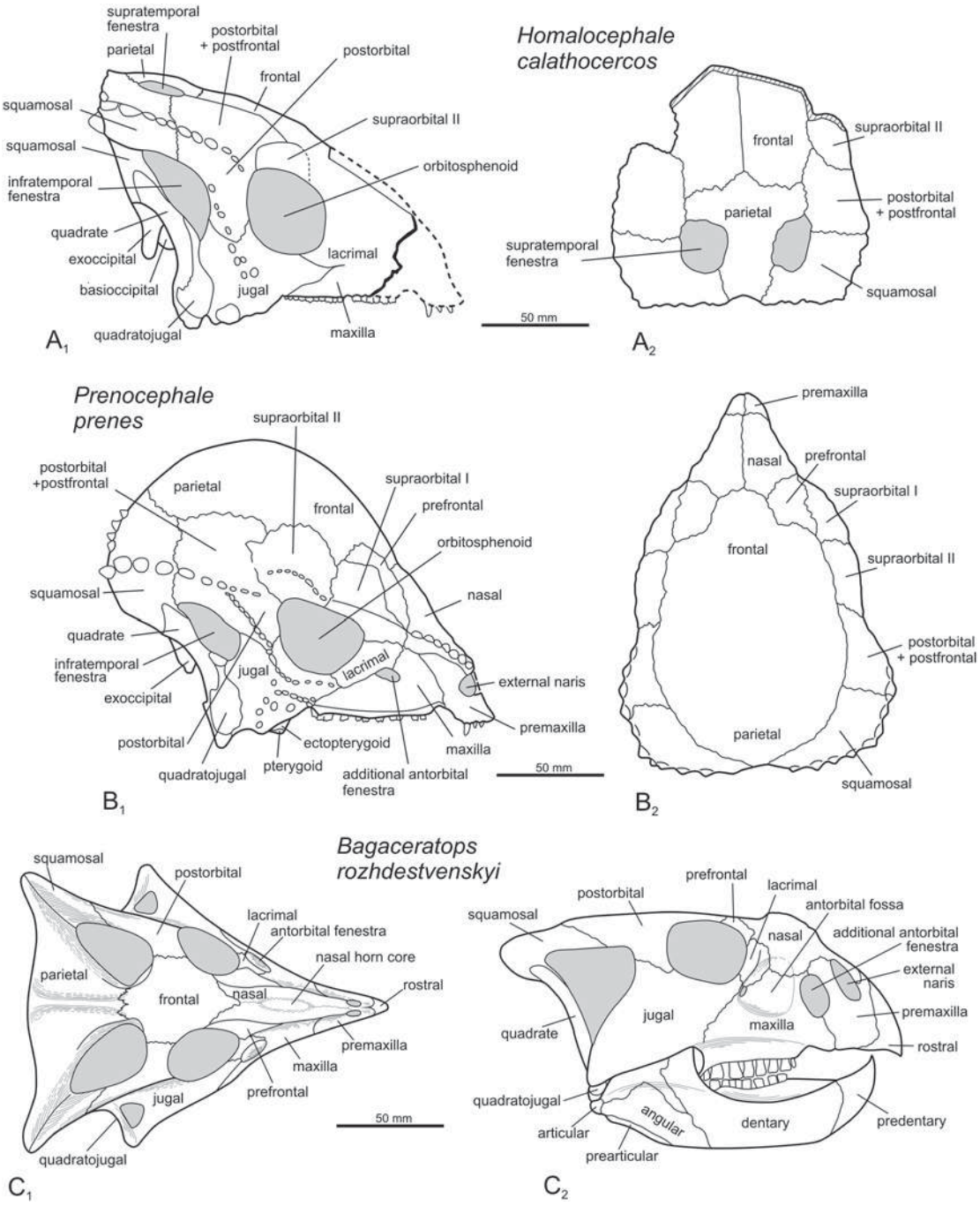
At the end of our stay at Altan Uul IV, we conducted excavations in outcrops of Altan Uul III, where we recovered an incomplete skeleton of another large *Tarbosaurus*. One rainy day, very rare in the Gobi Desert during summer, I was walking alone along the gullies of Altan Uul III and found an unusual skeleton consisting only of complete forelimbs and a shoulder girdle of an enormous size, along with fragmentary ribs. The limbs, as measured later in Warsaw, were 2.5 m long, ending in three powerful fingers armed with claws more than 30 cm long. The bones were scattered on a flat surface of a small hill. This was the first dinosaur skeleton, described in 1970, from materials collected by our expeditions. Halszka Osmólska and Ewa Roniewicz named it *Deinocheirus mirificus* and erected the new family of theropod dinosaurs Deinocheiridae based on this material (Osmólska and Roniewicz 1970). Further studies of various dinosaurs from Mongolia, including the ostrich-like Ornithomimidae, demonstrated that the carpus of *Deinocheirus* was most similar to that of ornithomimids (characterized also by long forelimbs), much more so than to the theropods with short arms. Unfortunately, no other remains of *Deinocheirus* have been found, in spite of intensive fieldwork in the Gobi Desert by numerous expeditions from a variety of countries. The original of this specimen, after description, was returned

4.8. Preparation of the skull of a sauropod dinosaur *Nemegtosaurus mongoliensis* from the Late Cretaceous Nemegt Formation (Nemegt locality, Gobi Desert, Mongolia) at the Institute of Paleobiology in Warsaw, by technical assistant Joanna Skarżyńska. Maciej Kuczyński, the technical organizer of the Polish-Mongolian Expeditions, watches her work.

Archive of the Institute of Paleobiology in Warsaw. Photograph by T. Zborowski.

to Mongolia and is displayed at the Natural History Museum in Ulaanbaatar (see plate 1C1).

On July 28, 1965, our camp at Altan Uul was dismantled, and the expedition moved eastward to the localities of Nemegt, where we remained until the middle of August. During the first days, as usual, we set up camp and were prospecting the terrain for fossil bones in order to decide where we should excavate. Nemegt seemed to us much richer in dinosaur bones than Altan Uul had been. Rinchen Barsbold (figure 4.4D), a Mongolian paleontologist and later the director of the Paleontological Center of the Mongolian Academy of Sciences in Ulaanbaatar, joined us at Nemegt. He soon became a well-known dinosaur specialist and was a great friend of us Polish paleontologists. He co-authored several papers with foreign paleontologists – Russian, American, Chinese, Japanese, and many with Polish dinosaur specialists, including Halszka Osmólska – and was always of great help to us during our visits to Mongolia. In 1965, he was with us from the time we began work at Altan Uul, and he turned out to be a very good dinosaur prospector, quite able to skillfully excavate them from the rocks in the field.



One day, when walking in a canyon (*sayr* in Mongolian), I noticed bones imbedded in a wall, some 3 m above the bottom of the *sayr*. I climbed up and noticed several relatively small dinosaur bones partly sticking out of the wall. I stood on a narrow ledge, and just in front of me, in a small crevice carved in the ledge by a seasonal stream, there was a block of sandstone weighing a few kilograms, containing several broken

ribs visible on the surface and a few phalanges about 3 cm long. I knew I had found a skeleton of a small dinosaur. I turned the block over and was left speechless! I had in my hands an almost complete, beautifully preserved skull of a small dinosaur, about 18 cm long (figure 4.9A), later named *Homalocephale*.

The bones of the cranial roof were over 1.5 cm thick, wrinkled and ornamented, and so well preserved that I could recognize the sutures between the frontal and parietal bones. Viewed from the side, very big orbits were "looking at me." The maxillary bone was well preserved, one side bearing a series of small flat teeth with vertical fan-shaped grooves. I was so amazed with my discovery that I did not notice that, on the ledge on which I stood and wanted to sit down, a brown viper was lying, almost touching my boots. The viper was evidently not enchanted by the unexpected presence of a big person next to her, and appeared nervous. The ledge was too small for both of us, so I decided to push the viper off with my hammer. Unfortunately, a few stones fell down at the same time, one of which killed the viper. Killing one reptile by accident, I started with some feeling of guilt to revive the existence of the other one. Returning for lunch, I took the skull with me. In the evening Teresa sat with me in my tent, and we searched the entire expedition's library in order to try and identify my new find. We decided that the skull belonged to an ornithischian pachycephalosaurid dinosaur, known from the Late Cretaceous rocks of North America but not recorded as yet from Asia. However, in contrast to all previously known pachycephalosaurids (e.g., the Canadian genus *Stegoceras*), in which the bones of the skull roof formed a high dome several centimeters thick, the cranial roof in my new find, although quite thick, was completely flat. The next day we started to recover the rest of the skeleton.

During the 1970 expedition Halszka found in Nemegt another beautifully preserved skull of a pachycephalosaurid dinosaur, designated by Maryańska and Osmólska in 1974 as *Prenocephale prenes* (figure 4.9B). It differed from the skull of *Homalocephale* in being larger and in having a high and strongly domed cranial roof. A third, less complete skull was found in 1971 in beds of the Baruungoyot Formation and was named *Tylocephale gilomorei*, described by Maryańska and Osmólska in 1974. Teresa and Halszka published a 1974 monograph of pachycephalosaurid dinosaurs in which they established a new suborder of ornithischian dinosaurs designated Pachycephalosauria (Maryańska and Osmólska 1974).

Our stay at Nemegt was unusually nice. There was a serene and merry atmosphere, and the wind blew all the time, making the heat bearable. We collected several more or less complete skeletons of *Tarbosaurus* and were quite satisfied with our discoveries as our expedition came to an end.

4.9. A and B. Skulls of two pachycephalosaurid dinosaurs found in the Nemegt Formation on the Gobi Desert. A. *Homalocephale calathocercos,* holotype skull with a flat roof without mandible, in lateral (A_1) and dorsal (A_2) views. B. *Prenocephale prenes* in lateral (B_1) and dorsal (B_2) views. C. The skull of *Bagaceratops rozhdestvenskyi* in dorsal (C_1) and lateral (C_2) views.

A and B. From Maryańska and Osmólska (1974). C. From Maryańska and Osmólska (1975). All in the Archive of the Institute of Paleobiology.

The 1970 and 1971 Expeditions

After the 1965 expedition we decided to suspend our exploration of the Gobi Desert for one year. We needed time for unpacking, preparation,

and preliminary analysis of the collected material. We returned to explore in 1967 and continued fieldwork until 1971. In 1967, 1968 (figure 4.4I), and 1969, the Institute of Paleobiology sent two- or three-person groups of paleontologists as part of a scientific exchange between the Polish and Mongolian Academies of Sciences. These groups worked only at Bayan Zag, not undertaking major excavations but concentrating on collecting mammals, lizards, and other small fossils from the outcrops of the Djadokhta Formation. In 1969 the Polish Academy of Sciences signed another agreement of cooperation with the Mongolian Academy of Sciences. This agreement called for us to organize two large Polish-Mongolian expeditions in 1970 and 1971. With the experience gained in the 1960s, organizing these new expeditions went smoothly. In 1970, 12 people took part on the Polish side, and 3 experienced paleontologists took part on the Mongolian side: Dashzeveg and Barsbold, both well known to us from previous expeditions and from their visits to Warsaw, and Altangerel Perle (figure 4.4G), a young dinosaur specialist. We also hired one Mongolian worker in Ulaanbaatar for the entire expedition – Sambu, who had also worked with us in 1965. Six extra workers were hired in the Gobi Desert.

In 1970 we were not the only paleontologists working in Mongolia. In 1969, returning from our "mini-expedition," I met in Ulaanbaatar colleagues from the Paleontological Institute in Moscow. They had just arrived in Mongolia to sign an agreement with the Mongolian Academy of Sciences for organization of five joint Soviet-Mongolian Expeditions for 1970–1974. Subsequently, the agreements were prolonged several times, right up to the present day. During the 1970 and 1971 expeditions, we conducted fieldwork in parallel with the Soviet-Mongolian group, sometimes not far away from one another, and we often visited each other. Barsbold (figure 4.4D), who was theoretically the head of the 1970 Mongolian group in our expedition, in fact spent most of his time with the Soviet-Mongolian Expedition. That year the Soviet group was enormous – comprising 60 people. They were divided into several subgroups, carrying out fieldwork in the Gobi Desert and other parts of Mongolia. These expeditions continue to today, not only in the Gobi Desert but also in the territories of northern, eastern, and western Mongolia. Their scientific results, published in Russian, have resulted in over 50 volumes.

In 1970 we started fieldwork later than usual, arriving in Ulaanbaatar in three successive groups during the second half of June and beginning of July. We began our work at Bayan Zag in early July. The main objective there was, as usual, to search for Cretaceous mammals. This was our sixth visit to this locality, and year after year we found fewer and fewer specimens. Although we were searching intensively with a large group during the two weeks, we found only six incomplete mammal skulls and a few more specimens of lizards and small dinosaurs. Our next destination was the locality Nemegt in the Nemegt Basin, where we excavated several skeletons of dinosaurs. One evening we were invited to a party put on by the Russian-Mongolian group. Another evening they visited us.

After supper we all sat long around the fire listening to beautiful Russian and Mongolian songs.

During the second half of our stay at Nemegt, we concentrated mostly on exploring the beds of the Baruungoyot Formation, which have also previously been referred to as the Lower Nemegt Beds (for example, see Gradziński 1970). This unit conformably underlies rocks of the Nemegt Formation, which have also previously been referred to as the Upper Nemegt Beds. The two formations look very different. The sandstones of the Nemegt Formation are light-colored, yellowish, sometimes almost white, and rich in dinosaur fossils, while the Baruungoyot Formation is intensively red and poor in fossils, so much so that Ivan Efremov, the leader of the Mongolian Expeditions of the Academy of Sciences of the Soviet Union in 1946–1949, designated them *nemaya seria*, which means "barren series." However, when mapping this series, Gradziński found fragments of egg shells and tiny broken bones, and so he suggested that the Baruungoyot Formation was similar enough to the rocks of the Djadokhta Formation that it might yield skeletons of lizards and mammals. In 1965 we found no important fossils in these rocks, just egg fragments.

In 1970 we decided to intensify our searching for mammals. On September 14 Halszka and I joined Wiesław Maczek, who drove us in a Muscel, a Romanian-made car, to outcrops of the Baruungoyot Formation situated a few kilometers eastward from our camp. There we separated, everyone going off on his own, looking intensely for mammals. The first two hours were just plain boring, as I could not find anything, but suddenly I noticed that Halszka was running toward me shouting: "I have found a skull." Indeed, she had found a beautiful skull of a small multituberculate mammal, preserved with both dentaries in occlusion. It belonged to a new genus and species, not known previously. It turned out that this small multituberculate was the most common mammal in rocks of the Baruungoyot Formation. I described it in 1974 as *Chulsanbaatar vulgaris* (see chapter 10).

Our enthusiasm was enormous. We returned for lunch and informed our colleagues about the new discovery. After lunch we drove with a larger group to Khulsan, where I found a fragmentary skull of a eutherian mammal. Two days later we decided to start searching in the lowermost part of the Baruungoyot Formation, which cropped out some 10 km eastward. Six of us searched for the whole day. It turned out that we were in a new El Dorado. During one afternoon we found five mammal skulls, eleven lizards, a nest of big eggs – different than those from Bayan Zag – and numerous small eggs about 5 cm long. It was clear that we had discovered a new locality, never searched before by paleontologists. We stayed in this new place until it turned dark, returning very late to camp. The following days brought more new discoveries at Khulsan. Altogether during ten days of searching until 25 September, when we had to break camp and return to Ulaanbaatar, we found 22 skulls of mammals; 80

4.10. A. Camp of the Polish-Mongolian Expedition at Khulsan in the Nemegt Basin, in 1971. The arrow denotes the cabin. B. Members of the 1971 Polish-Mongolian Expedition in the Gobi Desert. *From the left,* standing: Andrzej Baliński, Altangerel Perle, the late Jan Bijak, two Mongolian workers, Maciej Kuczyński, Edward Miranowski, Cyprian Kulicki; *sitting in the upper row,* Wojciech Skarżyński, Andrzej Elżanowski; *sitting in the next row,* Teresa Maryańska, Zofia Kielan-Jaworowska, Maria Ziembińska-Tworzydło; *lying,* Tom Jerzykiewicz, the late Andrzej Sulimski.

Archive of the Institute of Paleobiology in Warsaw. Photograph by W. Skarżyński.

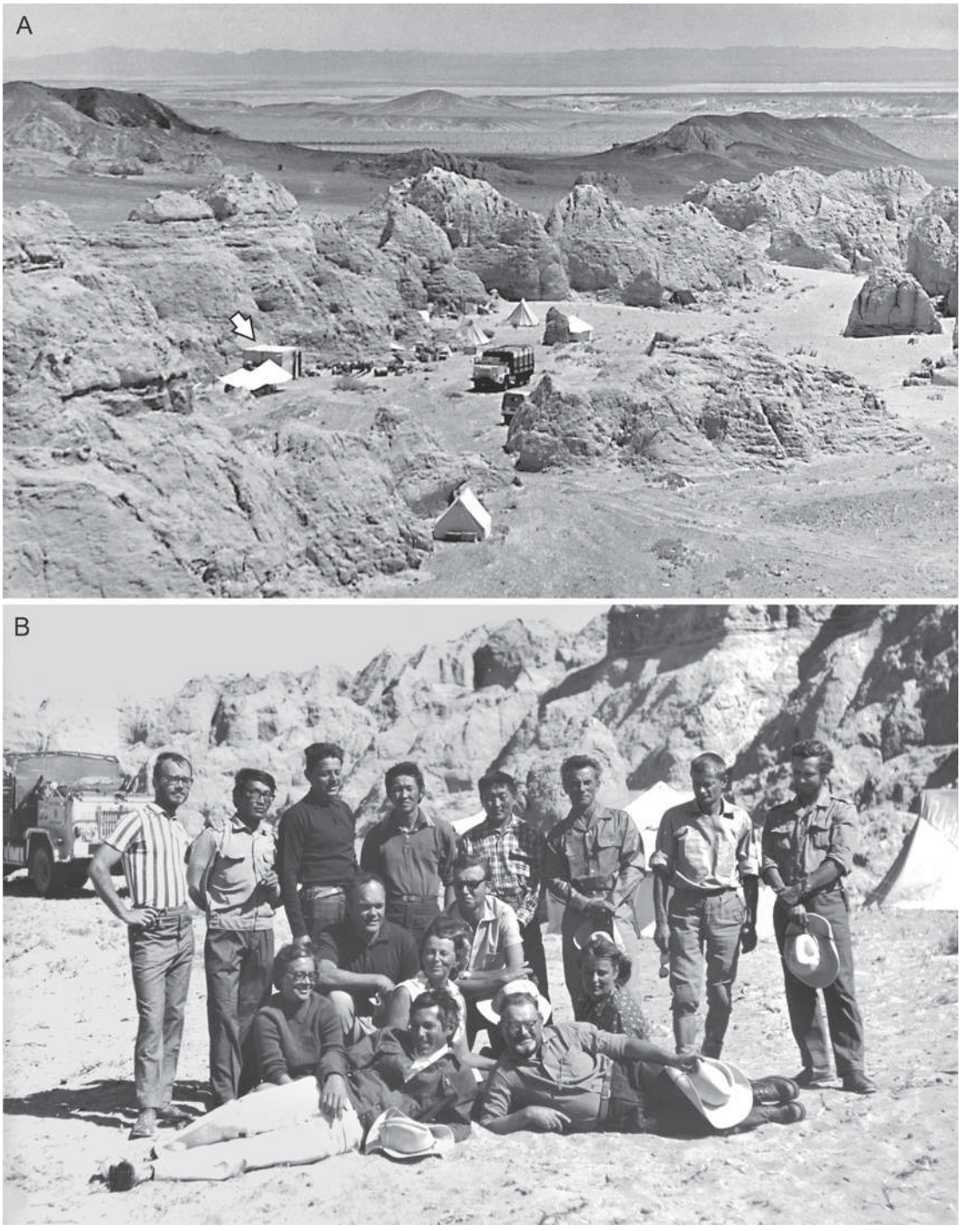
skulls of lizards, some of which had preserved complete postcranial skeletons; a large part of the skull of an ankylosaurid dinosaur; and numerous well-preserved turtles.

We had also noticed high on one of the walls a partial skeleton of a large ankylosaurid dinosaur, which we left to excavate the next year. One of the collected multituberculate skulls had been preserved without the lower jaws, and I was able to prepare its molar teeth. It turned out that it differed from the multituberculate skulls from Bayan Zag (see chapter 10) in having a greater number of cusps on the molars. As the evolution of some multituberculate lines involves a regular increase of the number of cusps on the molars, the new find might suggest a different (slightly younger) age of the Baruungoyot Formation than that of the Djadokhta Formation.

In 1970 most of the expedition members returned to Poland at the beginning of October, but I had to remain three weeks longer because of the prolonged negotiations with customs authorities. Teresa Maryańska and Maciej Kuczyński remained with me. Finally, I received permission from the Mongolian minister of trade to dispatch the collections to Warsaw according to our agreement with the Mongolian Academy. We left our trucks in Ulaanbaatar for the winter, along with some of our equipment, to await our return in the spring of 1971, and then we ourselves left for Warsaw on October 24.

The winter of 1970/1971 appeared very short to us. From the time of our leaving Mongolia until the dispatch of the new equipment to Ulaanbaatar we had only five months. The 1971 expedition team was considerably different from the previous crews (see figure 4.10.B). Some old "Gobians" who took part in several earlier expeditions could not join us this time. We had to recruit new people. Our group was, therefore, notably rejuvenated. The new paleontologists who joined us were Cyprian Kulicki and Andrzej Baliński, both invertebrate paleontologists from our institute. Maria (Marysia) Ziembińska-Tworzydło, a paleobotanist from the University of Warsaw, became an active member of the expedition and described the charophytes from the Paleocene and Late Cretaceous of the Nemegt Valley. In cooperation with Jadwiga Karczewska she published two monographs on the Charophyta from the Upper Cretaceous of the Nemegt Basin (e.g., Karczewska and Ziembińska-Tworzydło 1981), where earlier papers by the same authors are cited.

Andrzej Elżanowski, a student of paleontology, later a professor at Wrocław University, and subsequently a professor at the Zoological Institute and Museum of the Polish Academy of Sciences in Warsaw, also joined our team in 1971. He is now a well-known specialist of fossil birds. Elżanowski published three papers (1974, 1977, and 1981) in the series Results of the Polish-Mongolian Palaeontological Expeditions, two on the skull of a palaeognathous bird designated *Gobipteryx minuta*, from the Late Cretaceous Nemegt Formation, and one on a bird embryo from the same beds, possibly also belonging to *Gobipteryx minuta*. In addition, Elżanowski (1976) discussed the skull of


A
B

Gobipteryx in *Nature*. Ryszard Gradziński, our experienced geologist, and Jerzy (Jurek) Lefeld, our second geologist from the 1964 and 1965 expeditions (who published on the sedimentology of the Djadokhta Formation at Bayan Zag; see Lefeld 1971), could not join us, and both were replaced by their younger colleague Tomasz (Tom) Jerzykiewicz from the University of Wrocław, who subsequently settled in Canada. Tom published several papers on the sedimentology and stratigraphy of the Gobi Desert Cretaceous rocks, including one from our expeditions (Gradziński and Jerzykiewicz 1974). The old members of the expedition, Teresa Maryańska, Maciej Kuczyński, Andrzej Sulimski, and Wojciech Skarżyński, were also with us, along with a new medical doctor, the late Jan Bijak, and a new driver for the new trucks – the Big Star 66s (the "Star" is a well-known Polish-made truck and is found throughout eastern Europe). Altogether there were 12 Polish members and theoretically three Mongolian members: Barsbold, Perle, and the technician Sambu. But Barsbold was only in occasional contact with us, usually being with the Joint Soviet–Mongolian Expedition. Perle and Sambu were with us for the full expedition.

In 1971 we arrived in Ulaanbaatar at the end of April, and in the middle of May we left for the Gobi Desert, heading to the Nemegt Valley, first to Gurvan Tes, and then to Khulsan where we decided to set up our first camp (figure 4.10A). The weather this May on the Gobi Desert was quite unpleasant. It was cold, windy, snowy, and misty. Fortunately, Kuczyński had suggested that we take from Warsaw some extra boards and several square meters of plywood to build a small cabin in which the cook could prepare the food. Usually the kitchen was outdoors. This cabin also provided us with shelter during particularly bad weather. The cabin was constructed in three hours; it had a window covered with plastic foil and proved to be a very useful place. Later on, when we moved to other places, we dismantled the cabin and took it with us.

On the first field day we started searching for fossils in the "El Dorado" region, discovered during the previous year, while two trucks traveled continuously between the camp and Gurvan Tes, transporting the rest of the equipment. The first day was very lucky. I found three skulls of small multituberculates and two skulls of lizards. Teresa and Andrzej Elżanowski found a mammal skull each, and Andrzej Baliński reported the find of a big lizard with an associated postcranial skeleton sticking out the wall of one of the gullies, requiring excavation.

On the following days, we found more mammals and lizards and dinosaur skulls similar to *Protoceratops* but smaller, subsequently described by Maryańska and Osmólska in 1975 as *Bagaceratops rozhdestvenskyi* (figure 4.9C). The protoceratopsid material found by members of the Polish-Mongolian Expeditions enlarged knowledge about this group of dinosaurs. In addition to *Bagaceratops*, the new genus and species based on the very well preserved skull of the holotype specimen, and several younger skulls of the same species and fragments of the postcranial skeleton, Maryańska and Osmólska (1975) described a new

species of ?*Protoceratops*, named ?*P. kozlowskii*, and new specimens of *Microceratops gobiensis*. The new material of *Bagaceratops* derives from the Hermiin Tsav Formation (previously referred to as Khermeen Tsav Formation; see Maryańska and Osmólska 1975: 135); that of *Protoceratops kozlowskii* is from the Baruungoyot Formation at Khulsan; and that of *Microceratops* cf. *gobiensis* from a somewhat younger Late Cretaceous formation, called the Tsondolein Khuduk Formation.

In 1971 we began excavation of the large skeleton of an ankylosaurid dinosaur, found the previous year, preserved in the wall some 3 m above the bottom of the gully at Khulsan. Excavation of this skeleton was technically difficult. We had to construct wooden scaffolding with a platform, on which we worked when uncovering the skeleton (plate 2). It consisted of a large, beautifully preserved skull and the anterior part of the thorax covered with large scutes. This specimen was subsequently described by Teresa Maryańska (1977) as *Saichania chulsanensis*.

The last day of May 1971, we made a trip to outcrops called Hermiin Tsav, situated 40 km southwest from the westernmost end of the Nemegt Valley. In Hermiin Tsav there occur large outcrops of sediments belonging to the Baruungoyot and Nemegt Formations. We knew that the Soviet-Mongolian Expedition planned to conduct excavations in the Nemegt Formation of Hermiin Tsav, therefore we limited our work to examining the lower part of the beds cropping out there, which were red in color. We spent several days looking for mammals in the red sandstone. On the fourth day, we found the first mammal skull, belonging to a rather large multituberculate. The skull was 6 cm long with both dentaries preserved. I described it as *Djadochtatherium catopsaloides* in 1974, but later on I decided that it belonged to a new genus, which I called *Catopsbaatar*.

Some ten days later we went again to Hermiin Tsav. This time, in addition to one more skull of *Catopsbaatar* from the western part of the red picturesque sandstones, looking like a castle (named by us Hermiin Tsav I), we found a new small area of outcrops, situated on the west (named Hermiin Tsav II) and separated from Hermiin Tsav I by some 4 km of pediment. The new outcrops were not as dark red as the sandstone at Hermiin Tsav I, and they were full of small concretions and bone fragments. Here we found more skulls of mammals, similar to those in Khulsan, numerous lizards, the skull of a small oviraptorid (a peculiar toothless theropod dinosaur, a somewhat larger close relative of which was originally found at Bayan Zag by members of the Central Asiatic Expeditions), and several other fossils. Later, when we moved our camp to Altan Uul, the group led by Teresa Maryańska (figure 4.4E) went to Hermiin Tsav again.

In addition to the dinosaurs and Cretaceous mammals, we found and described fossils belonging to other groups of vertebrates, including turtles (described by Khosatsky and Młynarski [1971], and Młynarski and Narmandach [1972], among others). In 1972, Polish paleontologists began to publish on various groups of lizards (see, for example, Sulimski

1972, 1975; Borsuk-Białynicka 1984) and on Cretaceous frogs (Borsuk-Białynicka 1984).

In 1975 Jerzy Dzik, at the time still a student, described a spiroboloid millipede from the Baruungoyot Formation at the locality of Khulsan and erected for it a new genus and species *Gobiulus sabulosus*. Another group of invertebrates, common in the beds of the Nemegt Formation of the Nemegt Basin, are the ostracodes, described by Szczechura (1978, in which earlier papers by the same author and by Szczechura and Blaszyk are cited).

During our return from the second stay at Hermiin Tsav, I was in an open car, with the wind blowing for many hours on my left ear. By the time we arrived at camp I had a strong pain in the ear, which finished with a very violent hemorrhage from the ear. For the next few days I felt miserable. I had a fever and was deaf in the left ear. At that time we were busy winding up the camp at Khulsan and moving to Altan Uul IV. In Altan Uul we separated again. Teresa went once more to Hermiin Tsav with five other colleagues, and the remaining group started searching for dinosaur skeletons. I was ill all the time, with such strong pain in the ear that I stopped sleeping. As our doctor had accompanied Teresa to Hermiin Tsav, Kuczyński and Perle decided to take me to a doctor at Dalanzadgad. We drove there, and a Mongolian laryngologist examined my ear and concluded that the tympanic membrane had been broken. He said that I should not stay in a camp but rather return home. Teresa remained as the leader of the expedition during my absence. I left Dalanzadgad by plane to Ulaanbaatar, where I had to wait a few days for a plane for Warsaw. Barsbold, who met me in Ulaanbaatar, was soon leaving for the field and invited me to stay with his parents, Professor Rinchen and his wife. I knew both of them from their former visits to Warsaw. Rinchen was a great scientist, a historian of Mongolia, an ethnographer, and a linguist, knowing several languages, including Polish. In spite of my ear problems, this stay was very memorable, full of interesting conversations from which I learned a lot about the history of Mongolia, Lamaism, and Buddhism.

After some three weeks of treatment in Warsaw the membrane healed up. I sent telegrams to my colleagues to the address of the post office in Dalanzadgad and flew back to Ulaanbaatar and from there to Dalanzadgad. I calculated that the expedition was probably moving to, or already settled in, Tögrögiin Shireh, which was scheduled to be our last place of work for the season. My calculation was right. In front of the hotel in Dalanzadgad I noticed the well-known Muscel car of our expedition, and soon I met Kuczyński and Skarżyński returning from the post office, where they had retrieved my telegrams. The expedition was already in Tögrögiin Shireh, and we drove there. On the way to Tögrögiin I learned from Skarżyński and Kuczyński about the great success of the expedition in finding mammals and other fossils at Hermiin Tsav and about a number of skeletons of different dinosaurs that had been excavated at Altan Uul.

Although some rare mammals have occasionally been found at Tögrögiin Shireh, in spite of intensive searching we did not find a single mammal fragment there in 1971. But we did make a spectacular discovery there. Andrzej Sulimski found the skeleton of a beautifully preserved small carnivorous dinosaur, *Velociraptor mongoliensis.* When we started to uncover it, it turned out that the skeleton had two tails. We could not understand this. Further excavation revealed that the *Velociraptor* was preserved together with another skeleton – of an herbivorous dinosaur, *Protoceratops andrewsi.* With its forelimbs, the *Velociraptor* embraced the skull of *Protoceratops.* In a short paper, which I published in 1972, co-authored with Rinchen Barsbold, we suggested that two animals might possibly have died during a fight. The photograph of the "fighting dinosaurs" has been subsequently published in numerous popular articles all around the world. However, the conclusion that the two dinosaurs might have died during the fight was challenged by Halszka Osmólska in a paper, which she published in 1993. On the basis of analyzing the state of preservation of two skeletons, Halszka concluded that the *Velociraptor* had found the dead body of *Protoceratops* as a scavenger, rather than as a predator, and then died of some unknown cause, before finishing its meal. I am now convinced that Halszka was right, as during the Nomadic Expedition of 2002 (see below) we found in Tögrögiin Shireh another specimen of "fighting dinosaurs." These were again two skeletons of *Protoceratops* and *Velociraptor* preserved together, but much less complete than those found in 1970. Because of our schedule in 2002, we could not remain in Tögrögiin Shireh longer to excavate the skeletons, and we only protected them against further weathering. Our Mongolian colleagues promised that they would come to Tögrögiin Shireh and excavate this find. The expedition wound up camp at Tögrögiin Shireh in the middle of August, and we returned to Warsaw in several groups, the last one in the middle of September.

Before my return to Warsaw, the president of the Mongolian Academy of Sciences, Professor Shyrendyb, asked me to meet with him. He apologized, saying that the Mongolian Academy of Sciences would not be able to arrange for our academies to continue the Polish-Mongolian Expeditions for the coming years because there were not enough Mongolian paleontologists to participate in both the Polish-Mongolian and the Soviet-Mongolian Expeditions. As mentioned earlier, beginning with 1970 the Soviet-Mongolian Expeditions worked side by side with ours. The news was absolutely crushing for me, but I tried to comfort myself and my colleagues, remembering that we had a number of fossils from Mongolia which we would be able describe during the coming years. In addition I tried to understand the politics that gave rise to this decision.

The collection of Mesozoic mammals assembled by us from the Cretaceous rocks of the Gobi Desert, comprising some 180 specimens, most of which are skulls often associated with postcranial skeletons, was at that time the largest collection of skulls of Mesozoic mammals assembled in any paleontological museum in the world. The situation changed in

1993 when the Mongolian Academy–American Museum Expeditions, led by Michael Novacek and Demberlyin Dashzeveg, discovered the locality of Ukhaa Tolgod in the southwestern part of the Nemegt Valley. During several years there, they collected several hundred skulls of Late Cretaceous mammals and other important fossils (Dashzeveg et al. 1995). So the largest collection of skulls of Mesozoic mammals is now housed temporarily in the American Museum of Natural History in New York.

However, our holdings also include valuable collections of dinosaurs, lizards, crocodiles, Cretaceous birds, and various Tertiary mammals, along with invertebrates such as diplopods and ostracodes, and rare plants, the charophytes. Beginning with 1969 we started to publish in *Palaeontologia Polonica* the series, Results of the Polish-Mongolian Palaeontological Expeditions, publishing ten big volumes through 1984. I published a number of papers on the mammals from the Gobi Desert and related forms, which I will cite in succeeding chapters that deal with particular groups.

Between 1976 and 1980, according to the agreement signed between our academies, we sent back to Mongolia four big shipments containing the original skeletons of dinosaurs, collected during our expeditions. Part of this collection is now on display in the museum in Ulaanbaatar. Although many years have now passed since the last expedition, we continue working on fossil material from Mongolia, often in cooperation with Mongolian colleagues.

The Nomadic Expedition, 2002

In 1990, an American-Mongolian tourist society, "Nomadic Expeditions," was set up by Mongolians and Americans who organized thematic expeditions to Mongolia. During most years, beginning in 1992, the society included paleontological expeditions to Mongolia in its roster. My husband Zbigniew (Zbyszek) Jaworowski, our granddaughter Zofia (Zosia) Jaworowska, at that time ten years old, and I joined one of the Dinosaurs of the Gobi Desert expeditions in August 2002. The leaders of the expedition were my colleagues, Canadian dinosaur specialist Philip Currie, whom I have known for many years, and Demchig (Badam) Badamgarav, a charming lady and geologist-sedimentologist who has been my Mongolian friend since the time of our earlier expeditions.

There were 17 "tourists" in the 2002 expedition, including 5 professional paleontologists: Philip Currie and his wife Eva Koppelhus, an amiable paleobotanist (see plate 1B); Rodolfo Coria, an Argentinean dinosaur specialist; Jørn Hurum, my former student and now a well-known Norwegian paleontologist specializing in dinosaurs, marine reptiles, and early mammals; and myself. Badam was the geologist on the expedition, and the remaining members were amateur paleontologists from Canada, England, and the United States, some with considerable experience in collecting and excavating fossils, in particular, dinosaurs. In addition there was a Mongolian guide, fluent in English, a Mongolian cook with

two helpers, and finally eight Mongolian drivers. There were 29 people altogether.

We arrived in Ulaanbaatar by plane, where in the airport our friend Barsbold, whom I had not seen for 31 years, was awaiting us. The first three days were spent visiting the city, museums, and people (see plates 1 and 3). Together with Jørn Hurum, I visited Demberlyin Dashzeveg, whose office was now at the Geological Institute of the Mongolian Academy of Sciences. We also spent two days examining collections at the new Paleontological Center of the Mongolian Academy of Sciences. We visited the Museum of Natural History downtown, where I saw with pleasure that part of the dinosaur exhibits were composed of the specimens collected during the Polish-Mongolian Paleontological Expeditions, including *Saichania chulsanesnsis*, *Deinocheirus mirificus* (plate 1), *Gallimimus bullatus* (figure 4.6), and *Homalocephale calathocercos* (figure 4.9A). The huge skeleton of the sauropod *Opisthocoelicaudia* (figure 4.7) still awaits mounting in Ulaanbaatar.

Nowadays Mongolian regulations discourage foreign institutions from taking dinosaur specimens out of the country. Every year, Philip Currie sends qualified technicians from his institute in Canada to Ulaanbaatar, and they work at the Laboratory of the Paleontological Center to prepare the best-preserved specimens collected during the previous expeditions. Philip also comes to study, take photographs, measure the specimens, and does much of his research writing on Mongolian specimens in Ulaanbaatar.

We left Ulaanbaatar by plane and landed in an airport close to a village west of Dalanzadgad, not far from Bayan Zag (see figure 4.3A, map of the Gobi Desert). In the airport parking lot, eight field cars with Mongolian drivers were waiting for us. Our first destination was a tourist settlement (Three Camel Lodge) built by Nomadic Expeditions, consisting of two central stone and wooden buildings with restaurants, a shop, entertainment hall, kitchen, and bathrooms (plate 3, tourist settlement on the Gobi Desert). The central part was surrounded by a number of comfortable yurts, our hotel rooms. We were assigned a nice yurt for our family.

After lunch, we drove to Tögrögiin Shireh and then to Bayan Zag. The visit to Bayan Zag, where I spent so many memorable field seasons, was disappointing. The Flaming Cliffs, famous for producing the first dinosaur eggs and a treasure trove of other fossils, used to be a calm, isolated, charming place. Now it is visited every year by hordes of tourists, who fly to several nearby airstrips where they are picked up by cars and driven to Bayan Zag. The result is miserable and has left the site looking dirty and devastated. Because there are no toilets for the large groups of tourists to use all summer, it was difficult to hike around, let alone to prospect for fossils. After having a supper served at sunset at the foot of the Flaming Cliffs, we returned to our yurts at the Three Camel Lodge. Both Zbyszek and I went to sleep. Zosia was full of vigor and went to the

entertainment hall to watch the Mongolian staff of the lodge performing folk dances and songs for our group.

The following day, we left for the Nemegt Basin, arriving in the evening at the now famous locality of Ukhaa Tolgod that had been discovered in 1993 by the American-Mongolian group led by Demberlyin Dashzeveg and Michael Novacek. It was getting dark as the tents were set up, and we only had time for a short walk around the site (plate 3). There was little time to search for fossils in the morning because we had to leave by noon. But it seemed that members of the American-Mongolian group, who had worked annually at the site since 1993, had been very effective in removing specimens from the surface. We did not find any Mesozoic mammal fossils in this, one of the most beautiful and fruitful localities in the world, which has yielded an enormous number of Cretaceous mammals and dinosaur skeletons sitting on the nests of eggs.

The journey to Hermiin Tsav lasted the whole of the next day. The old Russian-made four-wheel drive vans had difficulty climbing up the sandy hills and often needed the help of a dozen hands. Late in the evening, we arrived at the southern outcrops of the Nemegt Formation.

This was a completely different Gobi expedition than those Spartan ones that I took part in during the 1960s and 1970s. Paradoxically, it was more in the style of the great nineteenth-century geographical expeditions that were organized by rich sponsors. When we were resting in our small tent, with Zosia sleeping 5 m away in another one, Zbyszek told me about one of those old expeditions. During an expedition to the Ruwenzori Mountains in 1906, His Royal Highness Prince Luigi Amedeo of Savoy, the Duke of Abruzzi, gave each member of the team his own servant, one bottle of wine per day, and a folding bed. This was all transported on the backs of about 200 Ugandan porters up to an altitude of about 4500 m. Trash left by this expedition was still visible in the 1970s. This time we did not have individual servants, no beds, and no wine. However, our tents were not pitched by us but by the drivers, who also carried our luggage. And we had what Abruzzi's companions did not – any amount of cold drinks of all sorts from a refrigerator mounted in a Land Rover and powered by a Honda generator. The generator also powered lights under the canvas roof during the evening meals. Excellent food, based mainly on fresh goat meat and vegetables, was served by a courteous cook dressed in a sort of Japanese attire. We used to sit there all together until late in the night, discussing the day's events and finds (plate 3).

From time to time Philip Currie arranged evening lectures and free discussions on the paleontology of Gobi. Even though only ten years old, Zosia took part in these discussions, usually starting with "In my opinion . . ." My husband told us about the highly radioactive dinosaur and turtle bones from Nemegt. My stories were obviously about the Polish-Mongolian Paleontological Expeditions and Mesozoic mammals. Most of the audience were not professional paleontologists, but it would be difficult to find a more interested and competent group. Working together in the daylight, and chatting over the cold drinks and cakes in

the evening, united us into a merry and friendly company, much thanks to Philip and his wife's charming personalities.

During our few days at Hermiin Tsav, we excavated several partial skeletons of dinosaurs and a complete one of *Ingenia*, a small oviraptorid dinosaur. Philip, Jørn, and Rodolfo made a plaster jacket, weighing 200 kg, for the *Ingenia* so it could be transported safely with the help of workers to the cars and eventually to the Paleontological Center in Ulaanbaatar. Prospecting in the outcrops of red sandstone of the Baruungoyot Formation was less fruitful. However, I found the skeleton of a big lizard, with a skull measuring about 10 cm. This was also encased in a plaster jacket. Zosia searched for fossils with great enthusiasm and found a partial skeleton of a protoceratopsid dinosaur plus several smaller fossils. She helped excavate some other dinosaur skeletons and became good at making plaster jackets. I wanted to show Philip and my other colleagues our old locality that we designated Hermiin Tsav II. It is situated some 4 km east of the monument-like outcrops of Hermiin Tsav I. Hermiin Tsav II yielded many beautifully preserved specimens of mammals and small reptiles. However, this time our prospecting was again in vain. The small slope of Hermiin Tsav II had apparently been completely excavated by us previously, and all that we found there were only some tiny bone fragments.

The last locality where we set up the camp was Nemegt. As frequently occurs in the beds of the Nemegt Formation, we found several partial skeletons of dinosaurs. I was anxious to show Philip and my other colleagues the outcrops of Khulsan and our famous El Dorado. We drove there in large groups for three consecutive days. All the members of the expedition had hopes of finding a Cretaceous mammal for me, but unfortunately, we found not a single one during the whole expedition. In fact, after more than ten Nomadic Expeditions in the Gobi Desert, only two well-preserved skulls of Cretaceous mammals have been recovered. Both of these were interesting scientifically and were lent to me for description, which led to several publications (Kielan-Jaworowska et al. 2005; Hurum et al. 2006; Kielan-Jaworowska and Hurum 2006; Hurum and Kielan-Jaworowska 2008).

During our prospecting in the most eastern part of the Nemegt Basin, we found an accumulation of huge sauropod bones in the Nemegt Formation, indicating the presence of a large part of a skeleton. Unfortunately, because we had only a short time there with limited equipment, we were unable to uncover the skeleton. Big dinosaur skeletons had been excavated by the Mongolian Expeditions of the Soviet Academy of Sciences from 1946 to 1949 and by the Polish-Mongolian Paleontological Expeditions between 1964 and 1971. All subsequent expeditions, although collecting many important and often new dinosaurs, focused mostly on excavating smaller dinosaurs that were easier to handle logistically.

I had not been in Mongolia for 31 years, and enormous changes had clearly taken place in its westernized capital, Ulaanbaatar. However, few changes were evident in the Gobi. A most striking exception – and a

symbol of modern times – was the presence of satellite dishes and solar panels on top of almost all the yurts and the TV sets inside. The sun's energy was stored every day in batteries, and in the evenings Mongolian shepherds (*arats*, in Mongolian), after watering their camels and horses, watched local films or those produced in China, America, and Europe. The people themselves have not changed, however, and we were met with the same friendly hospitality as in the past. After such a long break, this visit was for me a rather sentimental journey and refreshed old memories. There was a new excitement in hunting fossils in the midst of a magnificent, sun-scorched Asia, kindly revealing to us the ancient dawn of the mammals.

The Nomadic Expedition of 2002 was very special to me, as this was the first time I had been in Mongolia with my closest friend – Zbyszek – and our amusing 10-year-old "scientist" Zosia – the mascot of the expedition.

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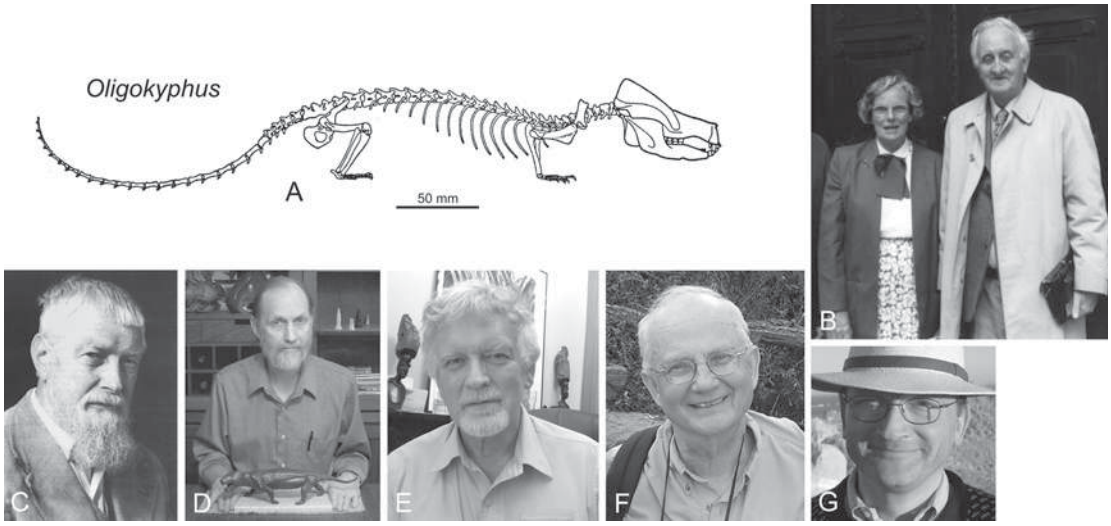


5.1. A. Reconstruction of the skeleton of *Oligokyphus.* B–G. Selected influential students of early mammals and synapsids. B. Doris M. Kermack (1923–2003) and Kenneth A. Kermack (1919–2000). C. Walter Kühne (1911–1991). D. Edgar F. Allin. E. Tom S. Kemp. F. James A. Hopson. G. Hans-Dieter Sues.

A. From Romer (1966: figure 291). B. Courtesy of John and Richard Kermacks. C. Courtesy of Renate Hahn.

Origins of Mammals and the Earliest Representatives of Mammaliaforms and Mammals

5

The Oldest Mammals and the Work of Walter G. Kühne and Kenneth A. Kermack

IN THE MORE THAN 500 MILLION-YEAR-LONG HISTORY OF VERTEbrates, mammals did not appear until quite late, some 225 million years ago. Although the first Mesozoic mammal was discovered as early as 1764 in England, its significance was not understood until more than 100 years later, in 1871, when Sir Richard Owen (1804–1892) published his great opus, the "Monograph of the Fossil Mammalia in the Mesozoic Formations." In spite of this and other significant publications that appeared in the nineteenth and first half of the twentieth centuries, the intensive search for Mesozoic mammals began in only about the middle of the twentieth century. Among known Mesozoic mammals, the oldest ones from the Late Triassic and Early Jurassic are extremely rare – they derive from a range about 35 million years long, between 225 Ma and 190 Ma.

Only 31 localities have been found on Earth that have yielded mammals from that time span. Ten of these occur in continental Europe, three in Britain, five in China, four in India, three in Africa, three in South America, one in Greenland, and two in North America. Mammals of this age have not yet been reported from Australia and Antarctica. Looking at maps of the almost worldwide distribution of the earliest mammals, one might get the impression that these early mammals are relatively well known. However, at the majority of these localities mammals are represented only by isolated teeth or single bones, and only a few places have yielded skulls and their parts or, more rarely, postcranial skeletons. I shall limit my review to the description of the more important sites and the well-preserved fossils from them.

The oldest mammals are of Late Triassic age and were first found in Great Britain in the middle of the nineteenth century by a Somerset geologist, Charles Moore (1814–1881). Moore discovered isolated teeth of haramiyidans, an enigmatic group of mammaliaforms, regarded by numerous paleontologists as related to the better-known multituberculates (see chapter 6). These ancient mammaliaforms were recovered from karst fissure fillings in Carboniferous limestone at Holwell in Somerset, England, on the southern side of the Bristol Channel. After a long break, Triassic mammaliaforms were found in Norian strata in Germany, where an incomplete mammalian ulna was recovered from latest Triassic rocks near Halberstadt.

In Britain, during the Second World War in 1941, Francis Rex Parrington (1905–1981) described two premolars from the Rhaetic fissure fillings in the Carboniferous limestone in Somerset, England, from the

previously mentioned locality of Holwell. He named these *Eozostrodon*. These two teeth had been found by Walter G. Kühne, the legendary German searcher for Mesozoic mammals, who contributed enormously to the discovery of early mammals in Europe, initially looking for them in Britain and later in continental Europe.

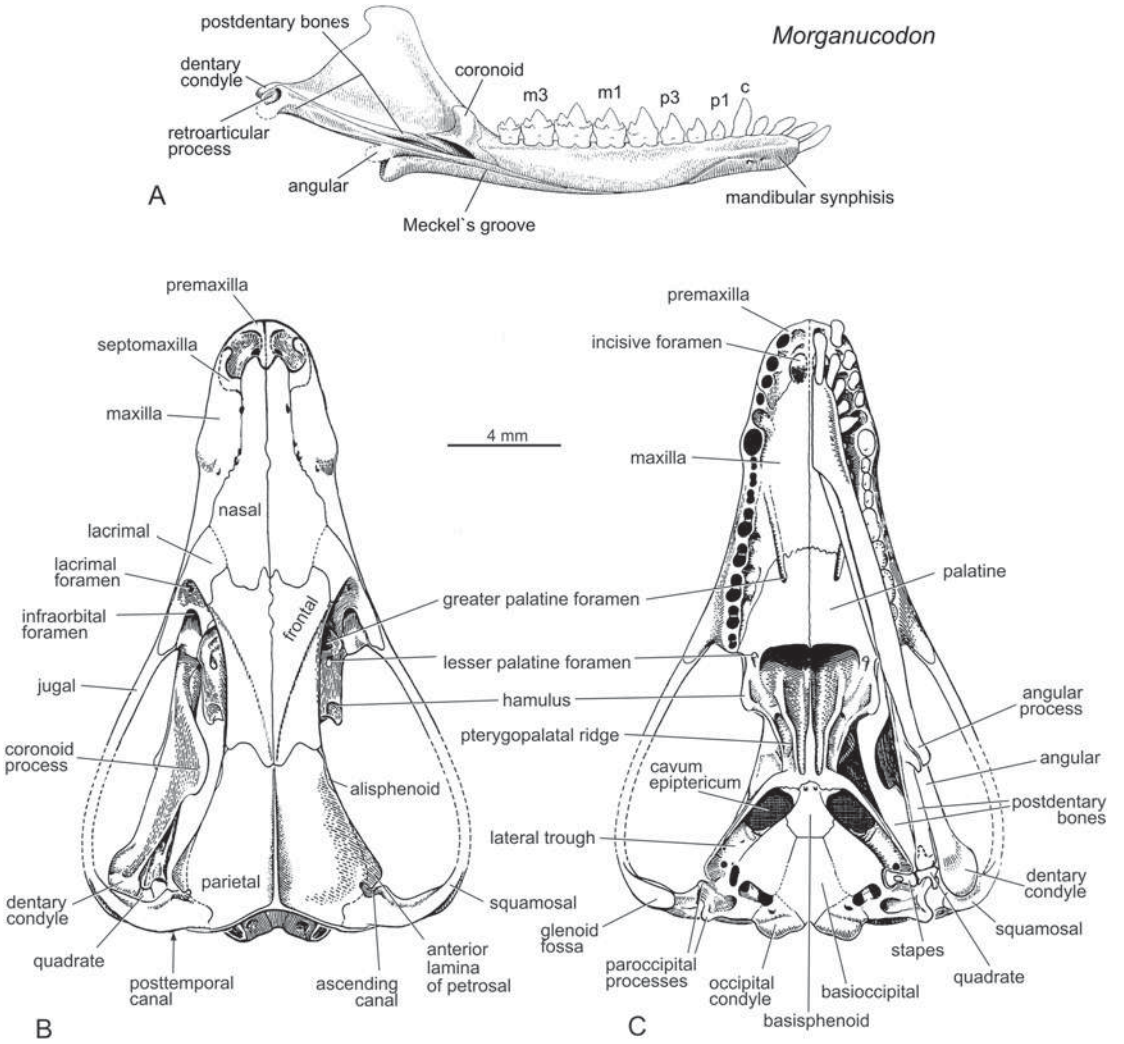
WALTER G. KÜHNE

Walter G. Kühne was born in Berlin in 1911 (and passed away, also in Berlin, in 1991; figure 5.1C). He started paleontological studies at the Friedrich-Wilhelm Universität in Berlin, and in 1930 he moved to the University at Halle. Kühne soon acquired a reputation as a communist sympathizer there, and because of this he was removed from the university and imprisoned for nine months. Later he and his first wife, Charlotte, made their living by collecting fossils and selling them to museums and other institutions. In 1938 their situation became so precarious that the couple emigrated to Great Britain.

In the beginning of their stay in Britain the Kühnes continued to make their living by collecting and selling fossils. Walter Kühne was especially interested in searching for early mammals. In spite of his young age, he was an experienced geologist, well prepared to search methodically for early mammals. He knew of Moore's earlier discovery of Mesozoic mammals at Holwell. Following Moore's example, soon after their arrival in Britain, the Kühnes started searching there. The couple began work there on a large scale. They washed and screened more than two tons of clay, from which they recovered several teeth. Then they moved to other quarries of Carboniferous limestone in England, exploiting the residue of several fissure fillings. The latter fissure fillings, situated on the northern side of the Bristol Channel, are of Early Jurassic age (Liassic, possibly Sinemurian). The Holwell fissure fillings discussed above are of Norian, or Rhaetian, age.

In August 1939, in a large and especially rich fissure in Windsor Quarry, of Early Jurassic age in the Mendip Hills, southeast of the Bristol Channel, the Kühnes collected numerous, albeit disarticulated, bones of the tritylodontid cynodont *Oligokyphus*. My friend, the late Professor Kenneth Kermack, related to me the story of how Walter Kühne, as a German citizen living in Britain, was interned at the beginning of the Second World War. The Germans invaded Poland on 1 September 1939, and on 3 September, Great Britain and France declared war on Germany. At the same time, Walter Kühne took his hammer and a geological map and went to the Atlantic coast in search of fissure fillings in the limestone cliffs. A patrol of soldiers guarding the coast noticed and arrested him, and he was interned in a camp on the Isle of Man.

His friends from the Natural History Museum and University College of the University of London helped him to obtain permission to come to the museum and continue his scientific work during the internment. Kühne assembled some 2000 isolated bones belonging to the Liassic



5.2. *Morganucodon* sp.
A. Lower jaw in medial view.
B. Skull in dorsal view. C. The same in ventral view.

Modified from Kermack, Mussett and Rigney (1973 and 1981).

tritylodontid *Oligokyphus* (figure 5.1A) from the karst fissures of Somerset. Additional material of *Oligokyphus* was collected during the war by his colleagues at the British Museum, under Kühne's remote guidance, and sent by the museum to the internment camp on the Isle of Man.

In 1944 Kühne was released from the camp and appointed an assistant lecturer at the University of London. There he developed a close relationship with the eminent British anatomist David Meredith Seares Watson (1886–1973). In addition to his work on *Oligokyphus*, after the war Kühne published information about his finds of different early mammals in Great Britain (Kühne 1946, 1949, 1950, and 1958). Kühne's impressive, meticulously rendered monograph on *Oligokyphus* was published after some delay in 1956 as a separate volume by the trustees of the British Museum. In 1952 the Kühnes returned to Germany, where Walter was granted a Ph.D. on the basis of his *Oligokyphus* monograph and became a professor of paleontology at the Free University in West Berlin.

Kühne's talent for finding fossils was unusual. He found several karst fissures full of bones in Great Britain and in other localities in continental Europe, later described by Rex Parrington, Georg Krusat, Bernard Krebs, Siegfried Henkel, and Kenneth Kermack. In 1959 he discovered a Jurassic fauna in the Portuguese coal mine Guimarota, which yielded multituberculates, eupantotherians, eutriconodontans, and several other early mammal groups, described by his collaborators Gerhard and Renate Hahn, Tom Martin, Bernard Krebs, and others. His discoveries influenced paleontologists in many countries to intensify their search for Mesozoic mammals and cast new light on the evolution and relationships of early mammals.

I had the pleasure of meeting Walter Kühne for the first time in the summer of 1969, when he came to Warsaw to visit the Institute of Paleobiology of the Polish Academy of Sciences and to examine our collection of Cretaceous mammals from the Gobi Desert. The second, perhaps more important, aim of his visit was to meet his teenage son, who lived with his mother (Walter's first wife) in East Berlin. With the political situation of the 1960s, Walter could not come to East Berlin, and his son could not travel to West Berlin. But the boy arrived at our home in Warsaw, and the next day Walter arrived from West Berlin and collected his son. Together they spent a short holiday in Poland. A third aim of Kühne's visit was his attempt to show us his methods for searching for Mesozoic mammals. With a group of my coworkers from the Institute of Paleobiology (at that time Paleozoology), we went with him to the area around Częstochowa in southern Poland to prospect the freshwater Early Jurassic sediments there, but in spite of washing and screening the sediments in various places, we did not find any Mesozoic mammals.

Later I met Walter and his second wife, Ursula, in London during the Early Mammals Symposium organized by Doris and Kenneth Kermack under the auspices of the Linnean Society (see below) in the summer of 1970. The following spring Walter invited me to present a series of lectures on Mesozoic mammals at the Free University in West Berlin. I lectured on Cretaceous mammals from the Gobi Desert, collected by the Polish-Mongolian Paleontological Expeditions, many of which had already been described and published. This visit was interesting to me, as it was a few years after Kühne had discovered the famous Late Jurassic (Kimmeridgian) fauna in the Guimarota coal mine in Portugal. For the first time, I also met Gerhard Hahn and his wife Renate, who worked on the rich collection of Guimarota multituberculates, which I discuss in Chapter 10.

In 1949, during his stay in Britain, Kühne described several mammal teeth from the Liassic fissure fillings in Duchy Quarry at Glamorgan in Wales and established the genus *Morganucodon*, which included a single species based on a single lower molar, *M. watsoni*. The name *Morganucodon* derives from Morganuc, the old name for South Glamorgan, which appears in the Domesday Book, completed in 1086, and the Greek *odous*, a tooth. Subsequently *Morganucodon* became one of the most

famous early mammals. Nine years later, Kühne (1958) described several teeth of *Morganucodon* and erected the family Morganucodontidae for them. After this relatively modest beginning, the fissure fillings in Wales were further exploited, first in the 1950s by Kenneth A. Kermack and his team from University College London.

KENNETH A. KERMACK

Kenneth A. Kermack (1919–2000; figure 5.1B) was a pioneer in the field of Mesozoic mammals in Great Britain. For most of his professional life he was associated with University College (Zoology and Comparative Anatomy) London. After Kühne returned to Germany, Kenneth and his crew from University College took over the monitoring and exploration of Welsh localities, assembling an enormous collection of mammalian teeth and bones, mostly of the primitive mammal *Morganucodon watsoni*, and also of a therian *Kuehneotherium*. The most important of his publications were two monographs on *Morganucodon* (co-authored with Frances Mussett and Harold W. Rigney) published in 1973 and in 1981. At University College, Kenneth taught vertebrate paleontology to generations of students and ran the master of science course in vertebrate paleontology. In addition, he trained a number of Ph.D. students, including, among others, Colin Patterson, Brian Gardiner, Susan Evans, Tony Thulborn, and Jerry Hooker. During his last 16 years he was seriously ill, suffering with diabetes and prostate cancer. His last paper, on some peculiar haramiyid/multituberculate-like teeth (coauthored with Doris M. Kermack, Patricia M. Lees, and John R. E. Mills) was published in 1998 (Kermack et al. 1998). During his whole life Kenneth was supported by his wife Doris Mary Kermack, née Carr (1923–2003) (figure 5.1B).

Doris Kermack was a British marine zoologist and vertebrate paleontologist. Doris graduated from London University and was granted her Ph.D. in zoology in 1953 at University College London on the basis of her thesis, "The Anatomy and Physiology of the Gut of *Arenicola marina* L." Her supervisor was Professor George P. Wells (1901–1985), the son of the famous science fiction writer H. G. Wells. At the beginning of her scientific life, Doris was engaged in studies on marine invertebrates and edited books and series on them. In March 1950 she got a position as lecturer at Imperial College London, and worked at this college until her retirement. In the second half of her scientific life she was engaged in studies on early mammals. She published several papers on early mammals in cooperation with her husband and his co-workers, the most important of which was a monograph on the Welsh pantothere *Kuehneotherium*. She was first author of the book *The Evolution of Mammalian Characters* (1984), coauthored with her husband. Doris was well known for her great organizational skills and activities. She was elected to the Linnean Society of London in April 1950 and was a Fellow until her death. She was the first Fellow of the society to be awarded the Linnean Gold Medal in 1988 in recognition of her services to the society. Doris had a sense of humor

and great personal charm. Doris and Kenneth Kermack left behind two sons (John and Richard) and four grandchildren.

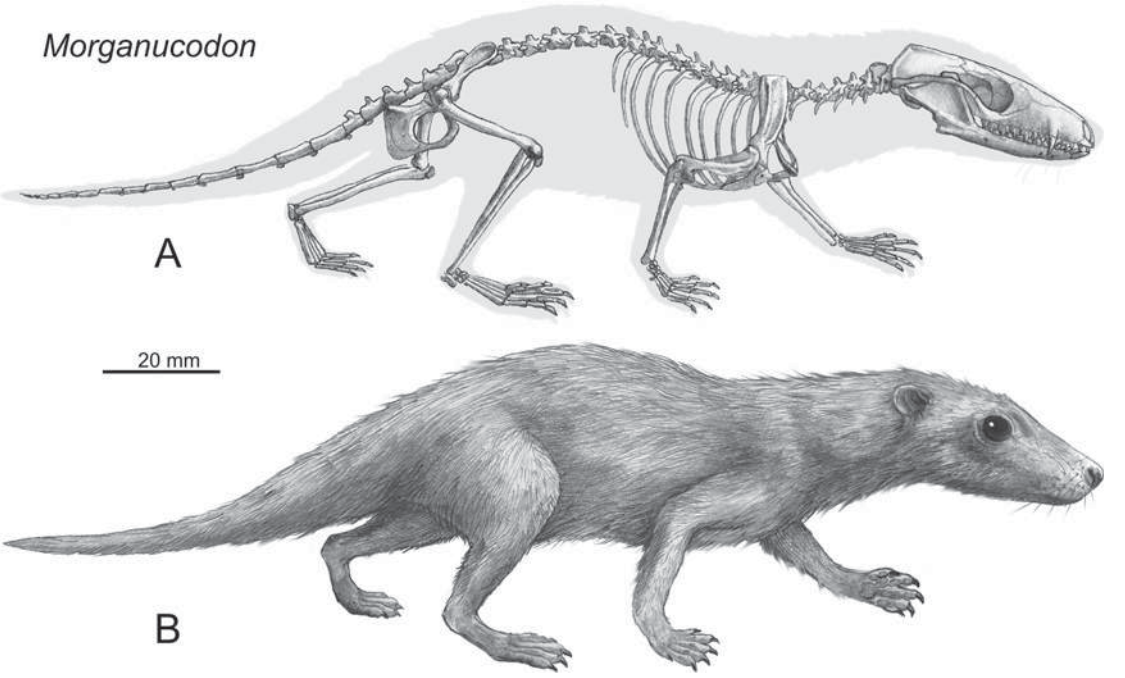
During years of fieldwork, Kenneth Kermack and his team assembled an impressive collection, including thousands of teeth, isolated bones of the skull, and postcranial skeleton belonging to *Morganucodon*, and bones of other early mammals; see also his paper published in 1988, in which he described in detail the localities in Britain yielding early mammals. In addition to the most common form, *Morganucodon*, the party recovered teeth, toothless fragments of the lower jaw of a "symmetrodontan" named *Kuehneotherium*, and several isolated teeth of haramiyidans.

The Chinese Adventure of Father Harold W. Rigney

At almost the same time that Walter Kühne and the Kermacks were looking for early mammals in Great Britian, another group of paleontologists began searching for early mammals in China. In 1946 Father Harold W. Rigney, an American paleontologist, was appointed rector of the Fu Jen Catholic University in Peking (now Beijing). In 1948 he sent an expedition led by Father Edgar O. Oehler, an associate professor of chemistry at the same university, to Yunnan Province, where Late Triassic sediments were known to yield small cynodonts. The expedition was financed by Father Ralph Thyken. Rigney himself had been interested in studying the ear region of the advanced cynodont *Bienotherium* found there previously, and he hoped to gather new material of this taxon. In August 1948, Father Oehler found a tiny (26 mm long) complete skull associated with the lower jaws of an early mammal, which was subsequently identified as belonging to *Morganucodon*. He sent this to Rigney at Fu Jen University.

The fate of Father Rigney was dramatic. On 1 February 1949, the Communist government was established in China, and on 25 July 1951, Father Rigney was arrested by the Communist security police. He spent over four years in prisons that were regarded as more cruel and humbling than the worst Stalinist jails in the Soviet Union. On 11 September 1955, due to the continuous interventions of his family and the international scientific community, Rigney was freed and returned to the United States, where he wrote his memoirs describing his days in prison (Rigney 1956).

Wilhelm Brull of the Fu Jen Catholic University managed to take the skull of *Morganucodon* out of China and returned it to Rigney in 1956 upon his own return to the United States. Rigney published a preliminary description of the skull in *Nature* in 1963, naming it *Morganucodon oehleri*. Subsequently, Kenneth Kermack, his assistant Frances Mussett, and Father Rigney further described this skull, together with the isolated bones from Wales, in two detailed monographs published in 1973 and 1981. Pamela Gill at the University of Bristol (pers. comm. 2012) has recently described work on *Morganucodon* going on now in Britain: "The skull of *Morganucodon oehleri* has recently been micro-CT scanned for study of the internal structure to see if further information can be gained that was not available in the 1970s to the team lead by Professor Kenneth Kermack. The scan data will be digitally reconstructed and studied for a



5.3. A. Reconstruction of the skeleton of a walking *Morganucodon* sp. B. Life reconstruction of the walking animal.

Original artwork by Oscar Sanisidro, emended by Aleksandra Hołda-Michalska.

Master's project at the University of Southampton, and then a model will be built for a biomechanical analysis of the skull using Finite Element Analysis (FEA), with Dr. Emily Rayfield at the University of Bristol."

The *Morganucodon* skull from China was one of the most important early mammalian fossils ever found. It was the first skull of an early mammal revealing anatomical details of the jaw joint developed during the reptilian–mammalian transition. In the spring of 1969, in connection with my studies of the skull structure of multituberculates from the Gobi Desert (see chapter 10), I arrived in London to discuss with Kenneth Kermack the skull structure of early mammals and to examine eutriconodontans and other early mammals in the British Museum (Natural History) collections. Kenneth had been working at his laboratory at University College London with Frances Mussett. Father Rigney resided at that time in the United States. I was most impressed by the excellent state of preservation of this famous skull of *Morganucodon* from China that these three authors subsequently described so well. The lower jaws had already been separated, partly by using acid preparation, so the double jaw joint could not be examined in place. However, the morphology of the lower jaws clearly exhibited a broad trough on the medial side, the "housing" for several "reptilian" bones, and demonstrated the double (composite) jaw joint. The beautifully prepared skull exposed the structure of the lateral wall of the braincase and the morphology of the orbit (figure 5.2).

The skull of *Morganucodon* was "mounted" in a small box on sand, so it was possible to rotate it using a fine brush and thus examine it under a binocular microscope. The lower jaws had been placed in other boxes. In addition to this wonderful skull, Kenneth and Frances had at their

disposal thousands of isolated bones of *Morganucodon watsoni* from the fissure fillings in Wales (figure 5.3).

After the two monographs by Kermack, Musset, and Rigney on the *Morganucodon* lower jaw and skull were published (1973, 1981), Kermack sent the Chinese skull back to Father Rigney in the United States, who subsequently deposited it at the Field Museum in Chicago. Later, additional *Morganucodon* skulls, though less complete than the first, were found at the same locality by Chinese paleontologists, and these are now housed at the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing.

London's Mammal Symposium 1970 and the Kermacks in Poland

In 1969, I spent six weeks in London, examining material mainly at the University College with Kenneth and Frances. During that time I co-authored with Kenneth a short article entitled "Therian and Non-therian Mammals" (see also chapters 9 and 10), which was published in 1971 as a chapter in *Early Mammals*, (Kermack and Kielan-Jaworowska 1971), along with papers presented at the Early Mammals Symposium. The symposium was held in June 1970 in London and was organized by Doris and Kenneth Kermack. I met there several paleontologists working on early mammals, including Harold Rigney. Probably the most interesting paper presented at this symposium was one by Alfred W. (Fuzz) Crompton (1971), "The Origin of the Tribosphenic Molar," which became a milestone in understanding the function of the tribosphenic molars. Fuzz presented at this symposium a relatively large model made of cardboard, consisting of simplified two upper molars with one lower molar fitting between them, moving against the uppers, clearly demonstrating how these teeth sheared food (see chapter 12). Of great interest, especially for students attending the symposium, was a chance to meet George Gaylord Simpson, the most famous vertebrate paleontologist at that time.

Kenneth Kermack, on his own or with his co-workers (especially with Frances Mussett), in addition to their main opuses describing the skull of *Morganucodon*, published several shorter papers of a more general character, discussing the issue of the origin of mammals and the interrelationships among the early mammals, including a paper on *Aegialodon dawsoni* (Kermack et al. 1965). *Aegialodon*, although represented by a single lower molar, played an important role in understanding the issue of the origin of tribosphenic molars (see chapter 12).

During my first visit to University College, Kenneth told me that he was anxious to visit Poland, for during the Second World War, as a young soldier, he served under the command of a Polish officer. During the war, a large part of the Polish Army, defeated by Germans in the early fall of 1939, left Poland and, through southern Europe and France, managed to reach Great Britain. At the end of war the Polish Army in the West numbered about 200,000 soldiers, including members of the Polish Air Forces, whose Squadron 303 shot down a record number of German planes during the Battle of England.

Another special reason for Kenneth's visit to Poland, in addition to examining our Gobi collection of Mesozoic mammals, was his hobby. He was especially interested in medieval battles and for a long time had dreamt of visiting the battlefield of Grunwald (or Tannenberg in German), where in 1410 Poles and Lithuanians, united in one state, defeated the Teutonic order. This was the greatest of medieval battles, in which, for the first time, artillery had been used. At the end of March 1970, before the Early Mammals Symposium in London, the Kermacks arrived in Poland in a Land Rover, with Frances Mussett and Patricia Lees-Fergusson, a very skillful technical assistant at University College. At the beginning of their stay, Kenneth remained with me to work in Warsaw, while the three ladies, accompanied by one of our institute technicians, drove the Land Rover to south Poland to prospect Early Jurassic localities for mammals. Unfortunately, no mammals were found this time, either.

After completing our work, we took the whole team, accompanied by my husband and our 11-year-old son, in two cars to the Mazury lakes region in northern Poland, where we visited the Field Station of the Institute of Genetics and Animal Breeding of the Polish Academy of Sciences at Popielno, overseen by my colleague, the late Zbigniew Jaczewski. This early spring at the Mazury lakes was unusually beautiful, and the ride in two chaises across the woods, which Jaczewski organized for us, was especially well remembered by everybody. We spent two days in Popielno, where we visited a breeding farm for the small horses known in Poland as "tarpan" horses and other animals, and we were introduced to the scientific work carried out by the Popielno team. On the way back to Warsaw we visited the Grunwald battlefield – finally fulfilling Kenneth's lifelong dream. Now every year on 15 July, the battle is replayed by armored "knights" coming for the anniversary from all over Europe.

The Kermacks and Frances Mussett visited Poland again in 1981 and attended the Second Symposium on Mesozoic Terrestrial Ecosystems, where Kenneth and Frances presented a paper, "The Ear in Mammal-like Reptiles and Early Mammals," published later in the symposium proceedings in *Acta Palaeontologica Polonica* in 1983.

Other Early Mammaliaforms

The year 1990 brought an unexpected find: Lucas and Hunt reported the discovery of an incomplete early mammaliaform braincase from the Carnian of Texas (225 Ma), named *Adelobasileus cromptoni* (figure 5.4). This specimen was some 10 million years older than the oldest mammal representatives known at the time. It was subsequently redescribed in the *Journal of Vertebrate Paleontology* by Lucas and Luo (1993).

The postcranial skeleton of *Morganucodon watsoni* from Wales has been reconstructed (see figure 5.3) from a great number of isolated bones, but because of the lack of proven articulation, some important details could not be reconstructed. Fortunately, at the beginning of the 1960s other morganucodontans were found in South Africa, in the Red Beds

5.4. *Adelobasileus cromptoni* from the Late Triassic (late Carnian) of Texas. Posterior part of the braincase in lateral view (A), half of the occipital plate in posterior view (B), and in ventral view (C).

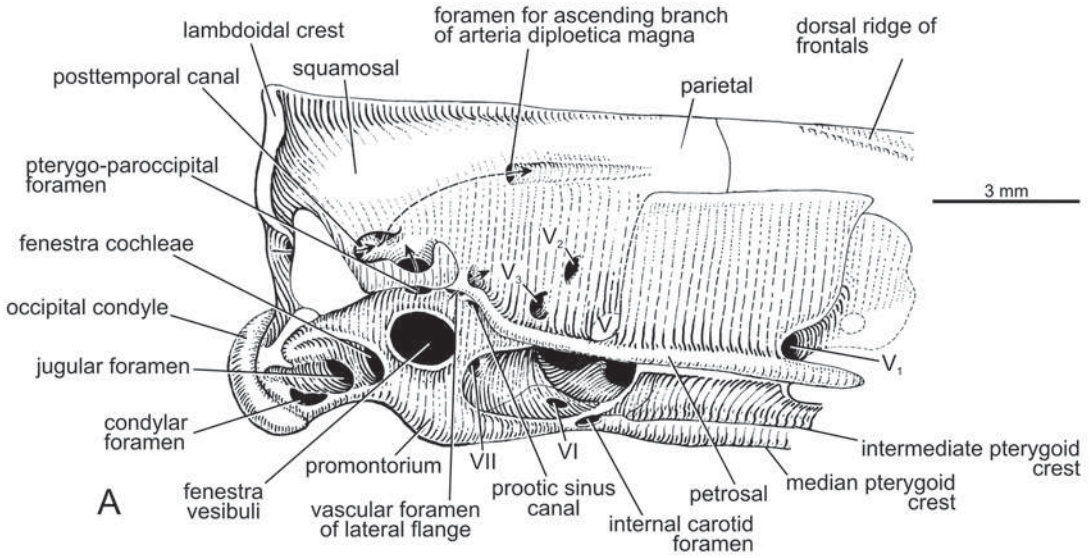
From Kielan-Jaworowska et al. (2004: figure 4.11).

of the Stromberg Series, originally referred to as Late Triassic age but subsequently recognized as Liassic (Early Jurassic). The first specimen was discovered in 1962 in Basutoland by an expedition led by Alfred W. Crompton, at that time the director of the South African Museum in Cape Town. It was a tiny skull of a juvenile mammal, which Crompton described preliminarily in 1964 as *Erythrotherium parringtoni*, named in honor of his supervisor from Cambridge University, F. R. Parrington. *Erythrotherium*'s dentition is quite similar to that of *Morganucodon*.

In 1964 Crompton left South Africa and became a professor at Yale University in New Haven, Connecticut. In November 1966, he organized a joint expedition by the South African Museum, Yale University, the British Museum (Natural History), and London University, which explored the Red Beds of Late Triassic age in the area of Hershel, along the border between Lesotho and South Africa. Fossils were rare and collecting conditions difficult. In December 1966, Ione Rudner, a technician from the South African Museum, found a tiny skull associated with a nearly complete postcranial skeleton. This was a new mammal, designated by Crompton and Jenkins (1968) as *Megazostrodon rudnerae*, in honor of its discoverer.

In 1974 Crompton, by that time at Harvard University, described in detail the dentition of *Erythrotherium* and *Megazostrodon*. Jenkins and Parrington (1976) described the postcranial skeleton of *Morganucodon*, referred to as *Eozostrodon*, as well as those of *Megazostrodon*, and *Erythrotherium*, and they discussed the habits of these earliest mammals. Based on tooth structures they suggested that morganucodontans were primarily insectivorous. At the time, the issue of whether the first mammals were arboreal or terrestrial was being widely discussed. In earlier papers, on the basis of observations on modern tree shrews and other extant mammals, Jenkins had argued that in the case of small mammals, terrestrialism and arboreality are not discrete phenomena. Small mammals often move easily between the trees and the ground. According to Jenkins and Parrington there is no evidence that the hallux of the hind foot in morganucodontans was opposable. In order to demonstrate the ability of morganucodontans to move between trees and the ground, the authors published a reconstruction (Jenkins and Parrington 1976) of the morganucodontan skeleton (based principally on the skeleton of *Megazostrodon rudnerae*) resting on the trailing roots of a tree. This drawing has been reproduced in nearly all paleontological textbooks and compendia published since that time. The authors did not notice, however, that taking into account the length of the morganucodontan skeleton (about 10 cm), that the diameter of the tree would have been about 6 cm, and such small trees never have trailing roots!

Only the isolated astragalus and calcaneus of the tarsus of morganucodontans have been preserved, as has a nearly complete pes of *Megazostrodon*, in which the astragalus and calcaneus were heavily damaged. The os calcaris, characteristic of nearly all early mammals (except for the therians), is described in chapter 8 ("Allotherians") of the book *Mammals*


lambdoidal crest
foramen for ascending branch of arteria diploetica magna
dorsal ridge of frontals
posttemporal canal
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pterygo-paroccipital foramen
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fenestra cochleae
V_2
V_3
occipital condyle
V
jugular foramen
V_1
condylar foramen
intermediate pterygoid crest
promontorium
VII
VI
median pterygoid crest
A
fenestra vesibuli
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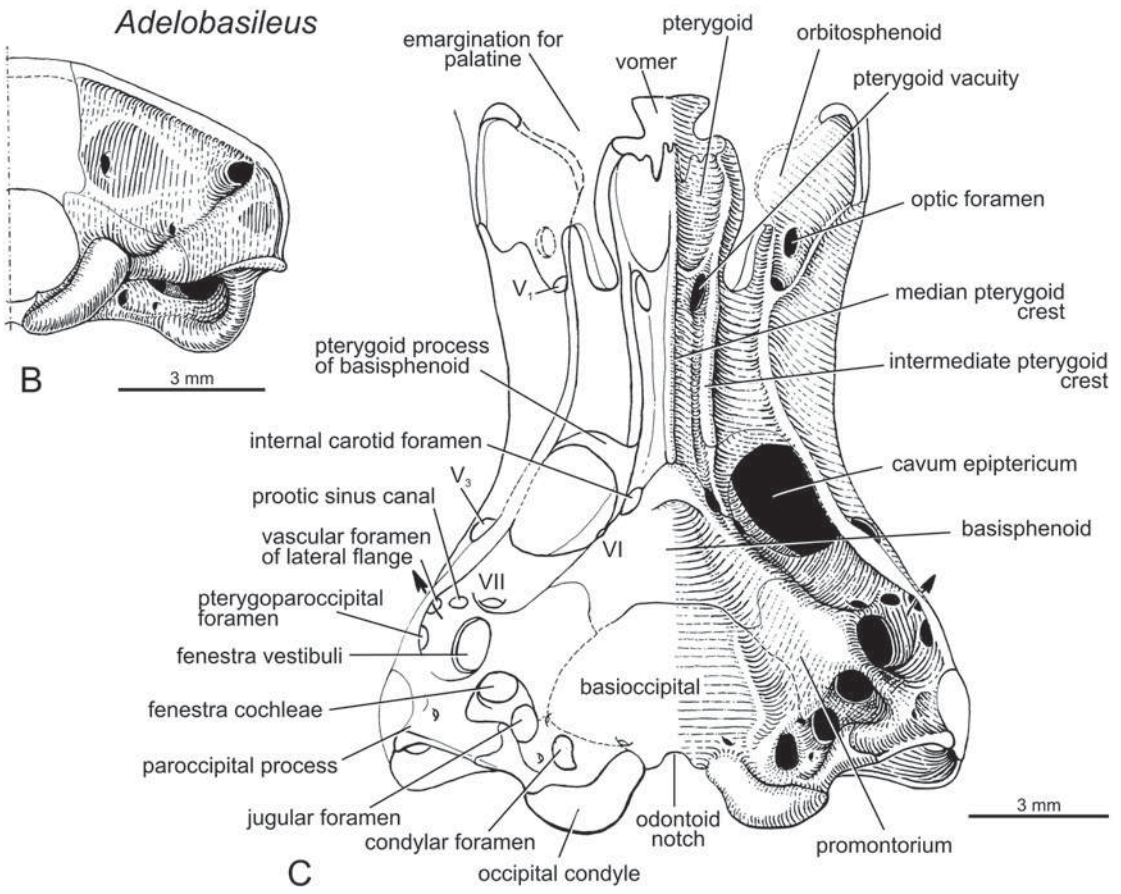
Adelobasileus
emargination for palatine
pterygoid
orbitosphenoid
vomer
pterygoid vacuity
optic foramen
V_1
median pterygoid crest
pterygoid process of basisphenoid
intermediate pterygoid crest
B
3 mm
internal carotid foramen
cavum epiptericum
V_3
prootic sinus canal
basisphenoid
vascular foramen of lateral flange
VI
VII
pterygoparoccipital foramen
fenestra vestibuli
basioccipital
fenestra cochleae
paroccipital process
3 mm
jugular foramen
odontoid notch
condylar foramen
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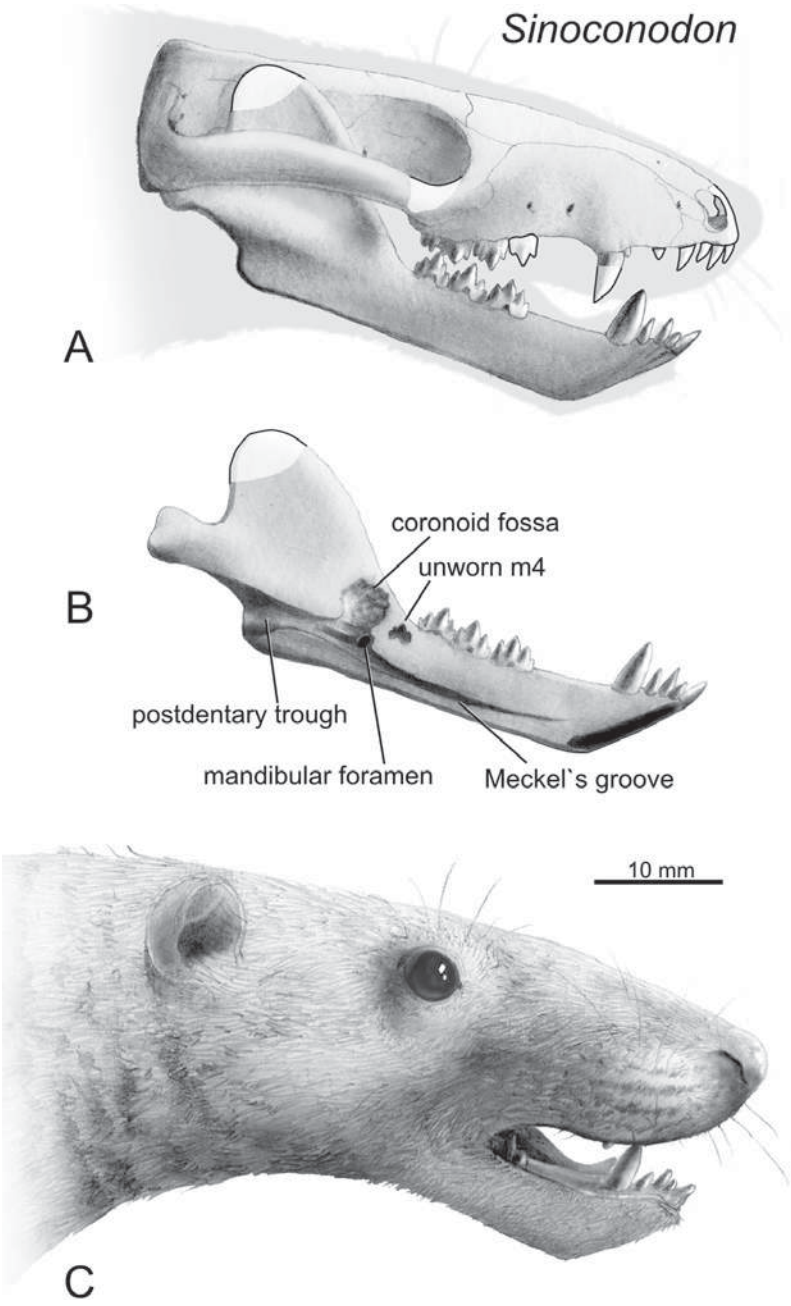
occipital condyle



5.5. Reconstruction of the skull (A) and head (C) of *Sinoconodon rigneyi,* and reconstruction of the left dentary in medial view (B). The drawing is based on the specimen CUP1 (Catholic University of Peking, China; original reference of Patterson and Olson 1961), which is the anterior part of the skull and lower jaw from the lower Lu Feng series. The series was originally referred by Patterson and Olson (1961) to the Late Triassic but subsequently recognized by Crompton and Luo (1993) as Early Jurassic.

Original artwork by Oscar Sanisidro.

from the Age of Dinosaurs, but it has not been found as yet in morganucodontans (Kielan-Jaworowska et al. 2004).

Among the early mammals, *Megazostrodon* differs considerably from *Morganucodon* and *Erythrotherium*. Because of this, in 1986 Gow erected a separate family of Megazostrodontidae. So far, 11 morganucodontan genera have been established, six of which have been placed in the Morganucodontidae, with the five remaining in the Megazostrodontidae. In addition to the three best-known genera discussed above, only the

North American *Dinnetherium*, set up by Jenkins, Crompton, and Downs (1983), from the Early Jurassic Kayenta Formation of North America, is reasonably well preserved. An almost complete dentition of *Dinnetherium* is known, set in a complete lower jaw and a partial skull. The seven remaining morganucodontan genera are known only from isolated teeth. During the Late Triassic and Early Jurassic, morganucodontans apparently had nearly a worldwide distribution. Because at this time the supercontinent of Pangaea existed, it seems likely that this group may eventually be found somewhere, for example, in South America and Australia.

Other early mammals from the end of the Triassic Period and beginning of the Jurassic belong to five groups: *Sinoconodon* (figure 5.5), morganucodontans, haramiyidans, the "symmetrodontan" *Kuehneotherium*, and *Hadrocodium*, all of which, except for *Hadrocodium* (figure 5.6), have a double (composite) jaw joint.

The Question of Hadrocodium

Luo, Crompton, and Sun (2001b) described the tiny Early Jurassic genus *Hadrocodium* and assigned it to Mammaliaformes, although it is evident from their figure 3 that it better suits the diagnosis of Mammalia *sensu* Rowe (1988) than that of Mammaliaformes. I am of the opinion that *Hadrocodium* (figure 5.6) differs from all mammaliaforms in having a mammalian dentary, no postdentary trough, a single dentary/squamosal (mammalian) jaw joint, the apparent presence of three ear ossicles, and a relatively large brain. I assign it tentatively to Mammaliaformes.

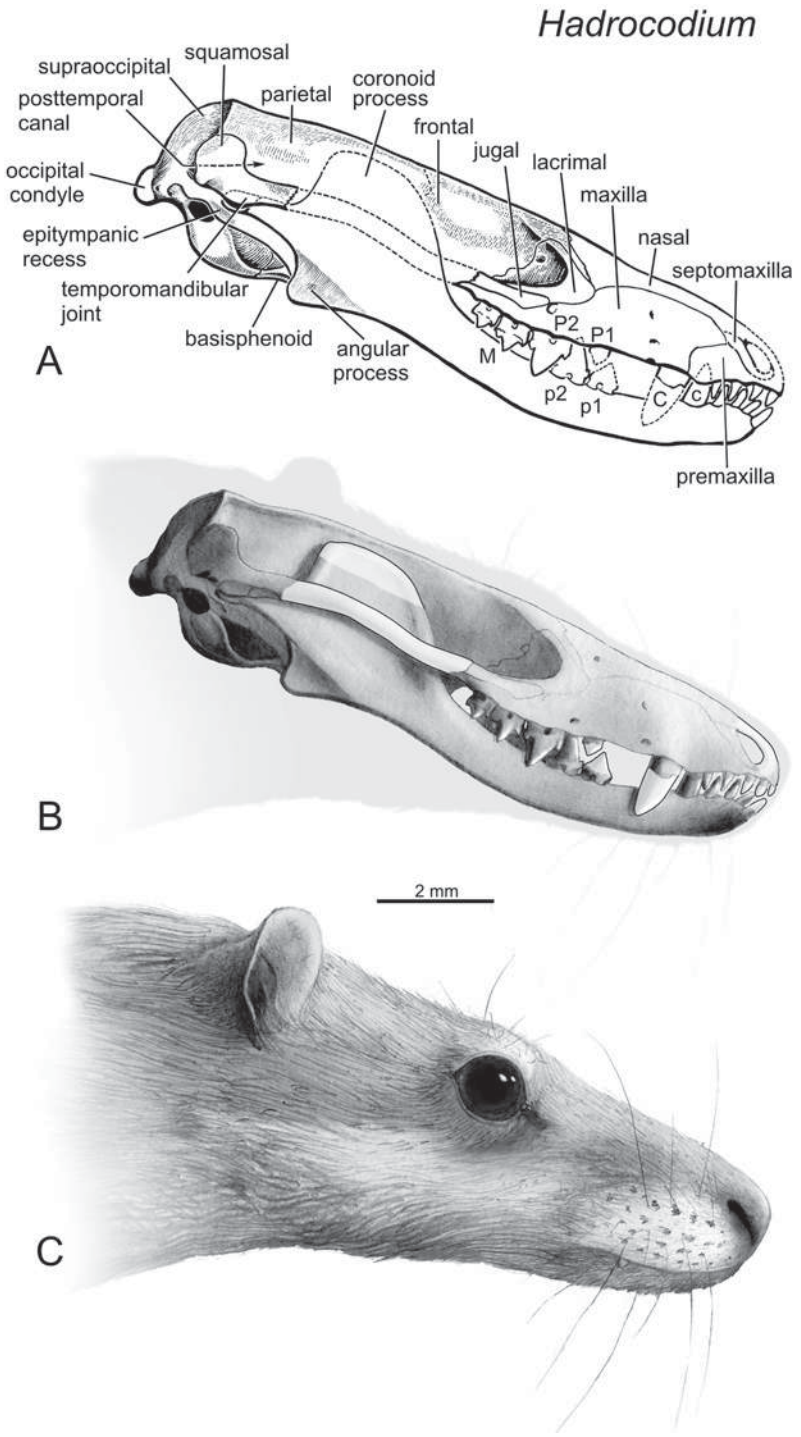
Perhaps it is proper to note at this point a more general problem faced in presentation of paleontological studies to a wider public. Sometimes we are forced to use a specific language and exotic names to describe tiny anatomical details and to discuss systematic issues spanning over hemispheres and mega-years. I am sure, however, that even the most complicated facts, finds, and theories can be expressed in plain words. One such complicated story is that of the evolution of the mammalian middle ear. When mammals made their appearance, they developed a new jaw joint, and the bones of the old reptilian joint evolved a new function, forming the new mammalian ear ossicles. This is one of the most fascinating transformations in vertebrate evolution. Let's begin our exploration of these earliest mammals with a bit of a mind-boggling journey—from jaw joint to refined hearing. This evolutionary change opened a new and previously unoccupied way of interacting with the world around them to this group of vertebrates.

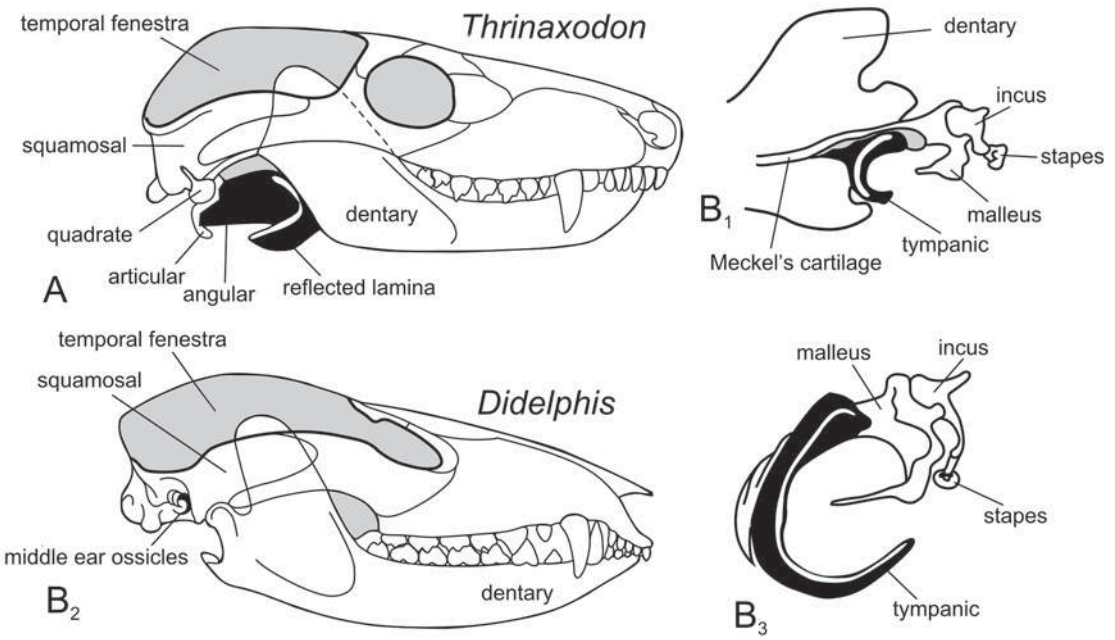
The Reichert-Gaupp Theory

Intermediate stages between large systematic units, such as the orders, classes, and phyla, are very seldom preserved. The origin of mammals from their non-mammalian cynodont ancestors is often quoted as the best documented transition from one class to the other (see Kielan-Jaworowska et al. [2004], especially chapters 3 and 4, for a detailed discussion).

5.6. *Hadrocodium wui.* A. Skull with mandible in occlusion in lateral view. B. Reconstruction of the skull in lateral view. C. Reconstruction of the head in lateral view.

A. From Kielan-Jaworowska et al. (2004). B, C. Original artwork by Oscar Sanisidro.





5.7. Comparison of the skulls of a mammal-like Early Triassic reptile *Thrinaxodon* (A) and a modern mammal *Didelphis* (B). B_1. The ear ossicles of a juvenile *Didelphis,* which are not as yet relocated into the middle ear and are situated to the rear of the dentary, as in *Thrinaxodon.* B_2. The skull of an adult *Didelphis.* B_3. The ear ossicles of an adult *Didelphis,* which have been relocated to the middle ear, as characteristic of all adult mammals.

Based on Hopson (1979, 1994) and modified.

The most important difference between the skeleton of reptiles and mammals concerns the structure of the lower jaw – the joint between the jaw and skull and the ear bones (ossicles) nested in the middle ear. In figure 5.7, these differences are represented by *Thrinaxodon*, an Early Triassic cynodont, and *Didelphis*, the American opossum. The reptilian lower jaw (figure 5.7A) consists of several bones, the largest of which is the dentary, which usually bears the teeth. In one of the bones – the articular, situated at the back of the dentary – there is a socket (referred to also as the articular fossa), which articulates with a condyle on the quadrate bone at the back corner of the skull. This is the craniomandibular joint.

In mammals (figure 5.7B_2), the lower jaw consists of a single bone, the tooth-bearing dentary. On the dentary there is a condyle that articulates with the glenoid fossa on the squamosal bone of the skull (which is a part of the temporal bone). This hinge has been referred to as the temporomandibular joint. In the reptilian middle ear there is a single auditory ossicle – the stapes (or columella auris). This is an ancient structure, ultimately derived from the hyomandibular, which was the link between the jaws and the braincase in fish ancestors of tetrapods. When fishes left the water and the skull of early tetrapods lost much of its mobility, this hyomandibular changed function, becoming the rod-like columella auris situated in the middle ear cavity. This apparently happened several times in different lineages. But in the middle ear of mammals, there are three ear ossicles – the stapes and two new ossicles, the incus and the malleus. The incus was derived from the reptilian quadrate or the skull component of the old reptilian joint, now lost – or transformed to new status as a joint between ear ossicles rather than between skull and jaw. The malleus was derived from the reptilian articular. In addition, the mammalian middle

ear incorporates yet another transformed element, the ectotympanic bone, which supports the delicate tympanic membrane. The ectotympanic is derived from yet another component, the angular bone, of the reptilian mandible (figure 5.7A).

For more than 150 years it was known that the bones constituting the reptilian mandibular hinge are equivalent (homologous, in scientific parlance) to the middle ear ossicles of mammals. The reptilian quadrate bone transformed into the incus; the articular and goniale (a dermal bone, which appears relatively late in ontogeny, homologized with the reptilian prearticular) became the malleus; and the angular bone of the reptilian mandible evolved into the ectotympanic. The malleus, the goniale part of the malleus, and the ectotympanic, which in reptiles are part of a complex of postdentary bones (the articular, prearticular, and angular, respectively), are in mammals attached to the mandible only in embryonic stages. In adults, these separate from the mandible and move into the tympanic cavity (figures 5.8 and 5.9). It is difficult to imagine that the discovery of these marvelous changes occurred as early as 1837, recognized by the German embryologist Karl Bogislaus Reichert (1811–1883), who had at his disposal only a primitive microscope and fine preparatory needles. He was able to trace the changes in the ear region in embryos of several living mammals. Seventy-six years later, Reichert's work was expanded by another German embryologist, Ernst Gaupp (1865–1916), who in 1913 published a comprehensive monograph on this subject. Since that time, the theory of the origin of mammalian ear ossicles from the bones of the reptilian jaw articulation has been known as the Reichert-Gaupp Theory. All these details were discovered by studying mainly extant reptilian and mammalian embryos, repeating in their development the evolutionary stages that had occurred in past reptilian lineages.

Edgar Allin

Comprehensive paleontological confirmation of the Reichert-Gaupp theory had to wait for many decades. Edgar F. Allin (figure 5.1D) from the University of Chicago, using a great variety of fossil material, elucidated the functional significance of the transformation of the articular and quadrate, which formed the reptilian jaw joint, into the malleus and incus of mammals.

Edgar Allin, a Canadian paleontologist and evolutionary anatomist, was born in 1930 in Edmonton, Alberta. In 1956–1963, Edgar studied medicine at the University of Alberta in Edmonton and graduated as an M.D. in 1963. In 1963–1965 he worked at two hospitals as a medical doctor. In 1965–1966 he studied postgraduate biology and physical anthropology at the University of Alberta in Edmonton and was granted a bachelor of science degree, and in 1966–1967 he was a postgraduate student in human biology at the University of Wisconsin. Beginning in 1961 he started teaching at various universities in the United States and Canada; his lectures covered gross human anatomy, osteology and comparative primate anatomy, neurology, and embryology. Beginning

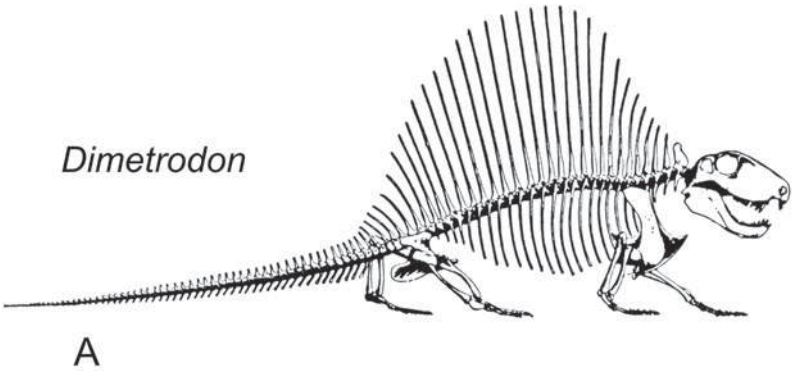
in 1984, when he was appointed full professor, he gave lectures on the origin of mammals at the Field Museum of Natural History in Chicago, mostly for graduate students. He became professor emeritus at the University of Chicago in 2007. He published some 112 scientific papers, the most important of which is probably the 1975 monograph in which he provided the first paleontological sequence of changes in the ear region from mammal-like reptiles to mammals, supporting the Reichert-Gaupp (1913) theory.

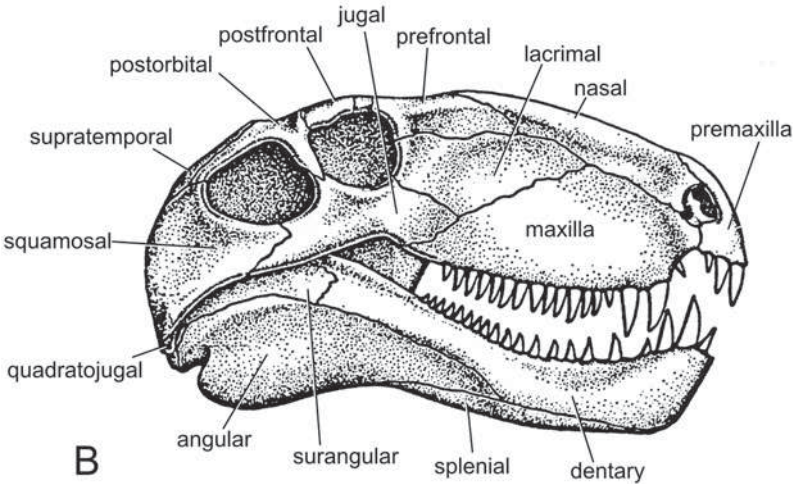
Before Allin published his benchmark paper in 1975, paleontologists generally thought that the ear in mammal-like ancestors of mammals was constructed the same way as in living reptiles and birds, with the tympanic membrane situated at the posterior wall of the quadrate, which in reptiles is an element of the jaw articulation (see, for example, Hopson 1966). According to this view, the single ear ossicle – the stapes – contacted the tympanic membrane posterior to the jaw articulation, and so transmitted the vibrations of the tympanic membrane to the inner ear. Allin suggested instead that in the evolutionary line leading to mammals, the middle ear was built quite differently from that of living reptiles.

Allin demonstrated that in the ancestors of mammals – the synapsids – the tympanic membrane was supported by a process on the angular bone called the reflected lamina and that the bones forming the reptilian jaw joint – the articular and quadrate – not only functioned in mastication but also had a role as part of the middle ear, transmitting airborne sounds. Allin's idea was not entirely new. As early as 1913, Gaupp suggested that the reptilian and mammalian tympanic membranes were not homologous. He was followed in this view by a few other anatomists. However, Allin was the first to provide the detailed anatomic analysis of the relevant changes in the structure of the lower jaw and ear region from the early synapsids, through intermediate stages of primitive and advanced therapsids (cynodonts) to early mammals.

In synapsids, the lower jaw consists of seven or eight bones, of which the largest is the tooth-bearing dentary. The remaining four elements are the articular, the prearticular, the angular, and the surangular – referred to as the postdentary bones – which are situated in a trough that extends posteriorly as a continuation of Meckel's groove, housing Meckel's cartilage. There are also three other elements located outside the trough: the splenial, the coronoid, and the anterior coronoid, which is lost in most reptiles. In early synapsids, the postdentary elements are prominent. In the Early Permian (about 280 to 290 Ma) pelycosaur *Dimetrodon,* for example, the dentary is relatively shallow and extends for about three quarters of the jaw length (figure 5.8B). The angular is a large bone, bearing at its posteroventral end a process referred to as the reflected lamina, regarded as a homologue to a much more prominent lamina in cynodonts, which played an important role in transformation of the synapsid angular bone into the mammalian ectotympanic.

Paleontologists believe that a group related to *Dimetrodon* gave rise to the therapsids. In the evolution of mammal-like reptiles, one observes





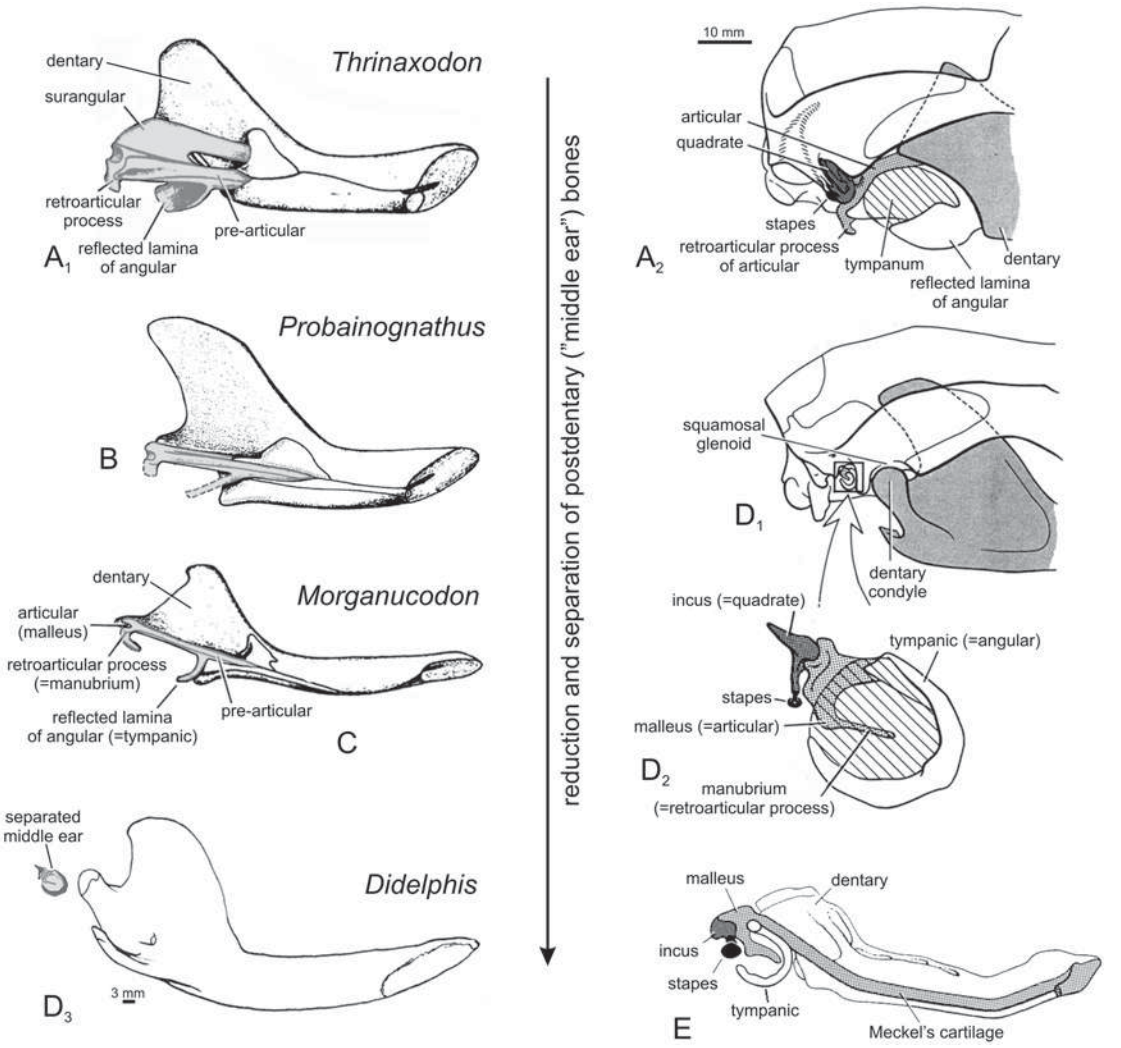
5.8. A. Reconstruction of the skeleton of the pelycosaurian *Dimetrodon,* characterized by unusually long neural processes of the vertebrae, apparently forming a skeleton for a sail, which might have served in regulation of the body temperature. B. Skull of *Dimetrodon* in lateral view, showing a shallow dentary, extending for two-thirds of the mandible length, and a very large angular, with a notch on the posteroventral part. The notch separates a process regarded as homologous to the reflected lamina of the therapsids and, in the future, of the mammals.

Modified from Romer by providing full terms (1966: figures 267 and 268 [lower left]).

5.9. Simplified reconstruction showing the evolution of the mammalian lower jaw from a reptilian ancestor and reduction of the postdentary elements. A. Cynodont *Thrinaxodon.* A_1. Medial view of the lower jaw. A_2. Lateral view of lower jaw joint and the postdentary elements attached to the dentary. B. Cynodont *Probainognathus,* medial view of mandible, showing the reduction of postdentary, or "middle ear," bones. C. Stem mammal *Morganucodon,* medial view of mandible, showing further reduction of postdentary, or "middle ear" bones. D. Marsupial *Didelphis.* D_1. The jaw joint in lateral view. D_2. Mammalian middle ear in lateral view, showing homology of middle ear bones. D_3. Mandible in medial view, with separation of middle ear bones from the dentary. E. Mandible in medial view, showing an early embryonic stage of a placental (with the attachment of Meckel's cartilage to the dentary).

From Kielan-Jaworowska et al. (2004: figure 3.10).

a successive enlargement of the dentary and the correlative reduction in size of the postdentary bones (figure 5.9). As demonstrated by Allin, in primitive cynodonts (such as the Late Permian procynosuchid *Levachia*, about 250 million years old) the posterior portion of the dentary is expanded, as is characteristic of advanced cynodonts, with development of a robust reflected lamina. In the Early Triassic *Thrinaxodon* (about 235 million years old; figure 5.7A), the reflected lamina of the angular is still a prominent process, posteroventrally encircling the space regarded by Allin as occupied by a large tympanic membrane. Characteristic of the lower jaw in *Thrinaxodon* (figure 5.7A) was the development of a high coronoid process and a distinct masseteric fossa, which gave this lower jaw a mammalian character, indicative of the presence of the masseter muscle. The masseter muscle serves to balance and strengthen the bite. In mammals the masseter works in concert with another muscle, the pterygoid, to aid in precise tooth occlusion. The coronoid process serves to increase the mechanical advantage of the main jaw-closing muscle, the temporalis, which also greatly increases bite strength.



Although this book is chiefly on early (Mesozoic) mammals, there are some synapsid specialists who should be mentioned: James A. Hopson, Tom S. Kemp, and Hans-Dieter Sues.

James A. Hopson, Tom S. Kemp, and Hans-Dieter Sues

James A. Hopson (figure 5.1F) was born in 1935 in the United States. He received his Ph.D. in 1965 at the University of Chicago and afterward worked for two years at Yale University. In 1967 he returned to Chicago, where he lectured in anatomy, and after several degrees became a full professor. He is now professor emeritus at the University of Chicago and at the same time a research associate at the Field Museum of Natural History. He has been working mostly on synapsids, the origin of mammals, and early mammals, but he has also studied the biology of dinosaurs.

An important student of synapsids and of the origin of mammals is the British paleontologist Tom S. Kemp (figure 5.1E). Tom was born in 1943, in Ellesmere Port, England, and he completed a Ph.D. in 1968

under the supervision of F. R. Parrington. His thesis, published in 1969, was on the functional morphology of the skull of gorgonopsian therapsids. After four years as assistant curator at the Museum of Zoology at Cambridge University, he was appointed curator of the zoological collections at the Museum of Natural History at Oxford University, where he has remained. In 1974 Kemp led a joint Oxford University–Geological Survey of Zambia Expedition to the Permo-Triassic of the Luangwa Valley, where was found, among many Late Permian therapsid specimens, the most complete skeleton of the basal-most cynodont *Procynosuchus*. Other important finds there included one of the best-preserved specimens of the mid-Triassic cynodont *Luangwa drysdalli* and an almost complete skeleton of *Dicynodon trigonocephalus*. Kemp's work has largely focused on the functional anatomy of therapsids and the macroevolutionary processes involved in the origin of mammals and of higher taxa in general. In 1982 he published the book *Mammal-like Reptiles and the Origin of Mammals*, which is still the only full-length, monographic treatment of this subject. Subsequently, in 2005, Kemp's *Origin and Evolution of Mammals* was published, which updated and extended the scope of the earlier volume. As a Fellow of and tutor at St John's College, Kemp has also always been heavily involved in teaching.

The third student of synapsids to be mentioned here is Hans-Dieter Sues (figure 5.1G), the American/Canadian vertebrate paleontologist, born in Germany in 1956. He received his undergraduate training at Johannes Gutenberg–Universität in Mainz (1975); after earning an master of science degree at the University of Alberta (1977), he moved to the United States and received a Ph.D. (1984) from Harvard University under Farish Jenkins on the basis of a dissertation on Early Jurassic tritylodontid cynodonts from Arizona. From 1992 to 2002, he was curator of vertebrate paleontology and later vice president for collections and research at the Royal Ontario Museum in Toronto. He subsequently became professor of zoology at the University of Toronto. From 2004 to 2009 he was associate director for research and collections at the National Museum of Natural History in Washington, D.C., and he now is senior research scientist in the Department of Paleobiology at this museum. Sues has published over 100 articles and book chapters. Impressive are his organizational and editorial activities. He served as president of the Society of Vertebrate Paleontology in 2004–2006, co-authored *Triassic Life on Land* (Sues and Fraser 2010) and *Terrestrial Ecosystems through Time* (Behrensmeyer et al. 1992), edited *Evolution of Herbivory in Terrestrial Vertebrates* (Sues 2000), and co-edited *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods* (Fraser and Sues 1994) and *Major Transitions in Vertebrate Evolution* (Anderson and Sues 2007).

In a Middle Triassic advanced cynodont, the chiniquodontid *Probainognathus* from South America (also around 235 million years old; figure

5.9B), the lower jaw appears very mammalian, having a large coronoid process. The dentary possesses a small posterior process that resembles the mammalian condylar process. It closely approaches the squamosal but does not contact it, and hence the new (mammalian) jaw joint is not present. A distinct angular process is also present, and the postdentary elements are strongly reduced in size, approaching the condition known among the earliest mammals. Finally, somewhat younger cynodonts, apparently close to the cynodont-mammal transition, are known to possess both the reptilian (quadrate-articular) and mammalian (squamosal-dentary) jaw joints.

Structure of the Jaw Joint in Morganucodon

As described by Kermack and his colleagues (1973, 1981) *Morganucodon oehleri* from China has a double (composite) jaw joint. It consists of the bones that make up the new mammalian jaw joint, the dentary, and the squamosal bone. In addition, on the medial side, the old reptilian joint remains, between the articular and the quadrate. Both joints functioned together, forming a single compound articulation. The postdentary elements are delicate, even in comparison with those in advanced cynodonts. Still, they lie in the postdentary trough and are not yet relocated into the middle ear, which is typical of true mammals. An intermediate fossil form between the condition in *Morganucodon* and true mammals with their single jaw joint is still to be found.

In the late 1950s Kermack and Mussett (1958) published preliminary descriptions of the *Morganucodon* lower jaw, wrongly attributing some *Morganucodon* specimens to Docodonta based on materials from fissure fillings, but the description of the skull and lower jaw from China was delayed until publication in 1973 and 1981, when two monographs were released by Kermack and his team. In the meantime, however, the British paleontologist Francis Rex Parrington, as early as 1941, described two premolars from the Rhaetic of Holwell in England as *Eozostrodon*. He studied the material collected by Walter Kühne, and described it in 1971, including several dentaries of *Morganucodon* from Glamorgan, referred to as *Eozostrodon*.

For many years controversy surrounded the possible synonymy of the genera *Eozoostrodon* of Parrington (1941) and *Morganucodon* of Kühne (1949). The controversy was resolved by William (Bill) A. Clemens (figure 10.1C), who in 1979 published an article in which he argued: "*Eozostrodon parvus* is the appropriate name for the morganucodontid represented in the fauna preserved in fissure fillings in Holwell Quarry, Wales [*sic*]. Its diagnostic dental morphology is not duplicated in the extensive samples of the most abundant morganucodontid known from Wales for which the name *Morganucodon watsoni* is appropriate" (Clemens 1979: 1).

The tiny ear ossicles characterizing mammals are seldom preserved in fossils, but, on the basis of the structure of isolated lower jaws, one can deduce if an animal had either a reptilian joint, a composite jaw joint (intermediate between the reptilian and mammalian condition), or a

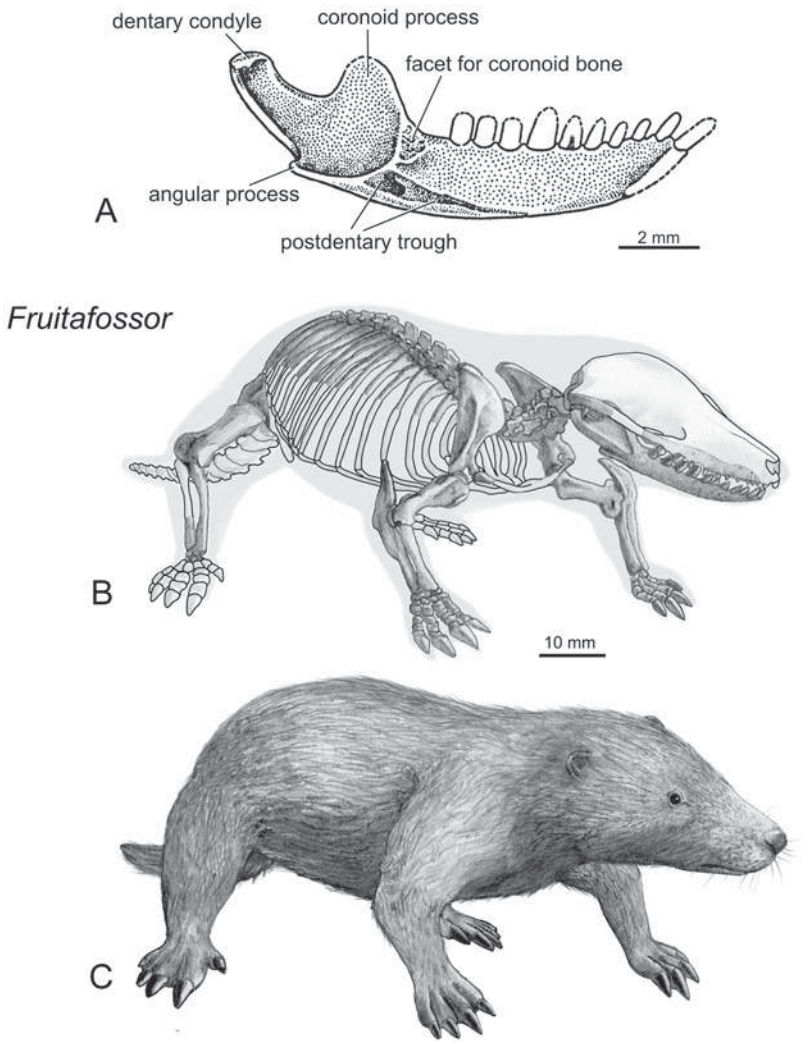
simple mammalian jaw joint. In advanced cynodonts and the earliest mammals with a composite jaw joint, the postdentary bones are housed in a trough in the dentary located on its medial side. The trough is literally a prolongation of Meckel's groove, in which Meckel's cartilage is located. At the bottom of the trough there are distinct facets corresponding to the particular postdentary bones. It follows that if the trough is preserved in a dentary, one can infer the postdentary bones that once were located there and conclude whether the animal had a composite jaw joint. If there is no trough and there is a dentary condyle, the jaw belongs to a mammal, which apparently had three ear ossicles in the middle ear.

The composite jaw joint, which represents an intermediate stage between the reptilian and mammalian lower jaw suspensorium, was first found in *Morganucodon* but subsequently was also recognized in another morganucodontan, as well as in another primitive mammaliaform, *Sinoconodon* from China, previously discussed (figure 5.5). This sort of jaw is also present in the "symmetrodontan" *Kuehneotherium*, in two docodontan genera *Haldanodon* and *Castorocauda*, as well as in the haramiyidans. These latter forms are discussed in other chapters.

The composite jaw joint is one of several plesiomorphic (primitive) characters present (as discussed above) in *Morganucodon*. Morganucodontans are, more than other mammaliaforms, similar to cynodonts in the structure of the lateral wall of the braincase. In cynodonts – for example, *Thrinaxodon* – three bones contribute to the structure of the lateral wall of the braincase. From the rear these bones are the squamosal, the prootic (in mammals, they are referred to as the anterior lamina of the petrosal), and the alisphenoid. Anterior to the alisphenoid the wall of the braincase is not ossified, producing a large orbital vacuity. The lateral wall of *Morganucodon* is of similar construction, the differences being only the proportions between particular bones and the orbital vacuity being relatively smaller than in *Thrinaxodon*.

Reconstructions of the life habits of extinct mammals are based mainly on their dentition, postcranial skeleton, assumptions concerning musculature, and a comparison with living forms. The dentition of *Morganucodon oehleri* consists of four incisors, a single-rooted canine (the upper distinctly larger than the lower), and eight cheek teeth, of which four are regarded as premolars and four as molars. The main cusps in postcanine teeth are arranged anteroposteriorly, as in eutriconodontans, and encircled by cingula with accessory cuspules. On the basis of superficial similarity of the dentition of eutriconodontans to that of morganucodontans, when discovered, morganucodontans were assigned to the "Triconodonta." Subsequent studies have demonstrated that the two groups are not closely related. The dentition of *Morganucodon* is indicative of an animal feeding on insects and other small invertebrates.

The cheek teeth of morganucodontans differ from those of therian mammals in having the main cusps arranged longitudinally, rather than forming a triangle as in therians. Another difference is that the main cusp of the lower molar in morganucodontans slices between two cusps on



5.10. *Fruitafossor windscheffeli.* A. Lower jaw in medial view, showing dentition and postdentary trough; modified from Luo and Wible (2005) by providing full terms for anatomical elements. B. Reconstruction of the skeleton, based on parts preserved in the holotype specimen; originally reconstructed by Luo and Wible (2005), modified here by reducing the distance between the hind legs and showing the right side of the specimen. C. Reconstruction of the animal by Oscar Sanisidro, modified by Aleksandra Holda-Michalska by reducing the distance between the hind legs.

A, B. Courtesy of Zhe-Xi Luo.

an upper molar, rather than between the two upper teeth as in therians. The solution "adopted" by therian mammals proved to be more efficient than that of morganucodontans, and it led to the development of the tribosphenic molar (chapter 12), from which originated all the types of differentiated dentitions seen in marsupials and placentals.

The Structure of Fruitafossor

The last taxon, which I tentatively include in this chapter, is *Fruitafossor windscheffeli*, described by Luo and Wible (2005) from the Late Jurassic Morrison Formation of Colorado (figure 5.10). Part of the cranial roof has been distorted, but almost complete dentition and postcranial skeleton are preserved.

Fruitafossor shows unusual similarities to present day xenarthran and tubulidentate mammals in having teeth with open roots, without enamel, and the forelimbs showing adaptations for digging. In addition,

the lumbar vertebrae show the so-called xenarthran joints, which occur in present-day mammals only in edentates. The lower jaw consists of a single bone and shows a dentary condyle that articulates with the squamosal of the skull, as typical for eutherian mammals. *Fruitafossor* resembles Early Jurassic *Hadrocodium* in having a mammalian jaw joint between the dentary and squamosal. However, where in *Hadrocodium* the postdentary trough is missing, in *Fruitafossor* there is a wide postdentary trough, but without traces of the reptilian bones, except for the facet for the coronoid. Maybe the fate of the quadrate and articular bones that formed the reptilian jaw joint might vary in different lines of mammaliaforms. We do not know whether in all the cases these bones changed into the mammalian incus and malleus or, rather, whether in some lines they simply disappeared. The affinities of *Fruitafossor* are puzzling. I tentatively place it in chapter 5, realizing that when more material is known, it might be placed in another group of mammaliaforms or early mammals.

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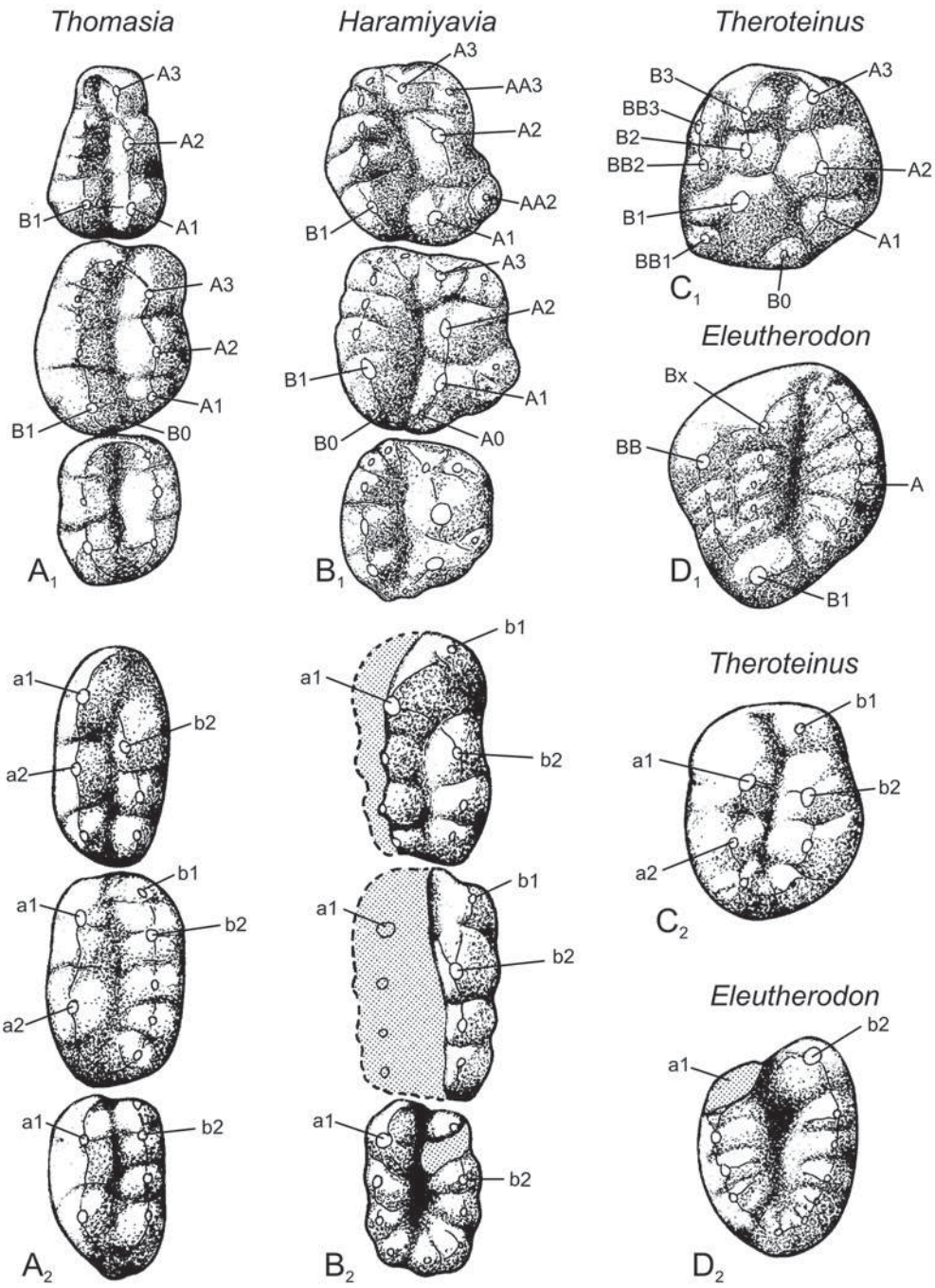
Thomasia
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Eleutherodon
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Theroteinus
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C2
Eleutherodon
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Haramiyidans and Probable Related Forms

6

AS EARLY AS 1847 PLEININGER ERECTED THE GENUS *MICROLESTES* with a single species, *M. antiquus*, based on a minute, double-rooted tooth boasting two rows of cusps. It derived from the Upper Triassic beds (Norian-Rhaetian boundary) of Dagerlof, Württemberg, Germany. The name *Microlestes* was already occupied, as were other names subsequently erected to replace it, and it was later assigned to *Thomasia* Poche, 1908.

Teeth of this type are common in the Late Triassic–Early Jurassic of Europe, and they resemble those of multituberculates in having numerous low cusps, arranged in rows. They differ from those of multituberculates in having cusps of various heights. The teeth referred to as *Thomasia* are relatively narrow. In addition to *Thomasia*, broader teeth assigned to the genus *Haramiya* also occur in the same sediments. Simpson (1947) placed both *Thomasia* (figure 6.1) and *Haramiya* in the family Haramiyidae.

Hahn (1973) erected a separate suborder for the Haramiyidae, a Haramiyoidea, placed within the Multituberculata, and later (in Hahn et al. 1989) raised it to ordinal rank as Haramiyida. Heinrich (1999, 2001) described the genus *Staffia* based on isolated teeth from the Upper Jurassic (Kimmeridgian) Tendaguru beds of Tanzania (see figure 6.2C). The teeth of *Staffia* were obtained from the matrix, housed in the Natural History Museum in Berlin, collected by the German Tendaguru Expedition before the First World War, when Tanzania was a German colony (see Maier 2003). Kielan-Jaworowska et al. (2004) assigned *Staffia* to the Haramiyidae.

Studies on Mesozoic mammals in France are associated with the name of Denise Sigogneau-Russell (figure 6.2E). Denise defended her Ph.D. thesis in 1969, a part of which was devoted to the gorgonopsians (therapsid reptiles) of South Africa, where she spent two years. In 1976, when a Belgian amateur brought her a mammal tooth from a quarry in eastern France, she changed the direction of her studies and began to search for Mesozoic mammals. She sought them with great initiative in France, Portugal, Madagascar, and, finally, in Morocco. In 1991 she published a book on Mesozoic mammals (Sigogneau-Russell 1991).

The beginning of her work on Mesozoic mammals was at the locality Saint-Nicolas-de-Port in Lorraine (in northeastern France). In 1983 she published the first review (Sigogneau-Russell 1983a) of the fauna occurring there (whose remains were obtained by using the screen-washing technique). Subsequently she published a meticulous monograph

6.1. A Comparison of the left upper (A_1–D_1) and right lower (A_2–D_2) molariforms of *Thomasia, Haramiyavia, Theroteinus,* and *Eleutherodon* in occlusal views, illustrating cusp homologies postulated by Butler (2000). Numbering of cusps according to method introduced by Hahn and Hahn (1999). Labial is to the right and mesial above. On upper molariforms the cusps are numbered from distal to mesial and in lowers from mesial to distal, in accordance with their postulated homologies with *Haramiyavia.* On upper molariforms of *Eleutherodon,* the cusps BB and Bx are enlarged mesial cusps of the lingual (BB) and middle (B) rows, and A indicates the A (most mesial) row. Not to scale.

Modified from Butler (2000).

describing about 200 isolated teeth that she obtained from the deltaic sediments of Rhaetic (Late Triassic) age from the same locality (Sigogneau-Russell 1989). She recognized among the investigated teeth three types of upper incisors and one type of lower, as well as upper and lower premolars and molars of haramiyids. Research on these faunas included rewarding collaboration with Gerhard and Renate Hahn. Currently, Sigogneau-Russell studies the British Mesozoic faunas with Percy M. Butler (figure 6.2F). Owing to her scholarship and diligence, she has contributed enormously to the knowledge of early mammal evolution.

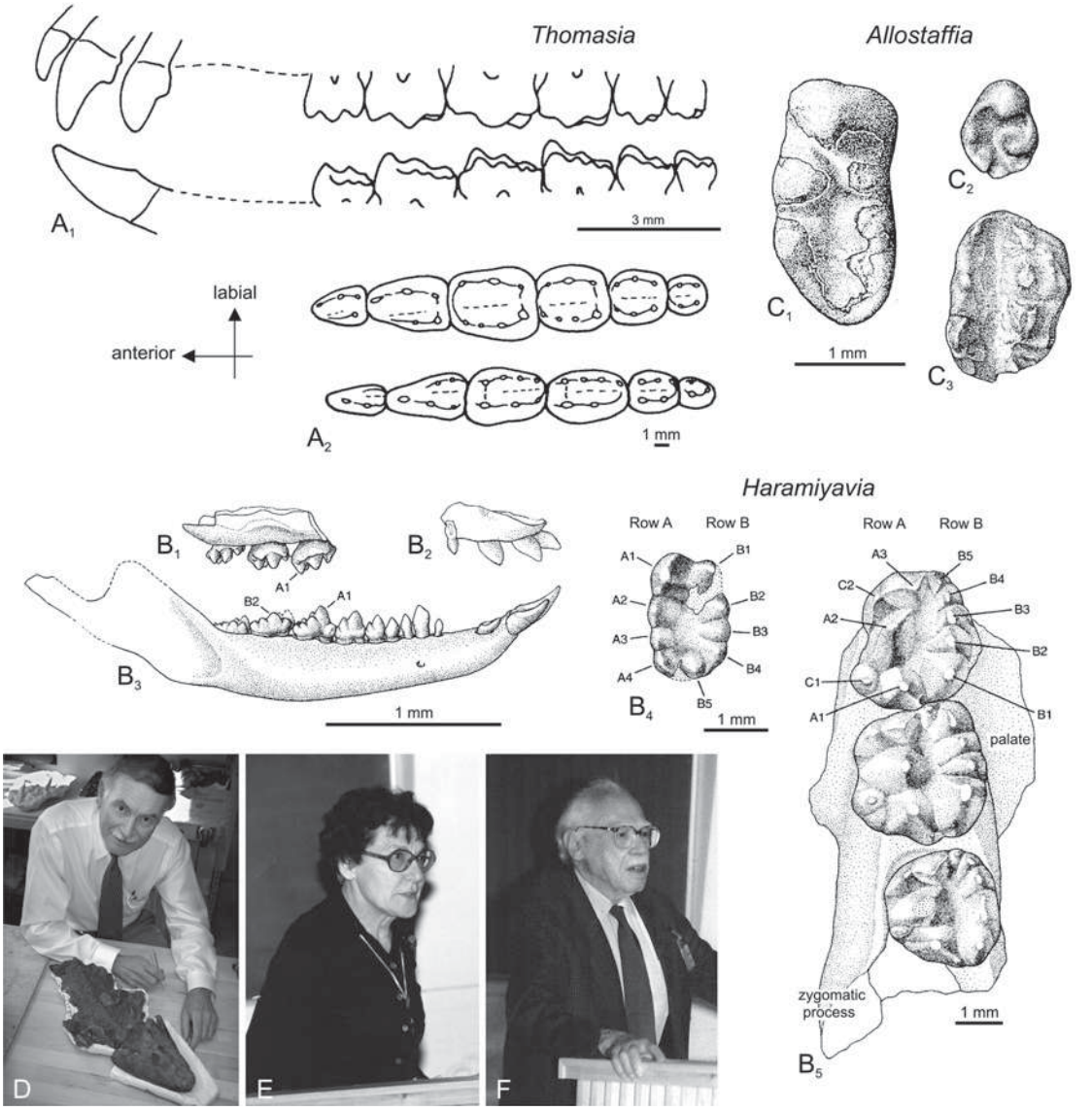
Farish A. Jenkins Jr. (1940–2012)

Farish A. Jenkins Jr. was born in New York and was the first scientist to employ cineradiography to study animal locomotion (figure 6.2D). Jenkins started university studies at Princeton, from which he graduated in 1961, and received his Ph.D. from Yale in 1968. In 1974 he was appointed professor of biology in the Department of Organismic and Evolutionary Biology at Harvard. In 1989 he was awarded the title of Alexander Agassiz Professor of Zoology. Jenkins published over 100 original papers, some of which are comprehensive monographs. He has been working on different groups of vertebrates, both fossil and extant, and most of his papers are innovative. He is also an active field researcher, mostly in Mesozoic deposits. He has described numerous Mesozoic mammals. Especially interesting have been his discoveries of the rich fauna in the Late Triassic Fleming Fjord Formation of East Greenland, which have yielded various vertebrates, most important of which are haramiyidan mammaliamorphs. As described earlier, haramiyidans were known previously only from isolated teeth, and here in the Fleming Fjord Formation they are represented by large parts of the skull with almost complete dentition. The study of this new material casts new light on the relationships of haramiyidans. Jenkins is widely known as a specialist of the postcranial anatomy (especially functional anatomy) of different vertebrates. His monograph on the "Postcranial Skeleton of African Cynodonts" (1971) is a benchmark paper concerning cynodont anatomy. A critical review of Jenkins's papers makes clear that it would be almost impossible to speak on the evolution of any group of vertebrates without citing one of them.

For one and a half centuries the Haramiyida were known only from isolated teeth. In 1997, Farish A. Jenkins Jr., from Harvard University (figure 6.2D), and colleagues described material from the Late Triassic of Greenland, including dentaries and partial maxillae with teeth they named *Haramiyavia clemmenseni*, assigning it to the Haramiyidae (figure 6.2B). Associated with these fossils were fragments of the postcranial skeleton, which were briefly described in the original paper but not

6.2. A. Reconstruction of the dentition of *Thomasia antiqua* (= *Haramiya butleri).* The number of cheek teeth is unknown; three upper and one lower incisor (based on Sigogneau-Russell 1989), two premolars, two anterior molars, and two posterior molars are reconstructed. Upper and lower dentition in lateral view (A_1). Left upper and lower dentition without incisors in crown view (A_2). B. *Haramiyavia clemmenseni,* right maxilla in lateral view (B_1); left premaxilla in inverted view (B_2); right dentary with teeth in lateral view (B_3); left lower molar in occlusal view (B_4); left upper molars in occlusal view (B_5). C. *Allostaffia aenigmatica,* right lower premolar (C_1); right lower posterior molar (C_2); upper molar, possibly M2 (C_3); all in occlusal view. D. Farish A. Jenkins Jr. E. Denise Sigogneau-Russell. F. Percy M. Butler.

A–C. From Kielan-Jaworowska et al. (2004: figure 8.2).



figured. Farish and his co-authors also noted that the dentary of *Haramiyavia* possessed a trough for postdentary bones, characteristic of all Late Triassic and Early Jurassic mammaliaforms, except for *Hadrocodium* (see chapter 5). Upon examination of wear facets on the teeth, Jenkins et al. (1997) further concluded that *Haramiyavia* had orthal (vertical) movement (where upper and lower molars alternate with one another so that each lower molar bites against two upper molars), and on this basis they excluded Haramiyida from Allotheria.

But Percy M. Butler (2000), an expert on mammalian occlusion and a specialist on haramiyidans, drew a different conclusion than Jenkins (see below). Before examining his opinion, I will discuss two groups of teeth similar to those of haramiyidans: the Rhaeto-Liassic

teeth of the Theroteinida from France and the Bathonian teeth of the Eleutherodontidae from England.

Sigogneau-Russell had figured and described two teeth from the Upper Triassic of Saint-Nicolas-de-Port, which she identified as ?Multituberculata indet. (Sigogneau-Russell 1983b). The teeth had an oval outline and three rows of cusps. The roots were preserved. Subsequently, in collaboration with R. M. Frank and J. Hemmerlé, she erected the genus *Theroteinus* with a type species *T. nicolai*, based on three apparently upper molars, and set up a new family for the species, Theroteinidae (Sigogneau-Russell et al. 1986). In 1989 Hahn et al. placed this family in a new suborder Theroteinida; characteristic of the theroteinids is their fully orthal occlusion.

Another group of strange teeth typifies the genus *Eleutherodon* (with a single species *E. oxfordensis*), described by Kermack, Kermack, Lees, and Mills (1998) from the Bathonian Forest Marble of Kirtlington, Oxfordshire, England. The genus *Eleutherodon* was based upon several upper and lower isolated teeth. Kermack et al. (1998) set up the family Eleutherodontidae, placed within the suborder Eleutherodontida, order *incertae sedis* (from the Latin, meaning "uncertain placement"), and assigned it to the Allotheria. Eleutherodontids, regarded as a family by Butler (2000), share with the Multituberculata and Haramiyida multicusped teeth with longitudinally arranged cusps and, with multituberculates, a backward power stroke of the dentary. The latter conclusion was based on position of the wear facets on the teeth. The upper molars are rhomboidal in outline, with three rows of cusps, and the lower molars are oval with two rows of cusps, which encircle the distal end and a median basin.

Butler (2000) revised all of the non-multituberculate allotherians, which he assigned to the order Haramiyida, erected by Hahn, Sigogneau-Russell, and Wouters (1989), and recognized within this order two suborders: Theroteinida, with a single family Theroteinidae, and Haramiyoidea, with three families: Haramiyidae, Eleutherodontidae (assigning family rank to the suborder Eleutherodontida), and a new family, Haramiyaviidae.

Kielan-Jaworowska et al. (2004) tentatively accepted Butler's idea on the relationship of haramiyidans and multituberculates. However, in addition to obvious differences in the structure of the masseteric fossa, and, apparently related to these, differences in the jaw movements, there are also differences between the two groups in the structure of the molar teeth. When observed from the side, the molars in *Haramiyavia* resemble more those of *Sinoconodon* and *Morganucodon* than those of multituberculates.

Percy M. Butler

Percy M. Butler, born in London in 1912, is a widely respected mammalian paleontologist in Britain (figure 6.2F). He entered Cambridge University in 1930 and graduated in 1934. After two years of postgraduate

research, he was awarded a Commonwealth Fund Fellowship to the United States (1936–1938), where he studied at the American Museum of Natural History under W. K. Gregory. Returning to Britain, Butler taught zoology at Exeter University College. After the war in 1946 he returned to academic life as lecturer in zoology at Manchester University. In 1958 he moved to Royal Holloway College, University of London, as reader and subsequently professor of zoology. He retired in 1972 to devote more time to research, a decision that has been justified by the fact that nearly half of his 100 published papers have been written since his retirement. His Ph.D. was entitled "Contribution to the Morphology of Mammalian Dentition." In it, Butler interpreted the series of tooth forms along the jaw as the result of embryonic growth fields. In a number of papers between 1937 and 1956, he applied "field theory" to a wide range of mammals, including those of the Mesozoic. Studying perissodactyls, Butler became interested in wear facets as indicators of cusp homology and the relation between the upper and lower teeth, on which he has since published several papers. A review of the Erinaceidae (1948) resulted in an invitation from L. S. B. Leakey to describe the Miocene insectivores from Kenya, and this led to a series of papers on fossil East African insectivores. After 1973 Butler published 14 papers on Mesozoic mammals. The last paper, with J. J. Hooker on Middle Jurassic allotherians, appeared in 2005, but there is still work in preparation.

Although Butler's diagnosis of Haramiyaviidae states that "the masseteric fossa does not extend below the molars as in multituberculates" (Butler 2000: 335), he still regarded the Haramiyaviidae as being in the line leading to the forms with fully palinal (horizontal) mastication. In my opinion this conclusion is not warranted by the available data. Reassessment of the relationships among the different groups of the Haramiyida and Multituberculata requires more complete materials, especially of groups known only from isolated teeth. That is why in this book I place the Haramiyida close to Morganucodonta, rather than within the Allotheria.

Since the book by Kielan-Jaworowska et al. (2004), not much has been published on forms discussed in this chapter. But two monographs need mentioning: the first of them is by Thomas Martin and Alexander Averianov (2010). They published a paper on the mammals from the Middle Jurassic Balabansai Formation of the Fergana Depression in Kyrgyzstan. The locality was discovered by the legendary Russian paleontologist Lev A. Nessov (see chapter 1 and figure 3.4). In 1994 I had the chance to participate in the description of a very modest collection assembled by Nessov's crew. This crew included, among others, my Ph.D. student from the University of Oslo, Jørn H. Hurum, and his wife Merethe Frøyland, at that time a student of geology. Although the collection was unusually modest, we decided to publish it (Nessov et al. 1994) as it contained the

first Jurassic mammal teeth ever found in Kyrgyzstan. Now Martin and Averianov (2010), although dealing with isolated teeth or their fragments, were able to identify at least ten taxa in Kyrgyzstan, belonging to the different groups. Although the fauna is of Middle Jurassic age, and generally resembles that of the Bathonian of England, the authors did not find in it the multituberculate-like teeth described from the Middle Jurassic of England (Kermack et al. 1998; Butler and Hooker 2005).

Another paper that should be mentioned here is by Martin, Averianov, and Pfretzschner (2010). This monograph describes the Late Jurassic (Oxfordian) faunas from the Qigu Formation, in the Southern Junggar Basin, Xinjian, in northwest China, studied as part of the Sino-German Expedition Project. From among five mammalian taxa, belonging to the three major groups (haramiyids, docodontans, and stem zatherians), the authors described an eleutherodontid haramiyid, dubbed *Sineleutherus zygomaticus*. This species is represented by isolated incisors, lower premolariform teeth, upper premolars, and upper and lower molars. I do not figure the teeth of *S. zygomaticus*, as its teeth were beautifully illustrated in Martin et al. (2010) in three SEM photographic plates, showing the details of the teeth, and I refer this paper to my readers.

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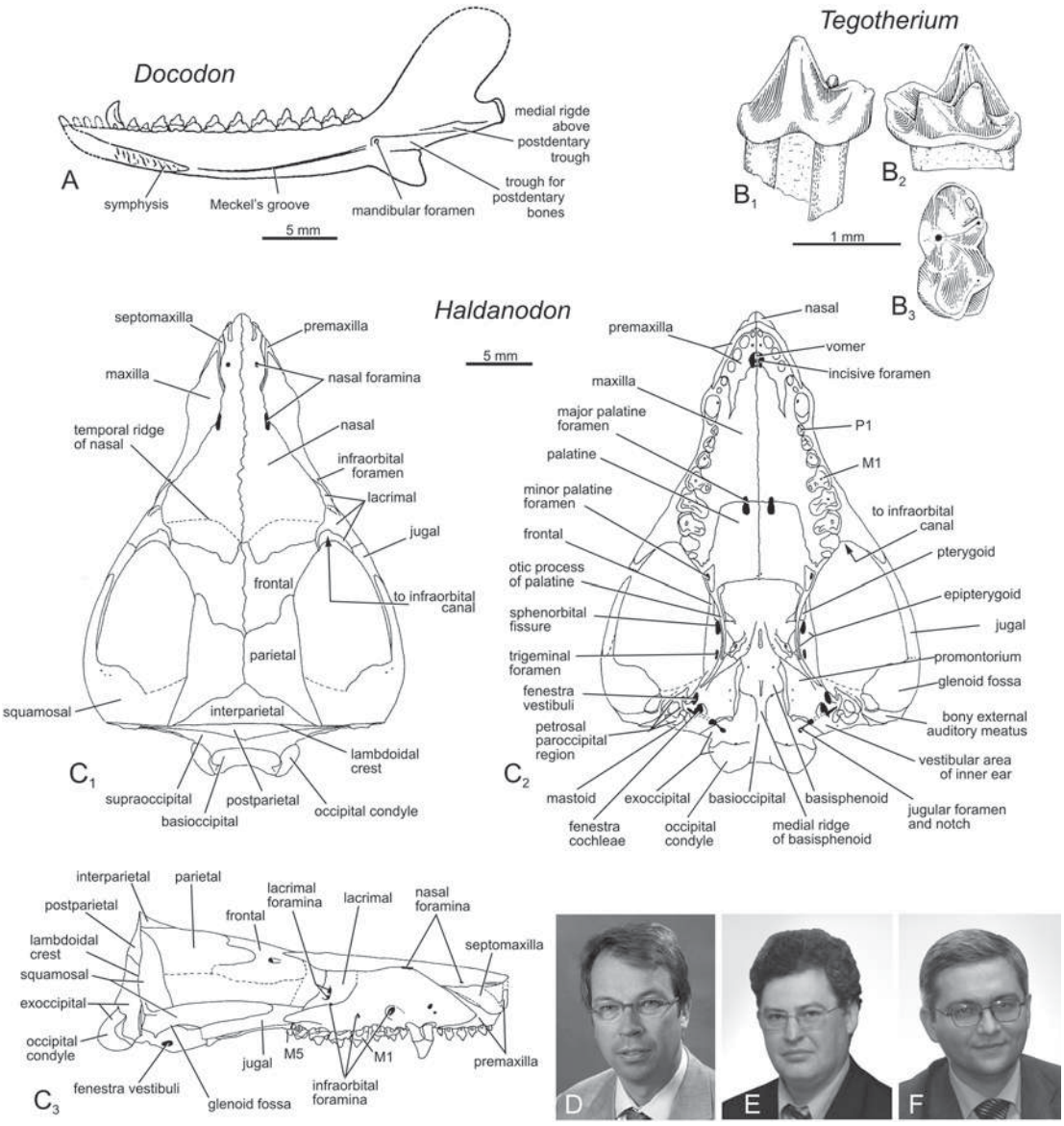

Docodon
A
symphysis
Meckel's groove
mandibular foramen
medial rigde above postdentary trough
trough for postdentary bones
5 mm
Tegotherium
B1
B2
B3
1 mm
Haldanodon
5 mm
septomaxilla
premaxilla
maxilla
nasal foramina
temporal ridge of nasal
nasal
infraorbital foramen
lacrimal
jugal
frontal
to infraorbital canal
parietal
squamosal
interparietal
lambdoidal crest
C1
supraoccipital
postparietal
basioccipital
occipital condyle
premaxilla
nasal
vomer
incisive foramen
maxilla
major palatine foramen
P1
palatine
M1
minor palatine foramen
to infraorbital canal
frontal
pterygoid
otic process of palatine
epipterygoid
sphenorbital fissure
jugal
trigeminal foramen
promontorium
fenestra vestibuli
glenoid fossa
petrosal paroccipital region
bony external auditory meatus
vestibular area of inner ear
C2
mastoid
exoccipital
basioccipital
basisphenoid
jugular foramen and notch
fenestra cochleae
occipital condyle
medial ridge of basisphenoid
interparietal
parietal
postparietal
lacrimal foramina
lacrimal
nasal foramina
frontal
lambdoidal crest
septomaxilla
squamosal
exoccipital
occipital condyle
jugal
M5
M1
premaxilla
fenestra vestibuli
infraorbital foramina
glenoid fossa
C3
D
E
F

Docodontans

7

THE DOCODONTANS ARE A GROUP OF VERY SMALL MAMMALIAFORMS, mostly mole size or even smaller, of Middle to Late Jurassic age. An exception with respect to size is the Middle Jurassic *Castorocauda lutrasimilis*, with a skull that measures 6 cm and a body about 42 cm long (Ji, Luo, Yuan, and Tabrum 2006).

Reigitherium from the Late Cretaceous of the Los Alamitos and La Colonia Formations of Patagonia, South America, has been assigned to the docodontans, but I regard it as a dryolestoidean. The characteristic feature of the docodontans is the presence of an extensive posterolingual trough on the dentary, housing the postdentary bones, as well as the presence of the double jaw joint. In a complete lower jaw of *Reigitherium* found by Rougier and his colleagues, no posterolingual trough is present, and the jaw joint is single. Rougier, Novacek, Ortiz-Jaureguizar, and Purerta in their abstract (2003, not cited herein) convincingly argued that *Reigitherium*, which originally was assigned to the Dryolestoidea by Bonaparte (1990), is better allocated there than to the docodontans.

The first docodontan was discovered in 1881 by Othniel Charles Marsh, who described a nearly complete lower jaw, dubbed *Docodon*. It occurs in the Jurassic Morrison Formation of Colorado and Wyoming. Characteristic of docodontans (figure 7.1A) are wide upper molars, rectangular or figure-eight-shaped in occlusal view, resembling those of advanced placental mammals. The lower molars are longitudinally elongated. Strong and prominent crests joining the molar cusps are also characteristic of docodontans. When in 1959 Walter G. Kühne and the young geologist Wolfgang Frey discovered the skull of a multituberculate mammal in the Guimarota Coal Mine (Kimmeridgian age) in central Portugal, they also found isolated teeth of various mammals (especially multituberculates; see chapter 10), and among these was the best-preserved skull of a docodontan, named *Haldanodon exspectatus* by Kühne and Krusat in 1972. The skull of *Haldanodon* was first described in English by the German paleontologist Georg Krusat in a monograph with a Portuguese title, published in the series Memórias dos Serviços Geológicos de Portugal in 1980. In 1991, after Jason A. Lillegraven had spent a sabbatical year in Berlin (1988–1989), he and Georg Krusat published a more detailed account of the skull and lower jaw of *Haldanodon*. Their study (Lillegraven and Krusat 1991) included details of the lower jaw suspensorium showing that there were numerous postdentary bones in a wide posterolingual trough of the dentary and a double jaw joint (figure 7.1).

7.1. A. *Docodon victor,* the first described docodontan, represented by a dentary with dentition. B. *Tegotherium gubini,* a lower molariform tooth, in labial (B_1), lingual (B_2), and occlusal (B_3) views. C. Reconstruction of the skull of *Haldanodon exspectatus,* in dorsal (C_1), ventral (C_2), and lateral (C_3) views. D. Tom Martin. E. Alexander Averianov. F. Alexy Lopatin.

A. From Kielan-Jaworowska et al. (2004: figure 5.3.A). B. Courtesy of the late Leonid P. Tatarinov, who sent me the original of his drawing. C. From Kielan-Jaworowska et al. (2004: figure 5.1.A–D), modified from Lillegraven and Krusat (1991).

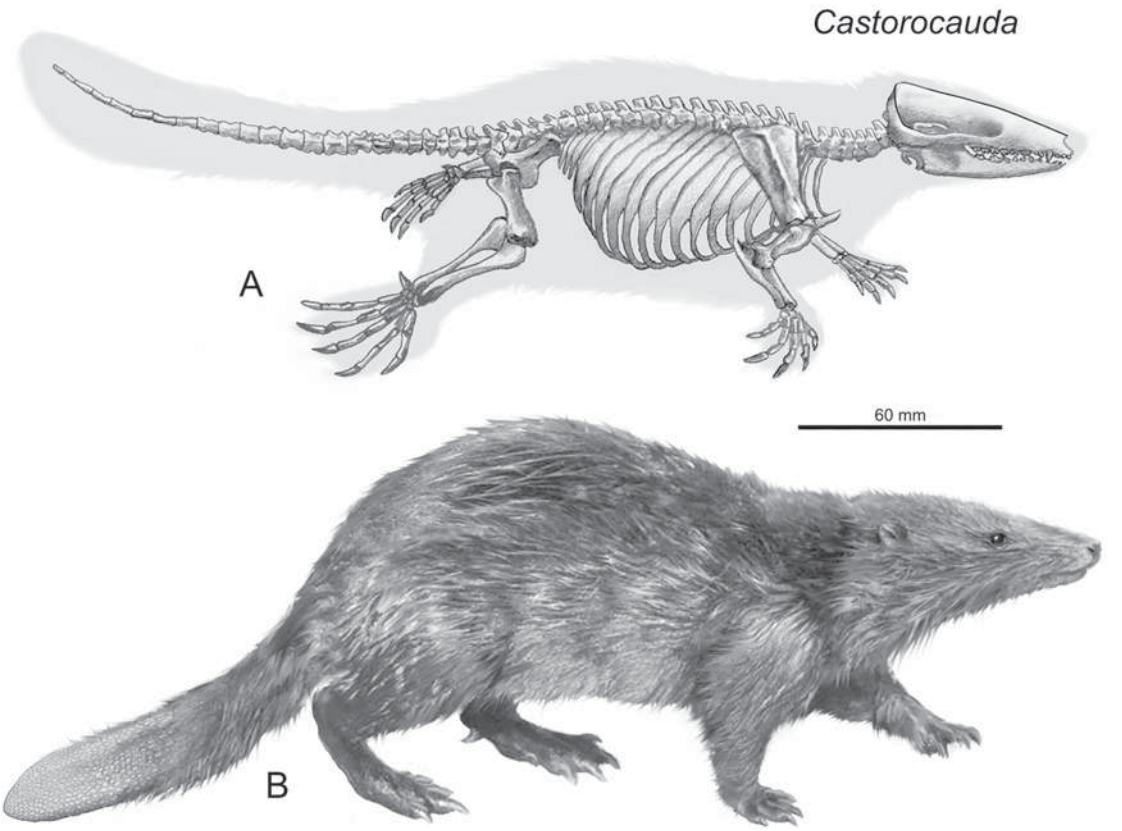
The Guimarota locality yielded several specimens of *Haldanodon*, among which there were fragments of skull associated with a large part of the postcranial skeleton, figured and briefly described by Georg Krusat (1991). Although the postcranial skeleton was not complete, the preserved bones, especially the femur and humerus, were found to be very robust, indicative of a fossorial (or burrowing) habit. Martin and Novotny, in the book edited by Martin and Krebs (2000), offered a general review of *Haldanodon*, with a life reconstruction painted by E. Gröning (Martin and Novotny 2000: figure 14.3). Martin (2005) re-described the skeleton of *Haldanodon* in great detail, together with several isolated bones found at the same locality.

Among the genera assigned to Docodonta, most of which are known from the dentition, of special interest is the highly specialized Middle Jurassic genus *Castorocauda* (figure 7.2). *Castorocauda lutrasimilis* was described by Ji, Luo, Yuan, and Tabrum in 2006, in an article published in *Science*. The beautiful reconstruction from this article (artwork by Marc A. Klingler) was used for an attractive cover of the journal. The only specimen of *C. lutrasimilis* (the holotype) was recovered from the Middle Jurassic Jiulongshan Formation of Inner Mongolia (Chinese People's Republic). There is no doubt that *Castorocauda* possessed swimming and burrowing skeletal specializations and a dentition adapted for aquatic feeding. Most telling is the structure of the tail vertebrae, which, combined with the presence of fur, clearly show that the tail was broad and flattened and partly covered with scales, quite analogous to the tails of modern beavers. In the holotype of *Castorocauda*, the spur has been found. *Castorocauda* is also the oldest mammal in which fur has been preserved.

The remaining genera of docodontans are known mostly from teeth or, at best, from a partial dentary with teeth. As far as the phylogenetic position of docodontans is concerned, the general conclusions spelled out in Lillegraven and Krusat's monograph (1991) are of special interest. The authors regard the docodontans as a sister taxon to all other mammals; in other words, docodontans represent an earlier stage of synapsid evolution than morganucodontans. This contrasts with the previously held opinion that docodontans were derived from morganucodontans (e.g., Simpson 1928a, 1929, 1959; Crompton and Jenkins 1979; and others).

The first docodontan from the territory of Mongolia was described by Tatarinov (1994) on the basis of a single lower molar (figure 7.1B), dubbed *Tegotherium gubini*, from the Late Jurassic of the locality of Shara Teg in the Trans-Altaian Gobi. Tatarinov originally assigned the tooth to the Symmetrodonta. Hopson (1995) argued that it resembles *Simpsonodon* from Oxfordshire (Kermack et al. 1987) and that together with *Borealestes* they form a clade of the docodontans, an idea that has been generally accepted.

Recently, several papers on docodontans have been published describing fossils from the territory of Russia, the countries of the former



7.2. A. Reconstruction of the skeleton of *Castorocauda lutrasimilis* in lateral view. B. Reconstruction of the animal in the same view.

Original artwork by Aleksandra Hołda-Michalska.

Soviet Union, and China and providing general discussions on docodontan phylogeny. After the death of Lev Nessov (see figure 3.4), his pupil Alexander Averianov (figure 7.1E) continued fieldwork in search of early mammals, working in Russia and in the countries of the Commonwealth of Independent States, including Kazakhstan, Kyrgyzstan, Tajikistan, and Uzbekistan.

Beginning with the paper by Averianov in 2004, a number of Russian authors, often working in cooperation with Tom Martin (figure 7.1D) from the University of Bonn, published extensively on the newly discovered docodontans. I am not able to cite all these papers, so I limit myself to those most recently published, referring readers to the literature cited there. In the first of these, Averianov (2004) discussed previously published interpretations of *Peraiocynodon inexpectatus*, erected by Simpson (1928a), and agreed with Butler (1939), who interpreted the four teeth preserved in the holotype of this specimen as deciduous. Averianov further argued that two taxa of docodontans from the British Middle Jurassic – *Peraiocynodon major* and *Cyrtlatherium canei* – are based on milk dentition. He also stated that *Simpsonodon oxfordensis* was a junior subjective synonym of *Cyrtlatherium canei* of Freeman (1979) and that *Peraiocynodon major* of Sigogneau-Russell (2003) is a junior subjective synonym of *Krusatodon kirtlingtonensis*, erected by Sigogneau-Russell

in the same paper. In this short paper, Averianov demonstrated his great knowledge and understanding of this group of early mammals.

In 2000 Averianov and Martin signed an agreement of cooperation with the Institute of Geology, National Academy of Sciences in Bishkek (the capital of Kyrgyzstan), and during fieldwork assembled a large collection of fossil mammals there. Martin and Averianov (2010) described a rich and diversified fauna (at least ten taxa or more) of rather poorly preserved mammals (isolated teeth or their fragments) from the Middle Jurassic (Callovian) Balabansai Formation of the Fergana Depression in Kyrgyzstan. The material was recovered by the screening-washing method. Previously, only one paper (Nessov et al. 1994) had been published on Mesozoic mammals from Kyrgyzstan. Especially rich is the fauna of the Docodonta, of which Martin and Averianov published nine plates of isolated teeth, taken by a scanning electron microscope.

Among the teeth identified, the docodontans are most numerous, represented by *Simpsonodon*, possibly two taxa; *Paritatodon* sp., the genus established by Martin and Averianov (2010) for "*Shuotherium kermacki*" of Sigogneau-Russell (1998) from the Bathonian of England; *Tashkumyrodon desideratus*; Tegotheriidae indet.; and Docodonta indet. In addition to the docodontans, there are eutriconodontan Amphilestidae indet.; *Ferganodon narynensis*, cf. *Ferganodon* sp.; Triconodontidae indet.; "symmetrodontan" Tinodontidae indet.; cladotherians Paurodontidae indet.; and Amphitheriidae indet. The occurrences of the Triconodontidae, Tinodontidae, and Paurodontidae in the Balabansai Formation represent the oldest-known records of these families. The assemblage discussed above is similar to the Bathonian mammals of the Forest Marble of England and the Itat assemblage in Siberia, showing a notable uniformity of the Middle Jurassic mammal faunas across Europe and Asia.

Also published in 2010 was a monograph by Averianov, Lopatin, Krasnolutskii, and Ivantsov on docodontans (see also the papers cited there). The authors erected a new species, *Simpsonodon sibiricus*; a new genus and species, *Hutegotherium yaomingi*; and discussed the previously described new specimen of *Itatodon tatarinovi*, all from the Bathonian Itat Formation of Krasnoyarsk region in West Siberia. They performed a phylogenetic analysis of 18 known docodontan and outgroup taxa and used 37 dental and mandibular characters. Their conclusion was that *Itatodon* is the most basal docodontan. The Docodonta were divided into the following families: the Docodontidae, with the genera *Docodon* and *Haldanodon* and with *Borealestes* regarded as a stem docodontid; the family Simpsonodontidae, which they erected for *Simpsonodon* and *Dsugarodon*, characterized by presence of an additional groove, situated dorsal to Meckel's groove; the Tegotheriidae, which they accepted, with *Krusatodon*, *Hutegotherium*, *Tegotherium*, and *Sibirotherium*. The last group is Docodonta *incertae sedis*, to which they assigned *Castorocauda*, *Tashkumyrodon*, and *Acuoduolodon*.

The papers of Russian paleontologists cited above enlarged our knowledge of the Middle Jurassic faunas of the world, in particular on the docodontans. Averianov et al. (2010: 121) noted:

> The Middle Jurassic mammals of Laurasia are now known from three principal assemblages: Forest Marble in England, Balabansai in Kyrgyzstan, and Itat in West Siberia. All these three assemblages are very similar and comprise docodontans, allotherians, eutriconodontans, "symmetrodontans," dryolestidans, and stem zatherians. The Middle Jurassic radiation of mammals has almost no roots in the known Early Jurassic mammal fauna and the evolutionary events which led to the formation of the principal groups of Mesozoic mammals (Docodonta, Multituberculata, Eutriconodonta, Dryolestida, and stem Zatheria) should have occurred sometime between the Sinemurian and Bajocian in Laurasia . . . most probably in Asia (Siberia?).

The third paper, published in 2010, by Martin, Averianov, and Pfretzschner, concerns the Late Jurassic mammal fauna of Junggar Basin, in northwest China. This fauna contains numerous teeth of the Docodonta, in addition to which there is a representative of the eleutherodontid haramiyids, an undetermined amphilestid triconodont, and the stem zatherian *Nanolestes*. The docodontans are represented by the common species *Dsungarodon zuoi* and by *Tegotherium* sp., the genus known from Mongolia. The mammalian assemblage, although represented by only five taxa, seems to be different from that of the Late Jurassic of Guimarota by the absence of multituberculates, which dominate in Portugal, and by the dominant presence of docodontans.

As the Russian and German paleontologists continue their searches in Siberia and also in the surrounding countries, with assemblages dominated by docodontans, one may hope that the understanding of this presently poorly understood group of mammaliaforms will soon increase.

Plate 1. A. Gandan, a Lamaist Buddhist cloister, on the hill above Ulaanbaatar. B. Philip Currie and Eva Koppelhus during the summer of 2000 in Denmark. C_1. The Natural History Museum in Ulanbaatar. In the photograph the author (*on the left*) and her granddaughter, Zosia, stand beneath the original of the forearms of the ornithomimid dinosaur *Deinocheirus mirificus*. C_2. Cast of the forearms of *Deinocheirus mirificus,* mounted at the Institute of Paleobiology in Warsaw.

A, C_1. Courtesy of Z. Jaworowski. B. Courtesy of J. H. Hurum. C_2. Archive of the Institute of Paleobiology in Warsaw.

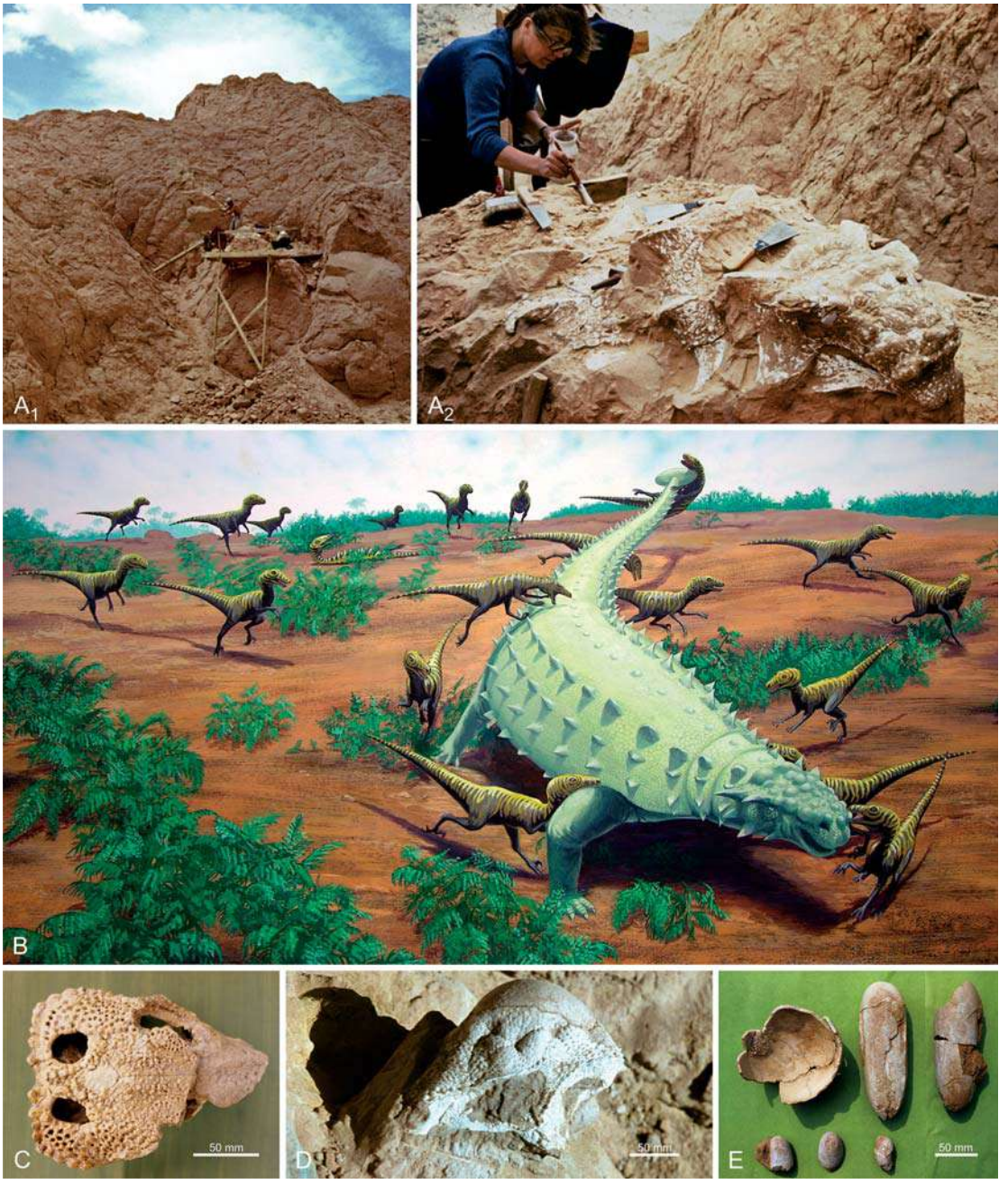


Plate 2. A. Excavation of the skeleton of the ankylosaurid dinosaur *Saichania chulsanensis* in 1971 at Khulsan, in the Nemegt Basin, in the Gobi Desert. As the specimen was preserved high above the bottom of the gorge, we were obliged to construct scaffolding with a platform to excavate it (A_1). A closeup of the excavation of the same skeleton with Teresa Maryańska working on the platform (A_2). B. Reconstruction showing *Saichania chulsanensis* chased by a herd of small carnivorous dinosaurs *Velociraptor mongoliensis.* C. The skull of a pachycephalosaurid dinosaur—*Homalocephale* in dorsal view. D. The skull of another pachycephalosaurid dinosaur *Prenocephale* in lateral view. E. Different sizes and shapes of dinosaur eggs found during the Polish-Mongolian Expeditions.

A, C–E. Archive of the Institute of Paleobiology, photograph by W. Skarżyński. B. Painting by Bogdan Bocianowski, original on display in the Paleontological Museum in Oslo. Courtesy of Hans-Arne Nakrem.

Plate 3. A. The hotel of the "Nomadic Expeditions" company, Three Camel Lodge, in the middle of the Gobi Desert. In the central part is the hotel's restaurant, a large meeting hall, shops, and bathrooms (A_1). Surrounding the central part are yurts, serving as guest rooms (A_2). B. The Jaworowski family (*left to right*: Zosia, Zofia, and Zbigniew) searching for mammals in Ukhaa Tolgod in 2002. C. Zosia has a friendly encounter (with a lizard). D. Zosia Jaworowska and Philip Currie making plaster jackets on the fossils. E. A fragment of the camp of the Nomadic Expedition, in 2002 in Ukhaa Tolgot.

A, C, and D courtesy of Zbigniew Jaworowski. B. Courtesy of Jørn H. Hurum.

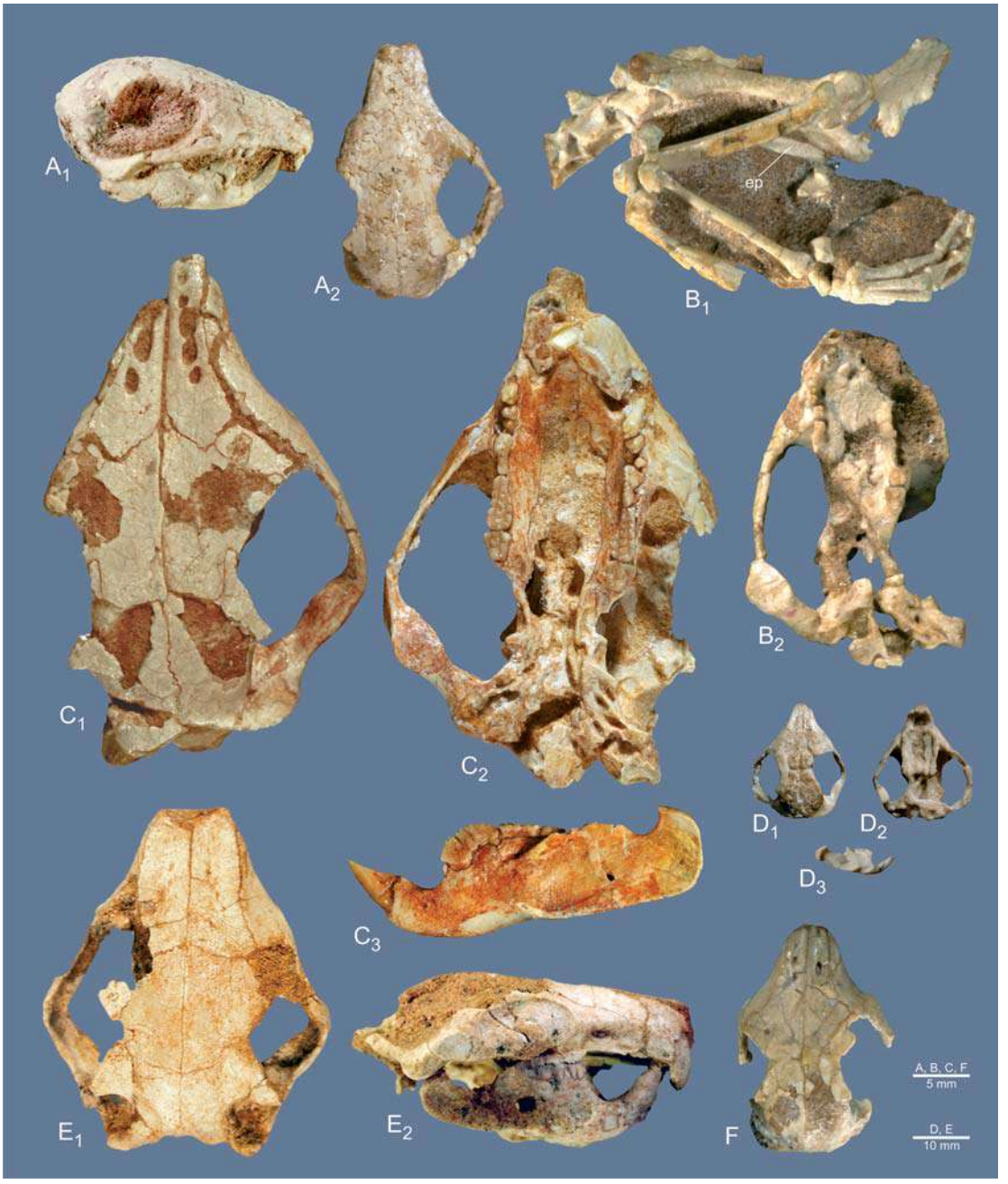


Plate 4. Multituberculate mammals from the Late Cretaceous of the Gobi Desert. A. *Sloanbaatar mirabilis.* Holotype. Skull preserved with lower jaws, in right lateral (A_1) and dorsal (A_2) views, both ×2. B. *Kryptobaatar dashzevegi.* Left hind limb preserved in anatomical arrangement, and a few lumbar vertebrae and damaged sacrum; please note the left epipubic bone (ep) preserved in situ (B_1). Incomplete skull of the same specimen in ventral view (B_2), both ×2. C. *Nemegtbaatar gobiensis.* Incomplete skull in dorsal (C_1) and ventral (C_2) views. Left dentary of the same specimen in outer view with all the teeth (C_3). D. *Chulsanbaatar vulgaris.* Nearly complete skull showing endocranial cast, in dorsal (D_1) and ventral (D_2) views. Right dentary of the same specimen in outer view (D_3), all ×1. E. *Catopsbaatar catopsaloides.* Skull in dorsal view (E_1) and the same skull with dentary in right lateral view (E_2), both ×1. F. *Kamptobaatar kuczynskii,* skull of the holotype in dorsal view, ×2.

Archive of the Institute of Paleobiology, Warsaw, photograph by W. Skarżyński.

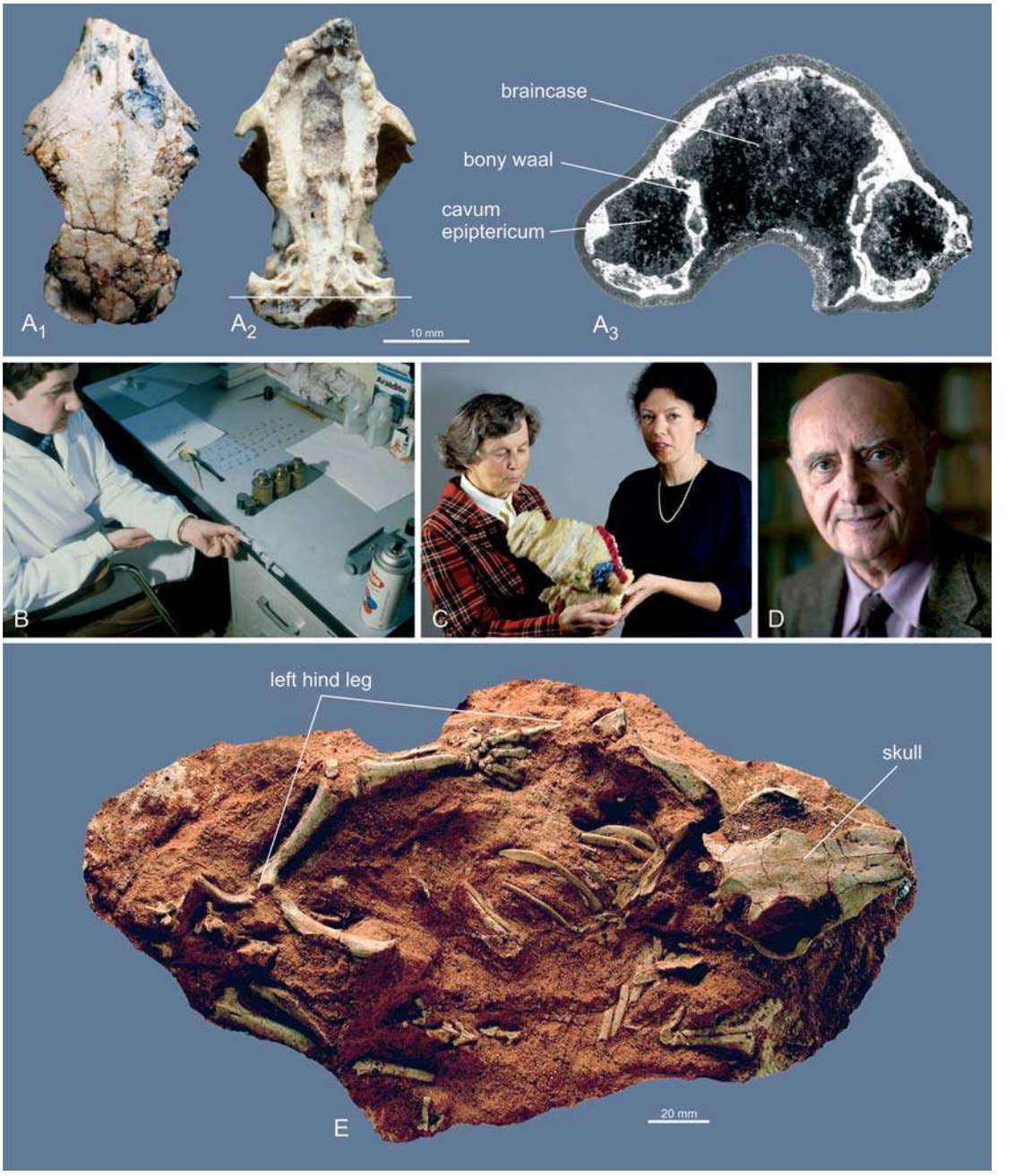


Plate 5. A. Skull of the multituberculate *Nemegtbaatar gobiensis* in dorsal (A_1) and ventral (A_2) views, both ×1.5. This is one of the skulls that I cut on the Jung microtome in the laboratory of Armand de Ricqlès at the University of Paris VI in 1982. The skull as preserved was 36 mm long. It was embedded in epoxy resin and then cut serially on the Jung microtome. I obtained from that skull 1370 sections, each 25 µm thick. The transverse line in A_2 shows the location of section no. 90 across the posterior part of the skull (A_3). The sections were numbered from back to front, about 4× enlarged. See the text for a detailed explanation of A_3. B. The technician, Françoise Alizard, sits next to the Jung microtome, putting consecutive sections between two glasses and writing the numbers on them. C. The author (*on the left*) and Cecile Poplin holding the wax model of the brain vasculature and nerves (×16), obtained from the sections of the skull. D. Armand de Ricqlès. E. The skull and distorted postcranial skeleton of the multituberculate *Catopsbaatar catopsaloides,* as preserved in the Red Beds of Hermiin Tsav, Hermiin Tsav locality, the Gobi Desert in Mongolia. *A_1–A_2.*

Archive of the Institute of Paleobiology, Warsaw, photograph by W. Skarżyński. A_3. Courtesy of Denis Serette. B, C, D. Courtesy of Armand de Ricqlès. E. Courtesy of Jørn H. Hurum.

Plate 6. Reconstruction of evening life on the Gobi Desert during the time of the deposition of the Djadokhta and Baruungoyot Formations, some 80 million years ago. Modified after the artwork of the late Karol Sabath, made in 2007. The inset key identifies the animals seen on the reconstruction by number. At the left lower corner, an insectivorous mammal, *Zalambdalestes* (number 1), a bit larger than an extant rat, hunts a beetle. To the right of *Zalambdalestes* is another, smaller insectivore, *Kennalestes* (number 2), on the lookout for supper. To the lower right, the herbivorous multituberculate mammal *Catopsbaatar* (number 3), having jumped upon a skull of a dead *Protoceratops,* is about to be attacked by the carnivorous dinosaur *Saurornithoides* (number 4). Behind them the feathered dinosaur *Oviraptor* (number 5) incubates its eggs. Three herbivorous *Protoceratops* dinosaurs (number 6), to the left, observe the scene. In the distance, three small, agile, carnivorous *Velociraptor* dinosaurs (number 8), 1.5 m long, with very long tails, chase the longer and four times larger ankylosaurid dinosaur *Saichania* (number 7). On the left, above the *Zalambdalestes,* a lizard (number 9) relaxes on the still-warm sand.

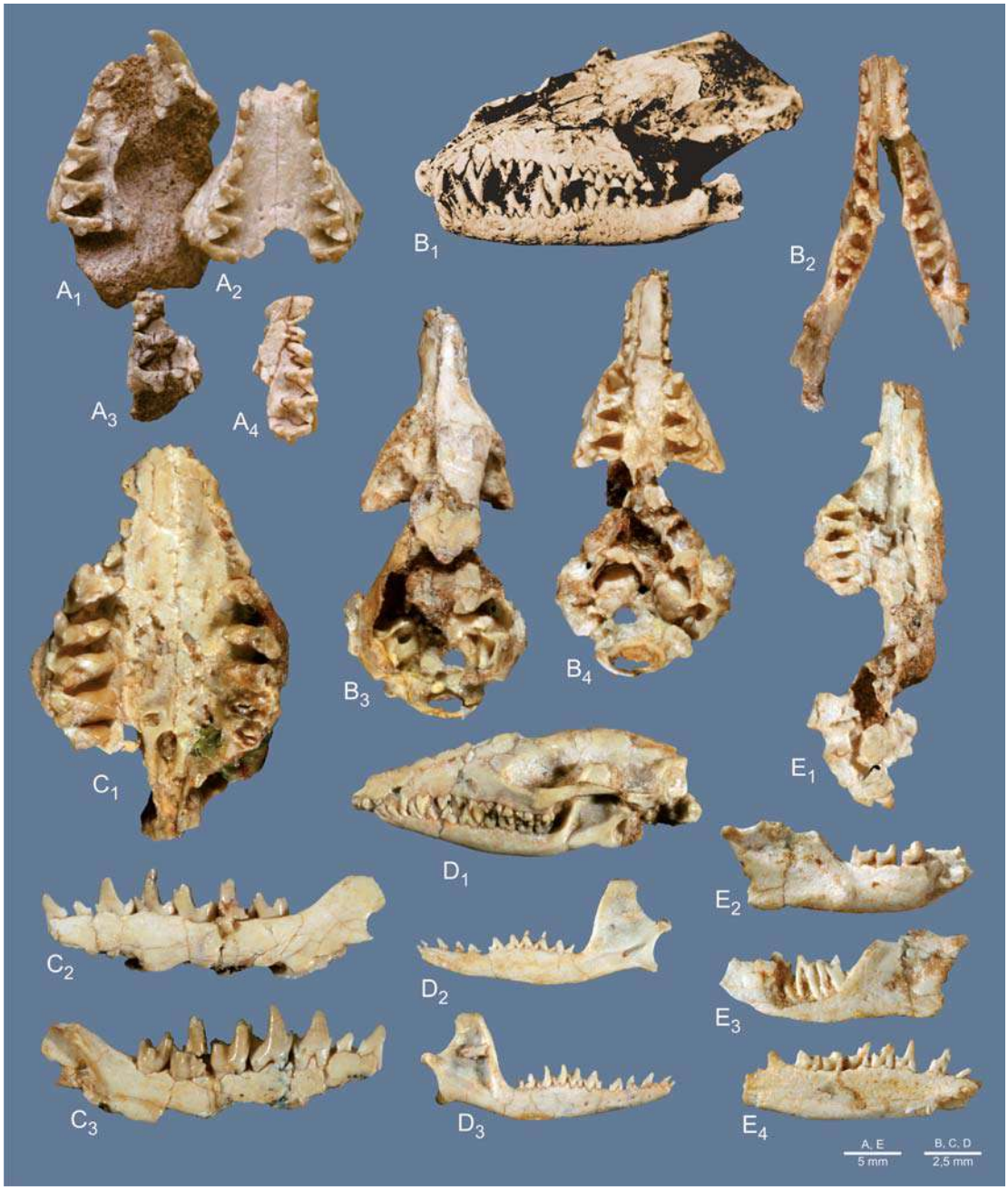
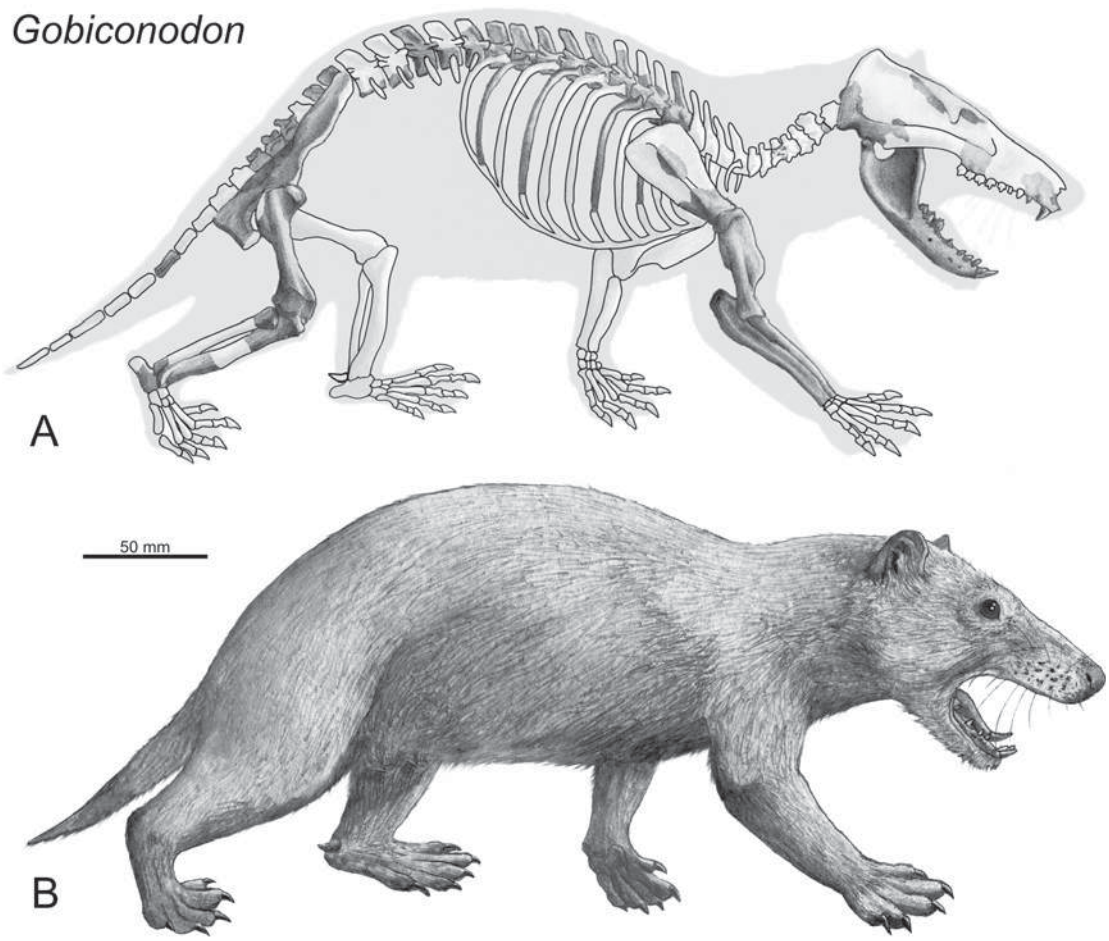


Plate 7. Djadochtatherian and eutherian mammals from the Late Cretaceous of the Gobi Desert. A. Four specimens of *Djadochtatherium pretrituberculare* (A_1–A_4), all showing incomplete upper dentition in coronal view (M4 is missing in all), ×2. B. *Kennalestes gobiensis,* two different specimens. The holotype, before separation of the mandible, in left lateral view (B_1). Fragments of the juvenile specimen of the same species after separation of the mandible (B_2–B_4). Both dentaries in occlusal view (B_2), joint anteriorly at the symphysis. The skull of the same specimen in dorsal (B_3) and ventral (B_4) views. C. *Zalambdalestes lechei,* rostral part of the skull in ventral view (C_1), incomplete left dentary of the same in inner (C_2) and outer (C_3) views. D. *Asioryctes memegetensis,* two different specimens. Skull with dentaries in occlusion (D_1). The right dentary of the other (holotype) specimen in inner (D_2) and outer (D_3) views, ×3. E. *Barunlestes butleri,* partial skull with both dentaries, the holotype. Partial skull in palatal view (E_1). Right dentary in outer (E_2) and inner (E_3) views. Left dentary in inner view (E_4).

Archive of the Institute of Paleobiology, Warsaw, B_1 by the late Maria Czarnocka, all others by W. Skarżyński and G. Dziewińska.



8.1. *Gobiconodon ostromi* from the Early Cretaceous Cloverly Formation, Montana. A. Reconstruction of the skeleton. B. Life reconstruction of the animal.

A. Modified from Jenkins and Schaff (1988), reversed and emended. B. Original artwork by Oscar Sanisidro, slightly emended by Aleksandra Hołda-Michalska.

Eutriconodontans

8

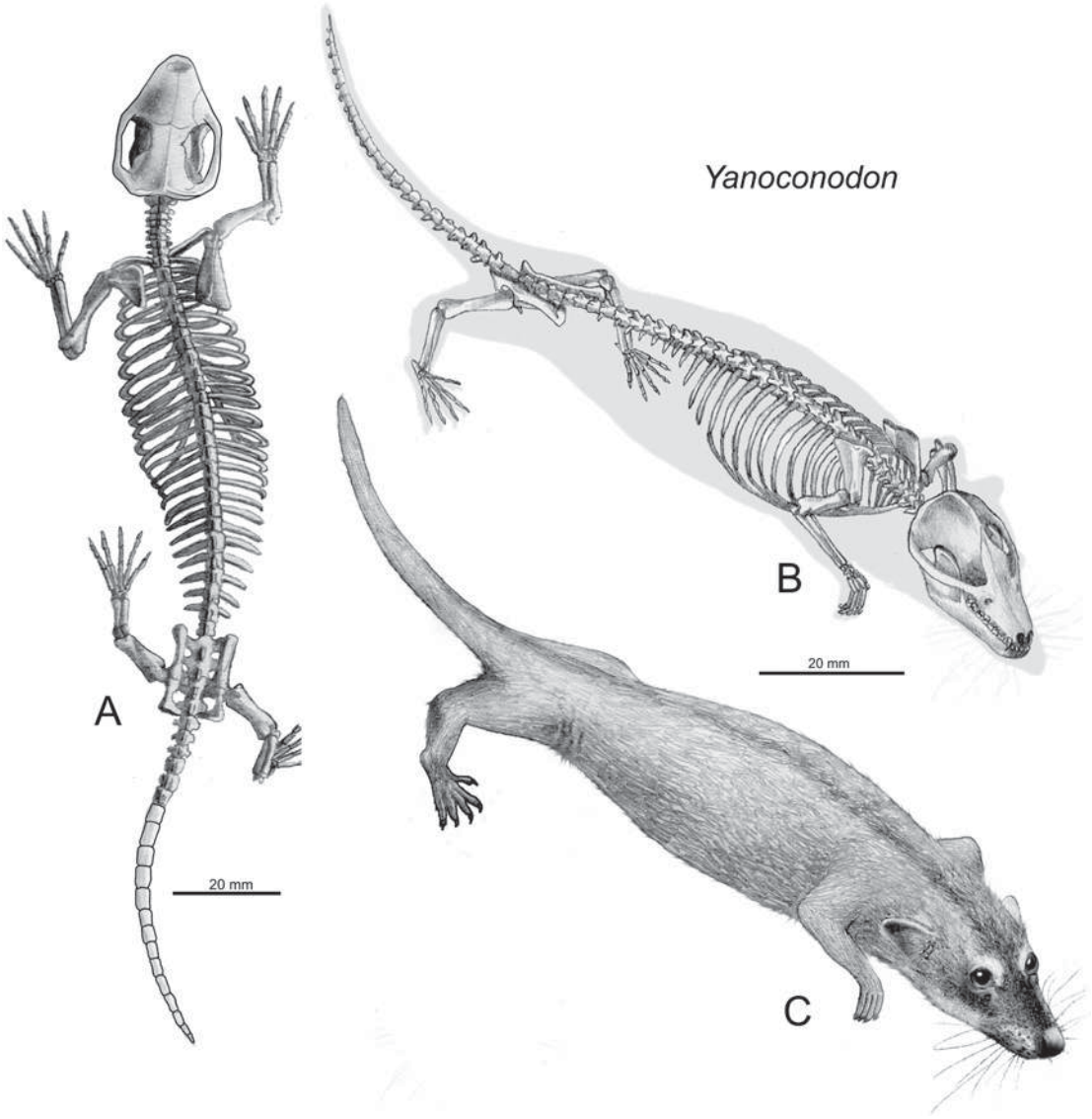
Introduction

THE DESCRIPTIVE TERMS "TRICONODONT TEETH" OR "TRICONodont mammals" were first used in the nineteenth century even before the formal taxon Triconodonta was proposed by Osborn (1888). Osborn assigned to Triconodonta all mammals in which the main three cusps on the molars were aligned from front to back on the tooth crown. Such teeth were known at that time mainly from the Middle and Late Jurassic. Simpson (1928a, 1929) in his two great monographs dealt only with Middle-Late Jurassic and Early Cretaceous triconodontans. Subsequent finds of older mammals from the Late Triassic and Early Jurassic began with the discoveries by Walter Kühne (1949, 1958) of triconodontans from the fissure fillings in Great Britain and the simultaneous description of early triconodontans from China (Patterson and Olson 1961; Rigney 1963). These new discoveries enlarged the scope of the triconodontans. Until 1973 students of the triconodont-like mammals seemed not to recognize the important differences in the skull, mandible, and tooth structure between Late Triassic and Early Jurassic mammals, on the one side, and those exhibited by Middle Jurassic to Early Cretaceous forms, on the other. They were all classified as belonging to a single group, the Triconodonta (e.g., Mills 1971; Jenkins and Crompton 1979; Lillegraven et al. 1979; and many others).

Kermack, Mussett, and Rigney (1973) were the first to recognize the Late Triassic and Early Jurassic triconodontans as a distinct group (for which they erected the suborder Morganucodonta) and to distinguish them from the Middle Jurassic–Early Cretaceous triconodontans. They assigned the Middle Jurassic–Early Cretaceous forms to their new suborder Eutriconodonta. The two new suborders were assigned by Kermack et al. (1973) to the order Triconodonta Osborn, 1888. In addition, Kermack et al. (1973) erected a new subclass, designated Atheria, which included the order Triconodonta, encompassing Triconodonta of Osborn, as defined above, and two other orders, the Multituberculata and the Monotremata. The subclass Atheria has not been endorsed by subsequent authors.

A well-known representative of the Eutriconodonta is *Gobiconodon ostromi*, erected by Jenkins and Schaff (1988; see figure 8.1). Ji, Luo, and Ji described (1999) a new eutriconodontan genus with a single species, *Jeholodens jenkinsi* from the Late Jurassic–Early Cretaceous of Liaoning in China. They left *Jeholodens* in a family *incertae sedis*.

Luo, Chen, Li, and Chen (2007a) described a new eutriconodontan genus *Yanoconodon allini* (figure 8.2) and set up a new family,



8.2. *Yanoconodon allini.* A. The skeleton in dorsal view, showing well-preserved lumbar ribs. B. The skeleton in dorsolateral view. C. Life reconstruction of the animal in the same view.

A. From Luo et al. (2007a: figure 1b, right); courtesy of Z. X. Luo. B and C. Original artwork by Oscar Sanisidro.

Jeholodontidae, to which they assigned *Yanoconodon* and *Jeholodens*. *Yanoconodon* shares with *Jeholodens* the structure and arrangement of the dentition and an ossified Meckel's cartilage. However, it differs from *Jeholodens* in retaining some plesiomorphic characters, the most important of which is the retention of lumbar ribs.

Kielan-Jaworowska, Cifelli, and Luo (2004) recognized the orders Morganucodonta and Eutriconodonta, but we did not unite them into a higher superunit. We provided a brief characterization of Eutriconodonta (Kielan-Jaworowska et al. 2004: 218), on which I base a diagnosis, given below.

Diagnosis. Eutriconodontans are generally large mammals relative to other members of their respective faunas, characterized by molars

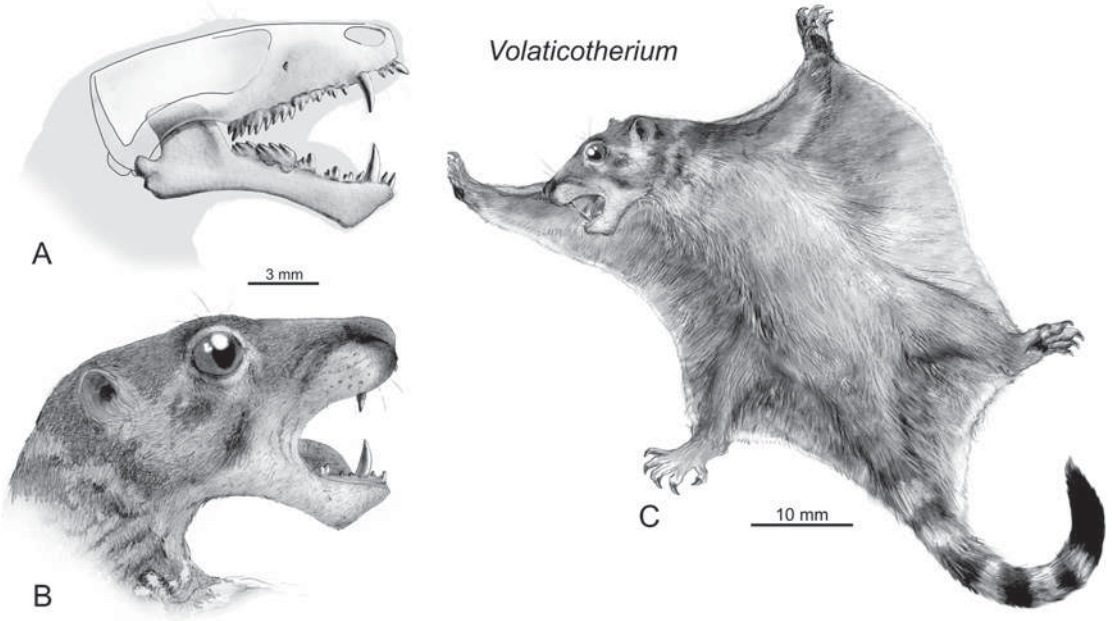
with three or four trenchant, serially arranged cusps (a plesiomorphy) that are more laterally compressed, with lesser development of accessory cuspules than in Morganucodontidae. The most noteworthy apomorphies distinguishing eutriconodontans from morganucodontans occur in the dentary, which in eutriconodontans has a well-developed pterygoid fossa and lacks (1) an angular process together with the posteroventral emargination of the dentary, and also lacks (2) a postdentary trough with overhanging ridge, associated with support of postdentary elements (articular, prearticular, angular, surangular) by the dentary (Allin and Hopson 1992; Rowe 1996). Presence of the postdentary trough and associated bones is a primitive feature, shared by morganucodontans and by the more distantly related non-mammalian cynodonts (Hopson and Barghusen 1986; Rowe 1988; Wible 1991; Allin and Hopson 1992; Luo 1994). The lack of postdentary trough in eutriconodontans is shared with crown group mammals. The dentary of eutriconodontans is more robustly built than in most contemporary mammals, further differing in the presence of a medial pterygoid ridge, sometimes called a pterygoid shelf or pterygoid crest (Simpson 1925b; Ji et al. 1999), which is also present in multituberculates (in which it is referred to as a pterygoideus shelf) and some spalacotheriid "symmetrodontans" (Miao 1988; Gambaryan and Kielan-Jaworowska 1995; Hu et al. 1998).

Comparisons. Kielan-Jaworowska et al. (2004: table 7.1) recognized 38 species of eutriconodontans belonging to 24 genera and 7 families (some of them *incertae sedis*). The best-known eutriconodontans are probably the members of the Gobiconodontidae, which include the largest Mesozoic mammals (e.g., *Repenomamus*, erected by Li et al. [2000], and some representatives of *Gobiconodon*).

In addition to the genera discussed above, and those cited by Kielan-Jaworowska et al. (2004), there are poorly known eutriconodontan genera known from the Middle Jurassic of Russia and Kyrgyzstan and the Early Jurassic of the Junggar Basin in China, discovered recently by Russian and German paleontologists and cited in respective papers in chapter 7. I do not discuss them here in detail as these are isolated teeth, or even fragments of them, and do not reveal much that is new on the structure and evolution of the Eutriconodonta.

The Issue of Volaticotherium

Meng, Hu, Wang, Wang, and Li (2006) described from the Daohugou beds in Inner Mongolia, in China, an unexpected Mesozoic mammal designated *Volaticotherium antiquum* (figure 8.3). With respect to the age of the Daohugou beds, Meng et al. (2006: 889) stated that "the Daohugou fauna is older than the Jehol Biota that dates to 125 Myr ago." Meng et al. (2006) erected for *Volaticotherium* a new family, Volaticotheriidae, which they placed in a new order, Volaticotheria. They diagnosed *Volaticotherium* as follows (2006: 889):



8.3. *Volaticothetrium antiquum* from the Daohugou beds in Inner Mongolia, China. A. Reconstruction of the skull with mandible in right lateral view. B. Life reconstruction of the head of an animal with snout open to bite. C. Life reconstruction of the entire animal in flight.

A, B. Original artwork by Oscar Sanisidro. C. Original artwork by Aleksandra Hołda-Michalska.

A small squirrel-sized mammal that differs from all known Mesozoic mammals in having the following features: small, ovoid-shaped head that lacks a neck; hallux diverging medially; proximal phalanges with pronounced flexor–sheath ridges; long tail with elongated and dorsoventrally flat caudal vertebrae and haemal arches; highly differentiated dentition with a dental formula of: I3-C1-P4-M3/i2-c1-p4-m2; incisors small and conical; canines long and sharp; molariforms with tall, sharp and posteriorly recumbent cusps that are aligned but are deeply separated; cusps of lower molariforms are more posteriorly recumbent and tightly packed than the uppers; cusp d of M1 labially overlapping cusp b of M2.

The order Volaticotheria (Meng et al. 2006) differs from all other early mammals in the presence of a patagium (flying membrane for gliding flight), which in *Volaticotherium* is covered with a dense fur. *Volaticotherium* is possibly most similar to early members of the Eutriconodonta, although it is much smaller than most eutriconodontan genera and shares with Eutriconodonta the single-boned mandible. It differs from other eutriconodontans in having specialized teeth, especially molariforms, which differ in having high, posteriorly recumbent cusps. Another difference is the presence of a posteriorly situated angular process, which is absent from the Eutriconodonta. Meng et al. (2006) provide a phylogenetic analysis of selected Mesozoic mammals (58 taxa and 435 characters), published as supplementary information to their paper. Unfortunately, *Volaticotherium* is represented by a single, incomplete specimen.

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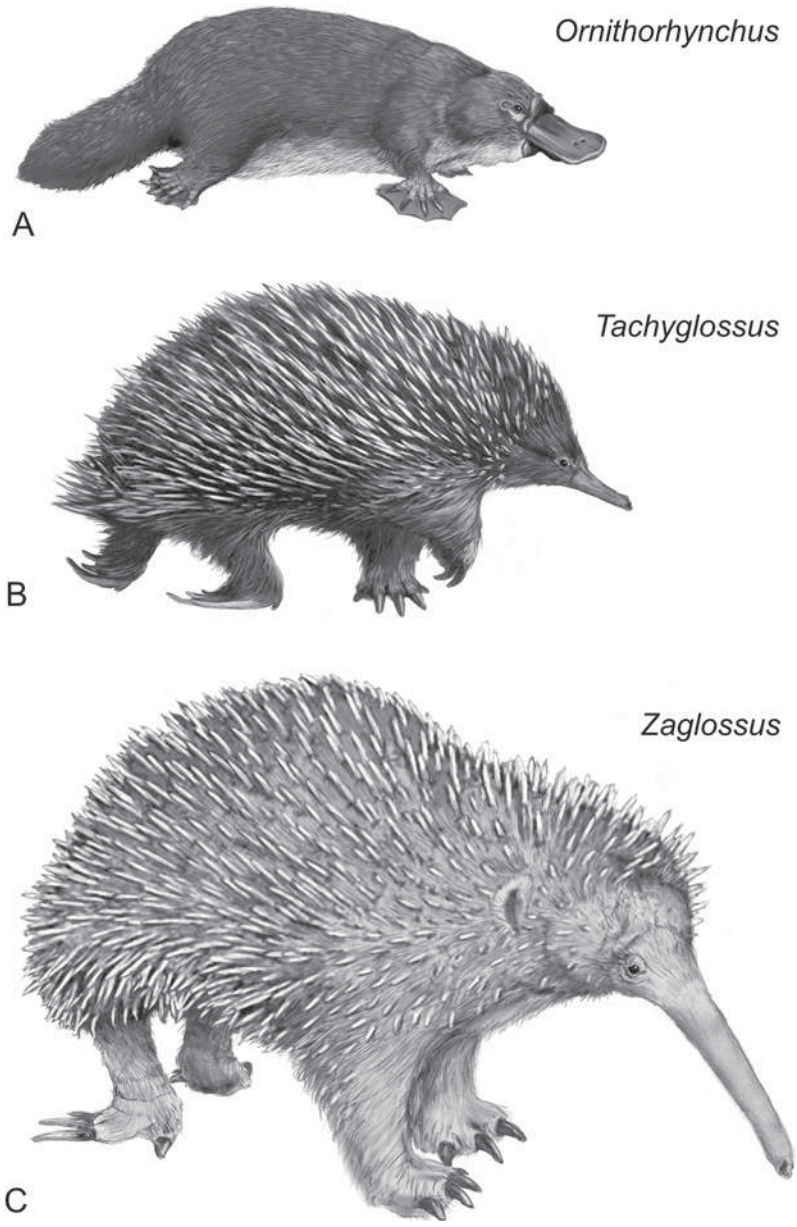


9.1. Present-day representatives of the Monotremata. A. Platypus, *Ornithorhynchus anatinus* (head and body length up to 45 cm, the tail 10–15 cm). B. Echidna, *Tachyglossus aculeatus* (head and body length 35–53 cm, tail 9 cm). C. Proechidna, *Zaglossus bruijni* (head and body length 45 cm–1 m).

Drawn on the basis of photographs published in various books. Artwork by Aleksandra Hołda-Michalska.

Monotremes and the Issue of Australosphenida and Tribosphenida

9

The Discovery of Monotremes and Their Place among Mammals

AT THE END OF THE EIGHTEENTH CENTURY THE FIRST INFORMATION about a strange animal from Australia – the platypus – reached the European zoological community (figure 9.1A). In August 1798, Captain John Hunter, the governor of the penal colony at Sydney, sent a skin of the platypus to the Literary and Philosophical Society of Newcastle-upon-Tyne, of which he was a member. He described it as a small amphibious animal of the mole kind that inhabited the banks of freshwater lakes, and he included a drawing of what it looked like in life. British scientists suspected that the unusual set of physical characters in the dry skin they received must be a hoax put together by some Australian taxidermist. European scientists also doubted whether the female of platypus laid eggs until it was later confirmed in Australia.

At that time another living monotreme – the echidna (*Tachyglossus aculeatus*) – had already been named by the English botanist and zoologist George Kearsley Shaw (1751–1813), who briefly described it in 1792 as "the spiny anteater" (figure 9.1B). A few years later Shaw (1799) named the platypus *Ornithorhynchus anatinus*, but he did not realize the true nature of the two mammals that he had described. He regarded the echidna as closely related to the placental anteater *Myrmecophaga* and stated that if it was not a species of *Myrmecophaga* "it forms a connecting link between the very distant genera of *Hystrix* and *Myrmecophaga*" (based on data of Griffiths 1968).

At the very beginning of the nineteenth century, the British physician Sir Everard Home (1756–1832) dissected a platypus and was the first to discover its unusual anatomy. In 1802 Home also demonstrated that the echidna and platypus are closely related. In spite of his merits in recognizing the nature of the monotremes, the memory of Sir Everard Home is rather negative. He was a pupil of his brother in-law John Hunter, and there is evidence that he plagiarized Hunter's work. In order to hide the evidence he also systematically destroyed John Hunter's papers.

Recent Monotremes

Recent monotremes (Monotremata) are an order of mammals made up of two families: the Tachyglossidae (echidnas or spiny anteaters) with two genera: *Tachyglossus* (the short-nosed echidna; figure 9.1B) and *Zaglossus* (the long-nosed echidna; figure 9.1C), and the Ornithorhynchidae, with a single genus *Ornithorhynchus* (the duck-billed platypus; figure 9.1A). The semi-aquatic *Ornithorhynchus* is the smallest monotreme, up to 45 cm in length. *Tachyglossus* and *Zaglossus* are powerful diggers

and attain lengths of 53 cm and 77 cm, respectively. However, the largest representatives of *Zaglossus*, unexpectedly discovered in December 2005 in the "Lost World" of the Foja Mountains in New Guinea by the Conservation International Expedition, are about 1 m long. *Tachyglossus* occurs on mainland Australia, Tasmania, and New Guinea, but *Zaglossus* is restricted to New Guinea; *Ornithorhynchus* occurs on mainland Australia and Tasmania. Traditionally the order has been placed in the subclass Prototheria, established by Gill (1872), but in the classification used in this book I assign Monotremata to the subclass Australosphenida, erected by Luo, Cifelli, and Kielan-Jaworowska (2001a).

Monotremes differ from other living mammals in that they lay shell-covered eggs, which are incubated and hatched outside the body of the mother, as in reptiles and birds. Female echidnas have a pouch, developed only during the period of incubation for the juveniles. In the platypus, the pouch never develops, and the female incubates eggs in a nest. Monotremes have large and complex brains, but they resemble reptiles in several characters of the skeleton. They differ from other living mammals in having cervical ribs, which occur also in some extinct groups of mammals. The pectoral girdle resembles that of reptiles more than that of other mammals in having precoracoid and coracoid bones and an interclavicle. They have marsupial bones in the pelvic girdle, thus resembling marsupials and many extinct groups of mammals, including Cretaceous eutherians. Monotremes have a cloaca, into which the posterior end of the intestine and the genital ducts open, as in reptiles and birds, but quite differently from modern marsupials and placentals, except for tenrecs.

Monotremes share with extant therian mammals the presence of fur, a four-chambered heart, and a single left aortic arch. They also nurse their young with milk secreted by milk glands, although they have no nipples. Monotremes have relatively constant body temperatures of 30–32°C, somewhat lower than that of other mammals. They additionally possess unique mammalian features of the skeleton such as (1) a single bone (the dentary) in the lower jaw, which articulates with the squamosal bone of the skull, (2) three ear ossicles, and (3) a cribriform plate in the nasal region.

Both the echidna and platypus are highly specialized. They are toothless as adults, but teeth do occur in the juvenile platypus. Sutures between the skull bones disappear early in life, and the snout is elongated into a beak, covered with a leathery sheath. Several "reptilian" bones, which are lacking in other modern therian mammals, such as the ectopterygoid and septomaxilla, are still present in monotreme skull. A unique feature is the presence of the so-called egg tooth – the prenasal processes of the premaxillae fused together, which are used for cutting the shell at the time of hatching. Monotremes are plantigrade and have strong claws and a pronounced sprawling posture. Males (in echidnas, also the females) possess a spur, which in the platypus is venomous (see below).

During the nineteenth and twentieth centuries, hundreds of papers and books on anatomy, systematics, and biology of monotremes were published. In September 1980 I had an opportunity to meet one of the great experts on monotremes, the late Professor Mervyn Griffiths, who came to Warsaw to attend the Second Symposium on Mesozoic Terrestrial Ecosystems, organized by the Institute of Paleobiology at Jadwisin near Warsaw. This happened 9 years after I published a monograph on the skull structure in Multituberculata (Kielan-Jaworowska 1971; discussed in chapter 10). In the 1971 paper I demonstrated some similarities in the skulls of monotremes and multituberculates. Professor Griffiths was interested in examining my multituberculate collection. He presented an interesting lecture at the symposium, "Lactation in Monotremata and Speculations concerning the Nature of Lactation in Cretaceous Multituberculata," which was later published in the proceedings of the symposium in *Acta Palaeontologica Polonica* in 1983 (Griffiths 1983).

For many years zoologists and paleontologists thought that monotremes differed so much from other Recent mammals that they probably originated from non-mammalian therapsids separately from the line leading to marsupials and placentals (modern Theria) and to other extinct groups of Mesozoic mammals. This opinion led to the concept of a polyphyletic origin of mammals, which dominated in paleontology from the middle of the previous century up until the early sixties. This was an idea based on the limited knowledge of Mesozoic mammals, known at that time mostly from dentitions.

Living in Europe, and working on the Cretaceous mammals from the Gobi Desert, I have not had a great chance to study the monotremes. Nevertheless, it happened that twice I studied them. First was in the late sixties of the twentieth century, when I began work on the skull structure of multituberculates (see chapter 10). My first work on the anatomy of the multituberculate skull was based on remains of two genera from the Late Cretaceous Djadokhta Formation at Bayan Zag on the Gobi Desert, which I dubbed *Kamptobaatar* and *Sloanbaatar.* The holotype skull of *Kamptobaatar kuczynskii* belonged to a juvenile specimen (the skull was 19 mm long) and was exquisitely preserved, showing the sutures between the bones, which in adult multituberculate skulls are, as a rule, obliterated. When comparing the structure of the orbit and lateral wall of the braincase in *Kamptobaatar* with that of Recent *Ornithorhynchus*, I noted a striking resemblance between the multituberculate and monotreme braincase.

Relationships and Skull Structure in Fossil Monotremes

The great British embryologist and paleontologist David M. S. Watson (1886–1973) studied the ontogeny of the skull of two monotreme genera, *Ornithorhynchus* and *Tachyglossus*, and demonstrated in 1916 that, in contrast to the skulls of eutherian and marsupial mammals in which the lateral wall of the braincase is formed by the alisphenoid and squamosal, in monotremes most of the lateral wall of the braincase is formed by the

petrosal (the so-called anterior lamina of the petrosal), lying anterior to the squamosal. In monotremes the alisphenoid is reduced to a small element, situated ventrally. I demonstrated (Kielan-Jaworowska 1971) that in multituberculates the lateral wall of the braincase has a structure similar to that of monotremes.

When studying the anatomy of multituberculate skull, I came across a paper by the British paleontologist Kenneth A. Kermack (see chapter 5), published in 1963, in which he described isolated petrosal bones of eutriconodontans, referred at that time to the Triconodonta, from the British Purbeck. At that time, too, the Purbeck Beds, now referred to as the Early Cretaceous Purbeck Limestone Group, were thought to be Late Jurassic in age. Complete skulls of eutriconodontans at that time were unknown, but Kermack, being an extremely careful observer, described their isolated petrosal bones in detail and concluded that they resemble those of the early mammal *Morganucodon* of latest Triassic and earliest Jurassic age (see chapter 5).

In a review article on early mammals (1967), Kermack coined the term "non-therian mammals" for a group of primitive forms where the lateral wall of the braincase was formed of bones different from those in the Theria. He assigned to "non-therian mammals" *Morganucodon* (which he attributed mistakenly to the Docodonta), triconodontans, Monotremata, haramiyidans (an enigmatic group of Triassic-Jurassic mammals, known at that time only from isolated teeth, showing similarity to those of multituberculates – see chapter 6), and Multituberculata (see chapter 10). At that time, the only described, reasonably well preserved multituberculate skull with a braincase was that of the Paleocene genus *Ptilodus*. Simpson described that skull in detail in 1937; however, he interpreted the braincase structure of *Ptilodus* on purely therian lines. One should acknowledge Kermack's intuition in recognizing – based on only fragmentary materials and despite the interpretation of the greatest early mammal authority at that time, George G. Simpson – that the multituberculate braincase might have a different structure than those of the Theria (Kermack 1963).

I visited University College London in the early summer of 1969 (see chapter 10), where Kermack had his laboratory. The multituberculate skulls from the Late Cretaceous of Mongolia, which I brought with me, made a great impression on Kenneth and his assistant Frances Mussett. I was similarly enchanted to learn that Kenneth and Frances were engaged in studies of the famous skull of *Morganucodon oehleri* from China, one of the most intriguing fossils of early mammals available at that time (see chapter 5). During my six-week stay in London, I examined all materials relevant to my comparisons with multituberculates, while Kenneth corrected the English of my monograph, and I returned to Warsaw with an almost completed monograph on multituberculate skull structure (published in 1971).

Kenneth and his wife Doris were organizing a symposium on early mammals in London in 1970. Kenneth suggested that we write a joint

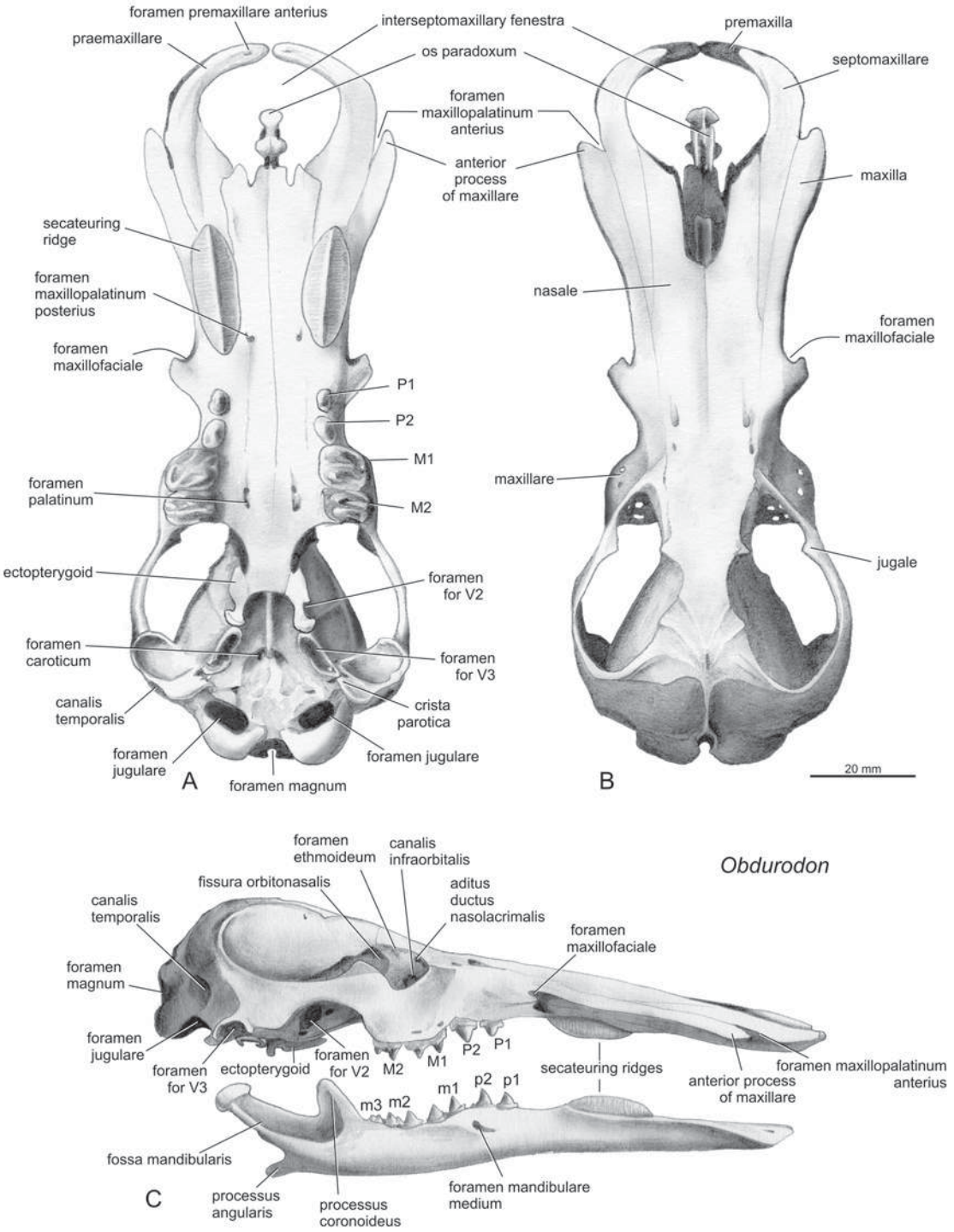
article on therian and non-therian mammals, and we wrote this short article during my stay in London. In that paper we proposed that there are two different patterns of braincase structure in mammals. One, characteristic of the "non-therian mammals," embracing monotremes, morganucodontans (assigned at that time wrongly to the docodontans), triconodontans, monotremes, and multituberculates, is typified by retention of the anterior lamina of the petrosal, in front of which in cynodonts and morganucodontans a relatively large alisphenoid is present. In multituberculates and monotremes the alisphenoid is reduced to a small ventral element, and most of the lateral wall is formed by the anterior lamina of the petrosal. In the second group, therian mammals (tribosphenidans in the terminology employed here), the lateral wall of the braincase is formed by the squamosal posteriorly and a relatively large alisphenoid anteriorly.

The informal terms "non-therian mammals" and "therian mammals" are semantically unfortunate, as the first includes *contradictio in adiecto* (contradiction in adjective = using words which exclude one another), and the second, a tautology. "Therians" (from Greek *therion*, a wild beast or a mammal) means "mammals," so the first expression means "non-mammalian mammals," and the second "mammalian mammals"! These terms have been used either as informal units or have been regarded as formal units, with "non-therian mammals" being equivalent to the subclass Prototheria – erected by Gill (1872) and originally set up to include only monotremes – and "therian mammals," being equivalent to the Theria – established by Parker and Haswell (1897) and embracing marsupials, placentals, and some extinct forms.

However, other authors by that time had began to support a monophyletic origin of all mammals, first based on studies of dentition and later on the study of origins of mammals, based on cladistic analyses of interrelationships among their clades. These latter studies, involving a multitude of anatomical characters, advocated a monophyletic origin of all mammals.

With respect to the position of monotremes, a new period in understanding their relation to other mammals began with the discovery of fossil representatives. Until the 1970s the only fossils of monotremes came from Pleistocene deposits of the Australian region. In 1975 isolated teeth of an ornithorhynchid dubbed *Obdurodon insignis* were described from the Miocene of Australia (Woodburne and Tedford 1975). This was later followed by a discovery of a complete skull in deposits of similar age of another species, *Obdurodon dicksoni*, described by Musser and Archer in 1998. This was the complete skull, associated with a dentary.

The exquisitely preserved skull of *Obdurodon* (figure 9.2) demonstrates that the main ornithorhynchid characters were already established some 23 million years ago. *Obdurodon* differs from *Ornithorhynchus* in retaining several plesiomorphic features, such as presence of a large septomaxilla (a bone characteristic of reptiles but lacking in modern therians), which is not fused with the premaxilla (as in *Ornithorhynchus*)


foramen premaxillare anterius
praemaxillare
interseptomaxillary fenestra
os paradoxum
foramen maxillopalatinum anterius
anterior process of maxillare
secateuring ridge
foramen maxillopalatinum posterius
foramen maxillofaciale
P1
P2
M1
M2
foramen palatinum
ectopterygoid
foramen for V2
foramen caroticum
foramen for V3
canalis temporalis
crista parotica
foramen jugulare
foramen jugulare
foramen magnum
A
premaxilla
septomaxillare
maxilla
nasale
foramen maxillofaciale
maxillare
jugale
20 mm
B
foramen ethmoideum
canalis infraorbitalis
Obdurodon
fissura orbitonasalis
aditus ductus nasolacrimalis
canalis temporalis
foramen maxillofaciale
foramen magnum
foramen jugulare
foramen for V3
ectopterygoid
foramen for V2
M2
M1
P2
P1
secateuring ridges
foramen maxillopalatinum anterius
anterior process of maxillare
m1
p2
p1
m3
m2
fossa mandibularis
C
processus angularis
processus coronoideus
foramen mandibulare medium

and the presence of teeth in adults. In echidnas, teeth are absent throughout life. *Obdurodon* did not bring much information on the origin and relationships of monotremes, as it is a typical ornithorhynchid, with teeth resembling those present in juvenile *Ornithorhynchus*, to which it is generally similar.

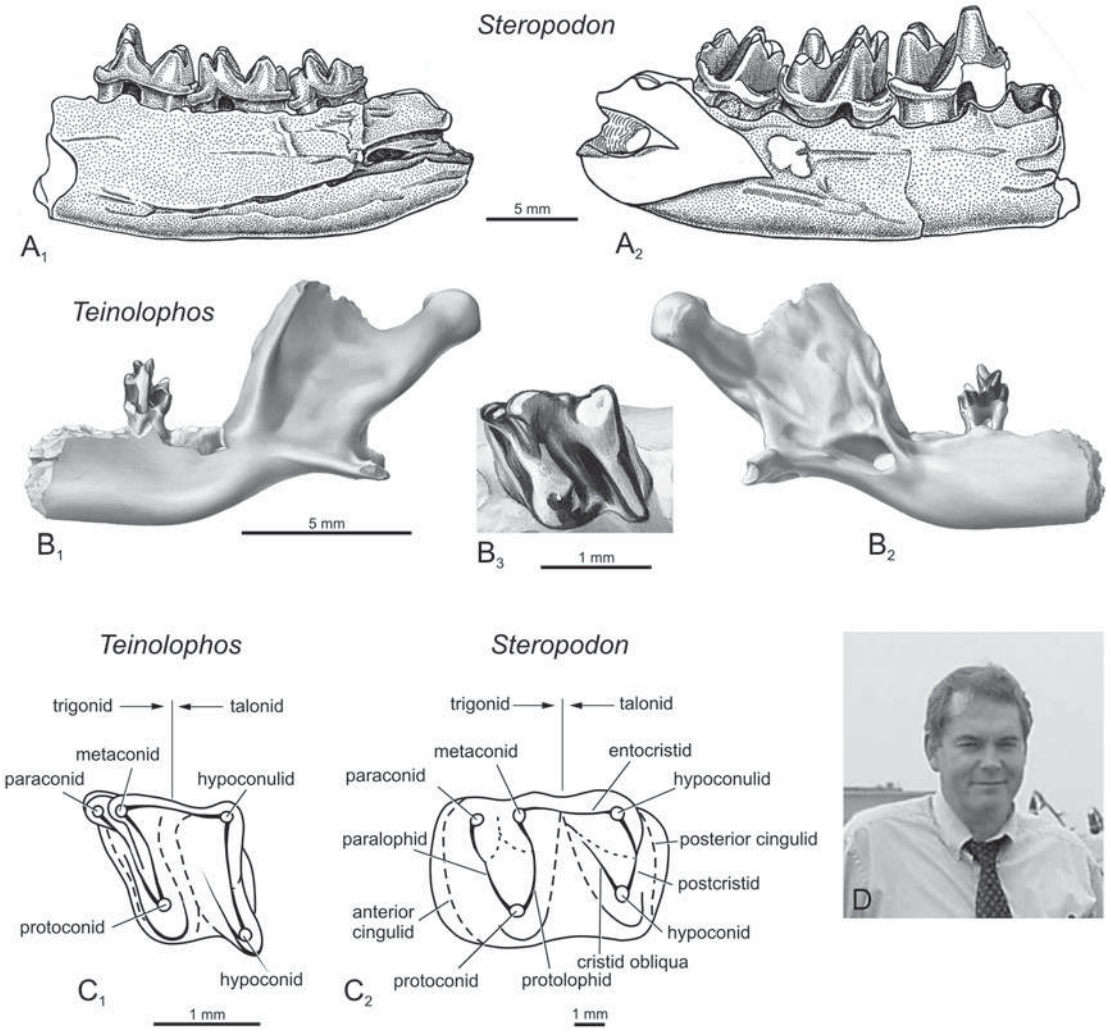
More important, however, was the discovery of Archer, Flannery, Ritchie, and Molnar (1985) in Australia of a toothed monotreme of Early Cretaceous age, represented by a fragmentary dentary with three molars, of the ornithorhynchid-like taxon *Steropodon galmani* (figure 9.3A). This unique specimen was found in an opal mine at Lightning Ridge in New South Wales, and like most other specimens from this same area, it is a natural pseudomorph in opal of the original fossil. This beautiful colored specimen made one of the most attractive covers of the journal *Nature*, in which *Steropodon* was described. The other group of Australian authors (Rich et al. 1999) reported the discovery of a new genus, *Teinolophos*, tentatively considered a "eupantotherian." The fossil consisted of the posterior half of a dentary with a penultimate molar. Tom Rich and his colleagues (2001b), after a thorough examination of the fossil and other specimens discovered after the first, revised their assignment of that specimen to monotremes rather than to "eupantotherians," and they submitted the paper to *Acta Palaeontologica Polonica*. The manuscript was accompanied with beautiful shadowed drawings of the specimen rendered by reconstruction artist Peter Trusler. I handed over the paper to our (now late) assistant editor, a talented artist, Karol Sabath. Karol decided that the conclusions of the authors on the monotreme nature of the specimen would be more convincing if accompanied by a schematic drawing of the occlusal surface of the molar of *Teinolophos* in comparison with that of *Steropodon* and made such a drawing, published in *Acta Palaeontologica* (Rich et al. 2001b: figure 2; see also figures 9.3B and C, in this volume).

Important data on the relationships of monotremes were provided by the dentary of *Steropodon*. Archer et al. (1985), who originally described *Steropodon* (1985), regarded the molars preserved in the dentary as tribosphenic (see chapter 12 for more information on the morphology and origin of the tribosphenic molar). In 1985, one of my Australian colleagues, Alexander Ritchie, sent me an epoxy resin cast of the dentary of *Steropodon*.

At the Institute of Paleobiology, we made an enlarged model of this cast. It happened that in early winter of 1986 I was visiting Washington, D.C., to attend the annual meeting of the International Union of Geological Sciences. I took the cast and model with me, and after the Washington meeting, I stayed for a short time at Harvard's Museum of Comparative Zoology to discuss this specimen with my friends Fuzz Crompton and Farish Jenkins. After examining the cast and comparing the teeth to various early mammals, we decided to send a short paper to *Nature* in which we argued that *Steropodon* appears to have been derived from the therian *sensu lato* stock before the tribosphenic molars made their appearance, from forms close to the Jurassic ancestors of

9.2. Skull of *Obdurodon insignis* from the Miocene of Australia. A. Ventral view of the skull. B. Dorsal view. C. Lateral view of the skull and the lower jaw.

From Anne M. Musser and Michael Archer (1998, figure 1 [a,], [b], and [c] on page 1065, all modified; figure [c] reversed).



Theria *sensu stricto* (see chapter 12). Our paper (Kielan-Jaworowska et al. 1987a) was published in *Nature*. Subsequent discoveries of Cretaceous mammals in Australia slightly challenged our conclusion.

In the mid-1990s, a new period in the evaluation of monotreme relationships began with fascinating discoveries of alleged placental mammals in Mesozoic deposits in Australia. In 1997 Tom Rich, his wife Patricia Vickers-Rich, and their colleagues reported in *Science* the discovery of a tribosphenic mammal from the Early Cretaceous (Aptian) of the Flat Rocks locality, situated 140 km southeast of Melbourne.

Tom Rich and Patricia Vickers-Rich

Tom Rich and Patricia Vickers-Rich (figure 9.4C, D) were both born and educated in the United States and then moved to Australia. They are among the most active paleontologists in the world. Patricia Vickers-Rich conducted research, in cooperation with various institutes in numerous

countries on Precambrian life, the origin of life and early evolution of animals, and vertebrate evolution in Australia, with special reference to the Mesozoic, including early mammals, dinosaurs, and birds. Referring to the numerous books that she has published or co-edited on the first of these subjects would be outside the scope of this book. But, among others, Tom Rich and Patricia Vickers-Rich are the authors of a charming book, Dinosaurs of Darkness (2000), which describes their arduous search for dinosaurs and early mammals in Australia, assisted by a great number of volunteers. The couple began searching in the late 1970s, at the westerly part of Australia's southern shore in a small gulf, which they called "Dinosaur Cove." In this gulf, small remnants of bones have been found. The search was more difficult than expected, as the Cretaceous deposits were situated far below the surface. To collect the fossils it was necessary to dig a tunnel. With a grant from the National Geographic Society, the heavy excavation work was possible. At the beginning, the work yielded some dinosaurs, pterosaurs, amphibians, and fish, but no mammals. Tom and Patricia did not give up and patiently searched other localities along the southern edge of Australia. They found their first Cretaceous mammal in 1997, at a more easterly situated locality called Flat Rocks, some 20 years after Tom and Patricia began their unstoppable searching.

9.3. A. Partial dentary with three molars of *Steropodon*. Lingual (A_1) and labial (A_2) views. B. Dentary with a single molar of *Teinolophos*. Labial (B_1) view, occlusal view of the molar (B_2), lingual view (B_3). C. Schematic comparison of the occlusal surfaces of *Teinolophos* (C_1) and *Steropodon* (C_2). D. Michael Archer.

A–C. From Kielan-Jaworowska et al. (2004: figure 6.5). D. Courtesy of Michael Archer.

The holotype of the first Australian taxon with tribosphenic molars, designated *Ausktribosphenos nyktos* by Rich et al. (1997), was a dentary with a rounded posteroventral margin and four teeth – three molars and the last premolar (figure 9.4). The authors regarded the new genus as similar to placentals and assigned it to a new mammalian order, Ausktribosphenida. The new finding was met with skepticism by some of the scientific community. I corresponded at that time with almost all the paleontologists working on Mesozoic mammals, who disagreed with the idea of Tom Rich and Patricia Vickers-Rich (see figure 9.4C and D) and their colleagues, but nobody was eager to write an article about it. So I suggested to Rich Cifelli, with whom I had already corresponded about writing a book together on Mesozoic mammals, that we should write a note about *Ausktribosphenos*. We sent the note for a private review to Zhe-Xi Luo, who introduced so many suggestions that we invited him to become a co-author of this note. This short paper by Kielan-Jaworowska, Cifelli, and Luo, "Alleged Cretaceous Placental from Down Under," was published (1998) in the Scandinavian journal *Lethaia*. In that paper, we argued that *Ausktribosphenos* cannot be a eutherian because of the structure of the mandible, in which there is a large trough on the lingual side, similar to those occurring in primitive mammals, with scars for several "reptilian" bones. In the line leading to placental and marsupial mammals, these reptilian bones disappeared during the Jurassic. We held that *Ausktribosphenos* might instead be a primitive stem mammal, possibly with its roots among early "symmetrodontans." This paper was

the first published by the three of us, and it began our close cooperation, resulting in several joint papers and, finally, in the comprehensive book *Mammals from the Age of Dinosaurs* (Kielan-Jaworowska, Cifelli, and Luo 2004; see the preface).

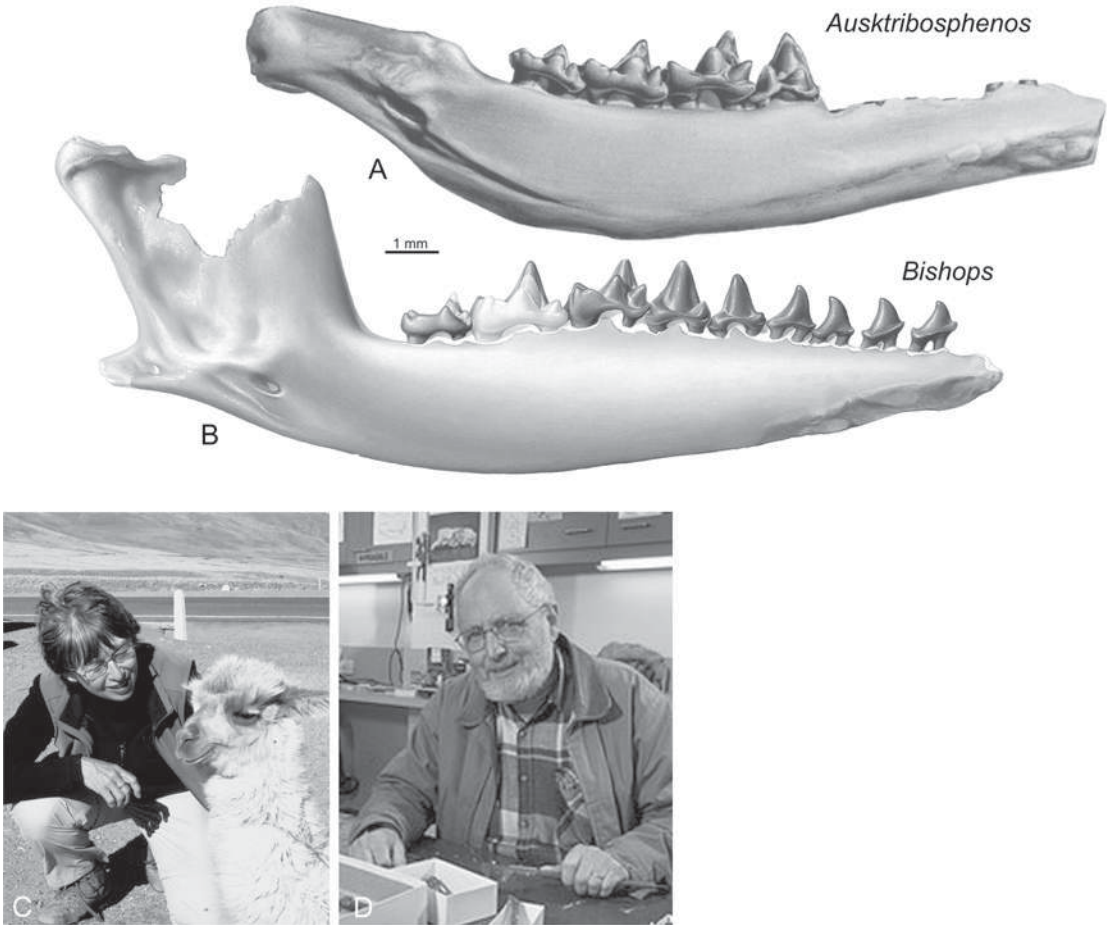
Luo (2007a, b), in his excellent reviews of Mesozoic mammal diversifications, recognized six "experiments" in the evolutionary path of early mammals and demonstrated their convergence with modern mammalian morphotypes. In this book I recognize two more "experiments" represented by the multituberculates and zalambdalestids (see chapter 14). Chapter 16 contains a summary of the evolution of mammaliaforms and early mammals in figure 16.1. Below I discuss three main anatomical innovations of mammals in Mesozoic times: (1) acquisition and loss of the extratarsal spur, (2) acquisition of tribosphenic molars, and (3) acquisition of three ear ossicles.

The Acquisition and Loss of the Extratarsal Spur

The venomous spur occurs in the extant male platypus (*Ornithorhynchus*) and is very dangerous (Fenner et al. 1992). In echidnas the spur may occur also in females, but is not as dangerous as in the platypus during its breeding season (Calaby 1968; Griffiths 1968, 1978; Grant 1995). In mammaliaforms and early fossil mammals, the spur has been rarely found because complete tarsi are seldom preserved (see figure 16.1: number 1). Among mammaliaforms, the spur has been found in a docodontan, *Castorocauda* (see Ji et al. 2006: figure 1B; and chapter 7, in this volume); in the Cretaceous eutriconodontan *Gobiconodon* (chapter 8 in this volume); in three Late Cretaceous multituberculates from Mongolia (*Kryptobaatar*, *Catopsbaatar*, and *Chulsanbaatar*; Hurum et al. 2006), probably in *Sinobaatar* from the Jehol biota (Kielan-Jaworowska and Hurum 2006: figure 4A); and in the "symmetrodontans" *Zhangeotherium*, *Maotherium*, and *Akidolestes* (Kielan-Jaworowska and Hurum 2006: figures 4D, E, and F, respectively). As the spur has never been found in either "eupantotherians" or in tribosphenidans (previously boreosphenidans; see below for explanation of synonymy), it seems that within the Theria *senu lato* it disappeared in "eupantotherians," or early tribosphenidans (see figure 16.1: number 1).

After our small *Lethaia* paper was published (Kielan-Jaworowska et al. 1998), Tom Rich arrived in Warsaw wishing to discuss with me some questions concerning *Ausktribosphenos* and early mammal relationships. Rich and his colleagues did not change their opinion after our challenge in *Lethaia*, and in 1999 they went even further, suggesting that *Ausktribosphenos* showed similarity to some hedgehogs (Erinaceidae) in having the ultimate premolar with a fully developed three-cusped trigonid and no talonid.

In 1992 a fossil monotreme was discovered for the first time outside Australia, in Paleocene beds of Patagonia (Argentina), dubbed *Monotrematum sudamericanum* (Pascual et al. 1992). The material is modest, consisting of two teeth (one upper and one lower molar). The teeth are



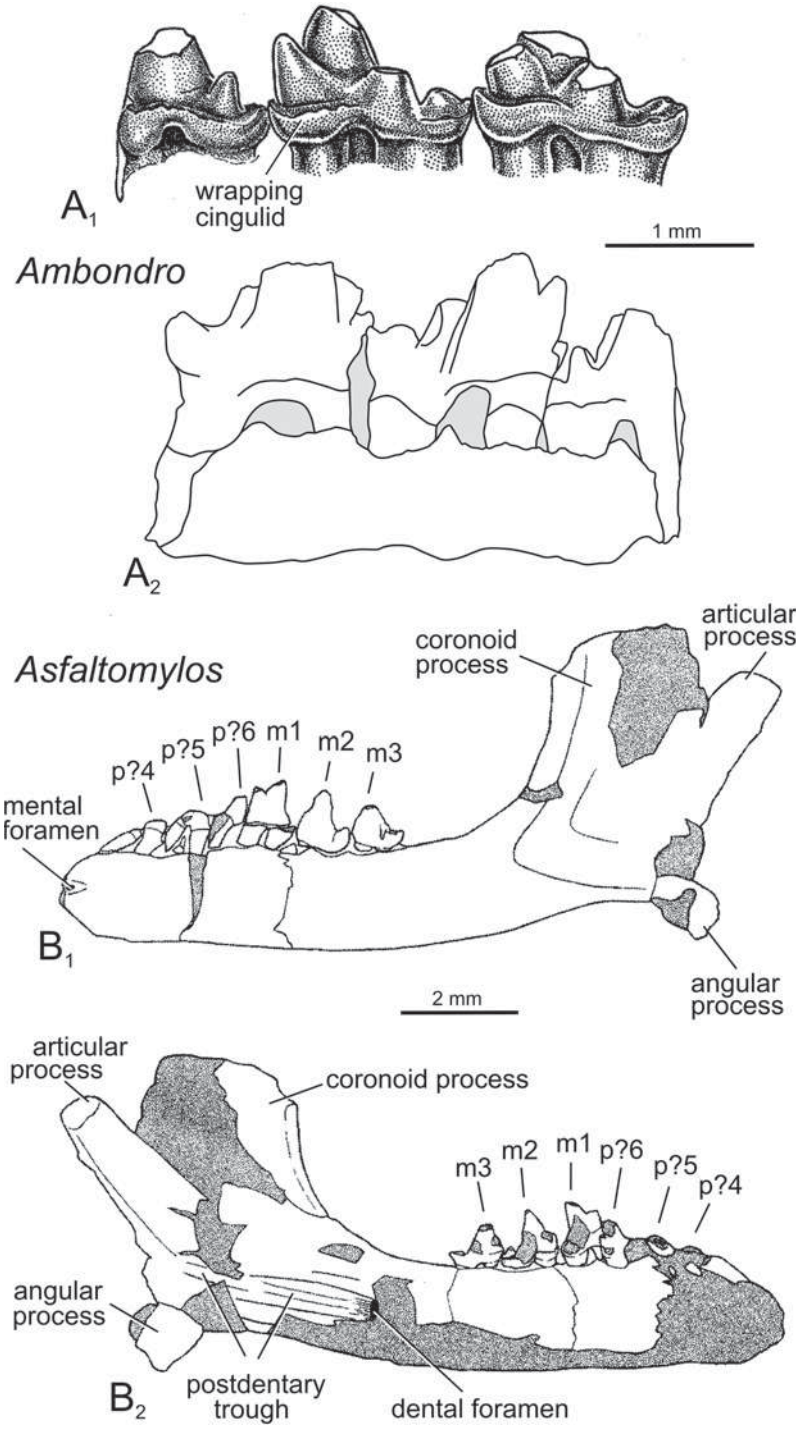
9.4. Two representatives of Australosphenida from the Early Cretaceous of Australia. A. *Ausktribosphenos nyktos,* right dentary in medial view, reversed. B. *Bishops whitmorei,* left dentary in medial view. C. Pat Vickers-Rich. D. Tom Rich.

A and B. From Kielan-Jaworowska et al. (2004: figures 6.1.B_2 and 6.2.A_3). C, D. Courtesy of Tom Rich.

well preserved and closely resemble the Australian *Obdurodon*, allowing assignment of *Monotrematum* to the Ornithorhynchidae.

One more ausktribosphenid taxon, *Bishops* (figure 9.4.B), was described by an Australian team in 2001 (T. H. Rich, T. F. Flannery, P. Trusler, A. Constantine, L. Kool, N. van Klaveren, and P. Vickers-Rich), with Tom Rich as the first author (Rich et al. 2001a). It was represented by a nearly complete dentary with six premolars (a condition not known in placental mammals) and three molars. *Bishops* differs from *Ausktribosphenos* in lacking a trough on the lingual side of the mandible, suggesting that the shallow structure present on the inner side of the dentary in *Ausktribosphenos* was a vestigial postdentary trough. However, no single upper tooth or maxilla of Australian non-monotreme ausktribosphenidans had at that time been found.

New discoveries were made about the same time in another part of the Gondwanan landmass, Madagascar. An American-Madagascan team, with John Flynn as the lead author, announced in 1999 the discovery of a new Middle Jurassic mammal *Ambondro mahabo* (figure 9.5A, in this volume), again represented only by a fragment of a dentary with three teeth, the ultimate premolar and two anterior molars of tribosphenic



9.5. Examples of two representatives of Australosphenida from Gondwana landmasses, outside Australia. A. *Ambondro mahabo,* from the Middle Jurassic of Madagascar, holotype, fragment of the dentary with three teeth, possibly the ultimate premolar and two molars in labial (A_1) and lingual (A_2) views. B. *Asfaltomylos patagonicus,* from the Jurassic of South America; dentary with three molars and three premolars, in labial (B_1) and lingual (B_2) views.

Both from Kielan-Jaworowska et al. (2004: figures 6.1.A and 6.3).

pattern. This discovery was of great importance, as the oldest fossils with tribosphenic molars known from the Northern Hemisphere were at that time Early Cretaceous in age. Thus, the new fossil extended the existence of mammals with tribosphenic molars back by some 25 or 27 Ma. Moreover, the new discoveries called into question the widely accepted opinion that mammals with tribosphenic molars, including ancestors of all living placentals and marsupials, arose on the northern continents.

Acquisition of Tribosphenic Molars

In order to elucidate the enigma of the origin of tribosphenic molars, we (Zhe-Xi Luo, Rich Cifelli, and myself) published an article in *Nature* in 2001, attempting a cladistic (phylogenetic) analysis of the relationships of the new Gondwanan fossils by comparing them to all known clades of Mesozoic mammals with tribosphenid (or pre-tribosphenid) molars (Luo et al. 2001a). As the new Gondwanan fossils were known only from the dentaries, lower premolars, and lower molars, we had to limit our analysis to these structures. The analysis comprised the distribution of 55 characters of the dentition and dentary in 21 mammal taxa, which included 19 of the oldest mammals from all around the world, 1 representative of extant marsupials (*Didelphis*), and 1 of extant placentals (*Erinaceus*). The results of the phylogenetic and morphometric analyses suggested that tribosphenic molars evolved independently at least twice: first, during the Middle Jurassic, in a clade endemic to Gondwanan landmasses, designated Australosphenida, of which only monotremes survive, and second, during the Early Cretaceous on the Laurasian continents, in a clade designated Boreosphenida (now Tribosphenida), which includes living marsupials, placentals, and their extinct relatives (figure 9.6). When we erected two new subclasses for mammals with tribosphenic molars (Australosphenida and Boreosphenida; see Luo et al. 2001a), knowledge of such mammals was limited. We thought that our "Boreosphenida" encompassed a larger spectrum of fossil mammals than the taxon Tribosphenida, earlier established by McKenna (1975). Now when more fossils with tribosphenic molars are described from various parts of the globe, I follow Davis and Cifelli (2011) and regard Boreosphenida Luo, Cifelli, and Kielan-Jaworowska, 2001 a junior subjective synonym of Tribosphenida McKenna, 1975.

In 2004 we set up a classification for mammals with tribosphenic dentition that included two subclasses (erected as infraclasses by Luo et al. [2001a]), Boreosphenida (= Tribosphenida) and Australosphenida (Kielan-Jaworowska et al. 2004). The Tribosphenida (former Boreosphenida) included mammals with primarily tribosphenic molars that originated in the Northern Hemisphere during the beginning of the Late Jurassic. The Tribosphenida included "tribotherians" Metatheria and Eutheria. The Australosphenida included mammals with primarily tribosphenic dentition that originated in the Southern Hemisphere during the Middle Jurassic and were assigned to the clade Yinotheria set up by Chow and Rich (1982). They differed from Tribosphenida in having

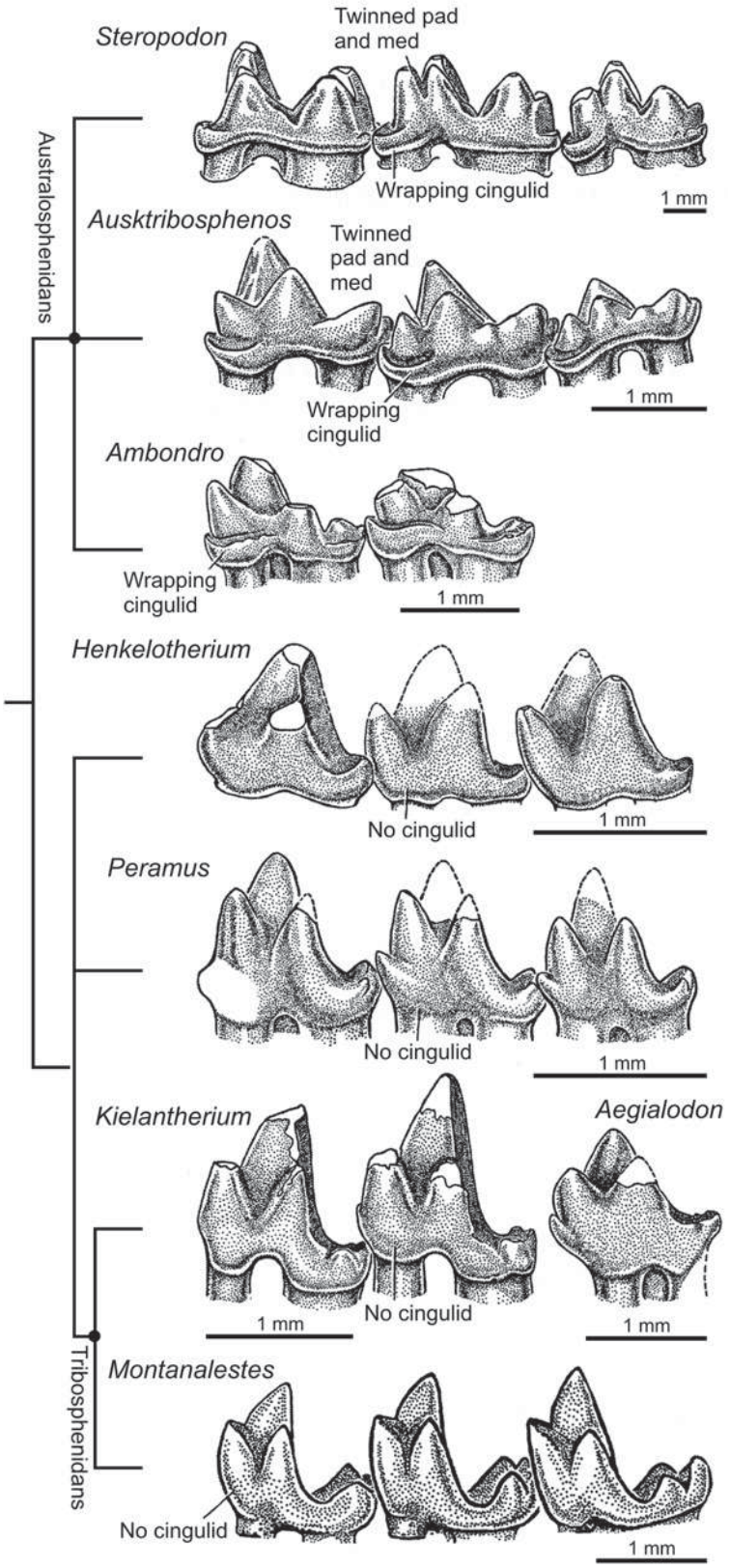
a continuous shelf-like mesial cingulid ("ridge") on the lower molars, rather than individual cingulid cuspules, and in having ultimate lower premolars with a fully triangulated trigonid, but no talonid, a feature not present in early Cretaceous tribosphenidans. Other differences included the greater number of premolars (up to six) in australosphenidans, rather than the three to five in tribosphenidans. The Australosphenida include *Ambondro*, *Asfaltomylos*, *Ausktribosphenos*, Monotremata, and tentatively also *Shuotherium*, a Northern Hemisphere form from the Jurassic of China (but see chapter 16).

Figure 9.6 presents a comparison of the lower molars of australosphenidans, pretribosphenids ("eupantotheres"), and tribosphenidans, all in lingual view. Lower molars of australosphenidans are characterized by a mesial cingulid wrapping around to the lingual side of the paraconid (pad) and a reduced height of trigonid relative to talonid. *Steropodon* and *Ausktribosphenos* share the derived feature of the twinned paraconid (pad) and metaconid (med) and the hypertrophied lingual cusp of the talonid. *Ambondro* and *Ausktribosphenos* share the derived features of a lingual cingulid on "molariform" premolars (not illustrated). None of these derived dental characters are present in the northern "eupantotherians" (*Henkelotherium*, *Peramus*), primitive tribosphenidans (*Kielantherium*, *Aegialodon*) or therians (*Montanalestes*).

One year after we published our cladistic analysis in *Nature*, we expanded our phylogenetic analysis, this time including 46 taxa of all major groups of Mesozoic mammals and 275 osteological and dental characters, and published it in a comprehensive paper in *Acta Palaeontologica Polonica* (Luo, Kielan-Jaworowska, and Cifelli 2002). According to this analysis, *Ausktribosphenos*, *Ambondro*, and, contra the Australian authors cited above, the Australian Cretaceous mammals (Australosphenida) do not belong to placental mammals; rather, they represent an ancient clade that originated during the Jurassic, more closely related to monotremes than to extant therians (tribosphenidans).

About this time, a new representative of the Australosphenida was found on a Gondwanan continent. In 2002, Rauhut, Martin, and Ortiz-Jaureguizar described in the journal *Nature* the first Jurassic mammal from Argentina, *Asfaltomylos patagonicus*, (figure 9.5B), represented by a well-preserved dentary with three premolars and three molars. According to these authors, the discovery of *Asfaltomylos* shows that australosphenidans were widely distributed on Gondwana before the end of the Jurassic and that the Middle Jurassic mammalian faunas of the southern and northern hemispheres differ considerably.

Our concept of a dual origin for tribosphenic mammals has been challenged by several authors. Some authors accepted the idea of *Steropodon-Ausktribosphenos* relationships but, argued against the australosphenidan nature of *Ambondro*. Others challenged the tribosphenic nature of monotreme teeth, arguing on the basis of an analysis of wear facets in *Monotrematum* that monotremes were derived from a non-therian ancestry. Rich et al. (2002) continued to note the similarity of Australian



9.6. Comparison of lower molars of australosphenidans, pretribosphenids ("eupantotherians") *Henkelotherium* and *Peramus,* and tribosphenidans in lingual views. Lower molars of australosphenidans are characterized by a mesial cingulid wrapping around the lingual side of the paraconid (pad) and a reduced height of the trigonid relative to the talonid. *Steropodon* and *Ausktribosphenos* share the derived feature of the twinned paraconid and metaconid (med) and the hypertrophied lingual cusp of the talonid. *Ambondro* and *Ausktribosphenos* share the derived feature of a lingual cingulid on molariform premolars (not illustrated). None of these derived dental characters are present in Northern Hemisphere "eupantotherians" (*Henkelotherium, Peramus*), primitive tribosphenidans (*Kielantherium, Aegialodon*), or therians (*Montanalestes*).

From Luo et al. (2001a), emended.

tribosphenic mammals, such as *Ausktribosphenos* and *Bishops*, to eutherians and did not support a relationship with monotremes. Woodburne et al. (2003) carried out a cladistic analysis of 51 mandibular and dental characters distributed among 20 taxa and concluded that the monotremes were a sister taxon of therian mammals with tribosphenic molars and that Gondwanan mammals with tribosphenic molars (assigned to Australosphenida by Luo et al. [2001a]), belong to basal placentals. Several authors also challenged our new taxon Boreosphenida for mammals with tribosphenic dentition that originated in the Northern Hemisphere, arguing that it would be better to use the earlier erected taxon Tribosphenida set up by McKenna (1975). I now accept this idea.

We continued to support the dual origin of tribosphenic mammals in our book *Mammals from the Age of Dinosaurs* (Kielan-Jaworowska et al. 2004). We presented there an enlarged phylogenetic analysis of 275 characters, distributed among 47 taxa. This new analysis gave support to our previous concept of the dual origin of tribosphenic mammals.

Recently our idea of the non-placental nature of Gondwanan Mesozoic mammals with tribosphenic molars received new support from paleogeographic studies. Hunter and Janis (2006) considered the geographic location of major placental clades at their first appearance (mostly Early Cenozoic) and demonstrated that a Laurasian origin would require fewer dispersal events than the southern-origin model. According to these authors, the paleogeographic data coeval with morphology-based phylogeny suggest the origin of Placentalia somewhere in Laurasia.

The existence of so many conflicting ideas on the nature of Gondwanan mammals with tribosphenic molars has its source, no doubt, in the lack of adequate fossil material. One should remember that *Ausktribosphenos*, *Bishops*, *Ambondro*, and *Asfalotomylos*, even after decades of prospecting, are known only from incomplete dentaries with partial dentitions. Tom Rich informed me recently (March 2010) that he found the first upper tooth – possibly the third premolar (P3) – of an ausktribosphenidan mammal at the locality Flat Rocks yielding lower dentitions in Australia. Fossil monotremes older than Oligocene are represented only by two isolated Paleocene molars from Argentina and a single dentary fragment with three teeth of Early Cretaceous from Australia, plus one molar with a dentary fragment (*Teinolophos)* from Australia. As long as the phylogeny of these early mammals is to be based on incomplete dentaries and fragments of the lower dentition, all the discussed views have to remain in the sphere of preliminary hypotheses.

Acquisition of Three Ear Ossicles

In 2005 Tom Rich, this time with a slightly different team (Hopson, Musser, Flannery, and Vickers-Rich) published in *Science* an interesting article on the independent origins of middle ear bones in monotremes and therians (Rich et al. 2005). They based their considerations mainly on the structure of the dentary of the Early Cretaceous monotreme *Teinolophos*. It is the oldest known monotreme, known from a dentary with a

well-preserved medial side and a single molar. As discussed in chapter 5, it has been well known since 1839 (the Reichert-Gaupp theory) that the bones building the reptilian jaw, the joint quadrate and articular, converted in mammals into middle ear ossicles. The quadrate bone became the incus; the articular and prearticular became the malleus; the angular became the tympanic ring; and the new joint between the dentary and the squamosal bone of the skull developed. Rich and colleagues demonstrated that in *Teinolophos* an extensive post-dentary trough has been preserved, and within it the angular, articular, and prearticular still occur. As in recent monotremes, three middle ear ossicles are present; their absence in the oldest monotremes, at a time when in therians the relevant bones had already moved from the mandible to the middle ear, demonstrates that the middle ear ossicles developed in monotremes independently of those in therian mammals.

The idea of an independent origin of ear ossicles in monotremes and therians is now generally accepted by specialists. This causes, however, the problem of how to define the mammals and where to put the boundary between mammaliaforms and mammals in the case of monotremes.

Recent Literature on Fossil Monotremes

Three years after Rich et al.'s (2005) paper, a five-author paper by an Australian and North American team (Rowe, Rich, Vickers-Rich, Springer, and Woodburne 2008) on the split between the ornithorhynchid and tachyglossied clades of monotremes was published in the *Proceedings of the National Academy of Sciences*. Another important paper, concerning all extant mammals (including monotremes), was published in *Nature* by a Canadian German zoologist, Olaf R. P. Bininda-Emonds, and nine co-authors, mostly zoologists, entitled "The Delayed Rise of Present-Day Mammals" (2007). Based on molecular data, the authors argued that the mass extinction event at the end of the Cretaceous, which eliminated the non-avian dinosaurs and most of the existing fauna, did not trigger the radiation of the present-day mammals. According to molecular data, present-day mammals made their appearance at least 93 million years ago, and after the mass extinction of non-avian dinosaurs (65 Ma), their evolution stagnated, and they began to differentiate intensively only much later, during the Eocene and Oligocene epochs, between 48 and 28 million of years ago. The conclusions of Olaf Bininda-Emonds and his co-workers challenged the hitherto accepted hypothesis that the end of the Cretaceous extinction event had a major direct influence on the diversification of present-day mammals. As far as the monotremes are concerned, according to the Bininda-Emonds et al. supertree (2007: figure 1), the split between the Tachyglossidae and Ornithorhynchidae took place 65 Ma ago, which does not agree with the recent paleontological data of Rowe et al. (2008), cited above. Rowe et al. (2008) demonstrated that these lineages diverged during the Early Cretaceous, some 47 million years earlier than the Cretaceous-Tertiary boundary.

As a rule, data obtained from molecular studies concerning the time of origin of a given group of mammals suggest earlier dates than do the data obtained by paleontologists. A comparison of the studies by Rowe et al. (2008) and Bininda-Emonds et al. (2007) shows a rare case in which the paleontological results suggest a considerably older time of origin than do the molecular ones.

On 8 May 2008 the journal *Nature* published an unusual article ("Genome Analysis of the Platypus Reveals Unique Signatures of Evolution"), authored by 89 geneticists from 32 scientific institutions in the United States, Australia, United Kingdom, New Zealand, Japan, Israel, Germany, and Spain. The authors demonstrated that the platypus exhibits a combination of reptilian and mammalian genomic characters. They stated:

> The 18,527 protein coding genes predicted from the platypus assembly fall within the range for therian genomes. Of particular interest are families of genes involved in biology that link monotremes to reptiles, such as egg-laying, vision, and envenomation, as well as mammal specific characters such as lactation, characters shared with marsupials such as antibacterial proteins, and platypus-specific characters such as venom delivery and underwater foraging. However, the repertoire of milk protein genes is typically mammalian, and the arrangement of milk protein genes seems to have been preserved since the last common ancestor of monotremes and therian mammals. (Warren et al. 2008: 181)

With regard to treating envenomation as a reptilian character, Hurum et al. (2006) and Kielan-Jaworowska and Hurum (2006) demonstrated that numerous early mammals with sprawling posture, assigned by them to Australosphenida (Luo et al. 2001a; Kielan-Jaworowska et al. 2004), were venomous. This concerns Multituberculata, Eutriconodonta, Symmetrodonta, and Docodonta.

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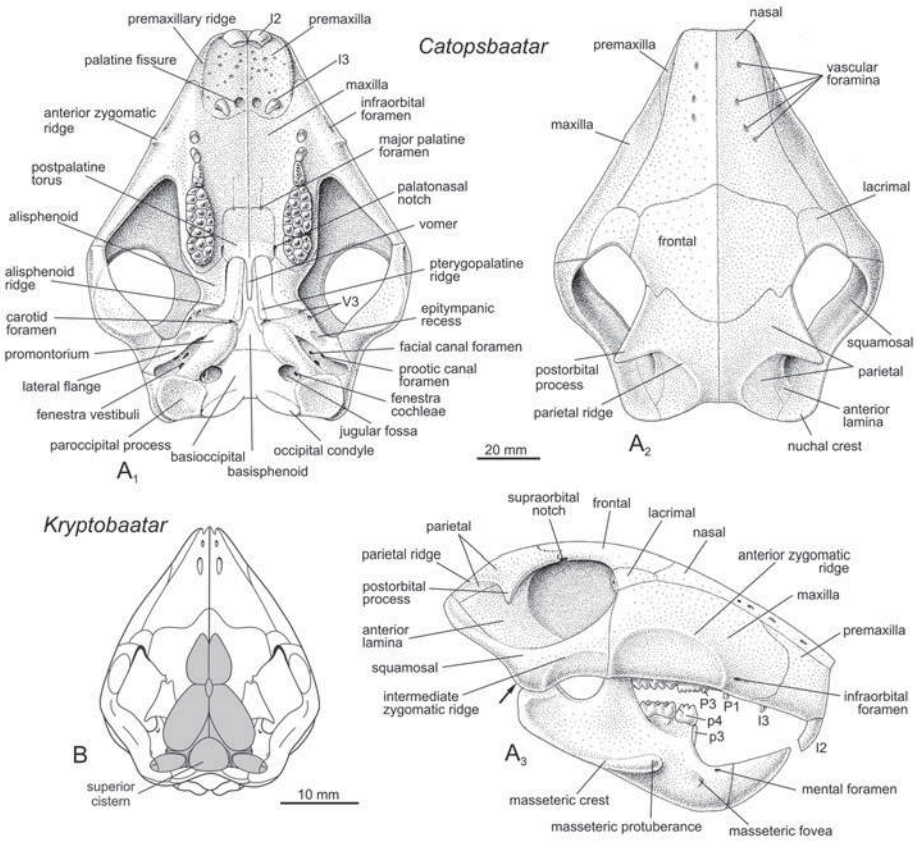


10.1. A. Skull of the Late Cretaceous djadochtatherioid (cimolodontan) multituberculate from Mongolia (Gobi Desert) *Catopsbaatar catopsaloides,* in ventral (A_1), dorsal (A_2), and lateral (A_3) views. The p4 (seen only in A_3) is small and reduced in size in comparison with other cimolodontans, with only three upper serrations, and lacks lateral ridges. B. Endocranial cast of a multituberculate *Kryptobaatar,* placed on the background of the skull. C–F. Multituberculate specialists: C. William A. Clemens. D. Petr P. Gambaryan. E. David W. Krause. F. Richard C. Fox.

A. From Kielan-Jaworowska et al. (2005). Artwork by Bogusław Waksmundzki. B. From Kielan-Jaworowska and Lancaster (2004: figure 3B). Artwork by Aleksandra Hołda-Michalska. C. Courtesy of W. A. Clemens. D. Courtesy of Peter Gambaryan. E. Courtesy of D. W. Krause. F. Courtesy of F. R. C. Fox.

Multituberculates and Gondwanatherians 10

MULTITUBERCULATES HAVE SOMETIMES BEEN CALLED "THE RODents of the Mesozoic" because of their superficial similarity to rodents, especially in the structure of the lower jaw and the arrangement of the dentition. Omnivorous or herbivorous, as today's rodents are, they likely occupied similar ecological niches. Most multituberculates were small, of shrew or rat size, with the exception of the Cretaceous *Bubodens* and the Paleocene *Taeniolabis*, which attained the size of beavers. Multituberculates are the best-known group of early mammals, represented by numerous complete skulls and large parts of the postcranial skeletons. In spite of this, multituberculate relationships and their origins are not clear. The controversial issue is whether they originated from the enigmatic Late Triassic–Early Cretaceous haramiyidans (see chapter 6) or, alternatively, from the line of mammals leading to therians.

Early Research on Multituberculates

The first multituberculates were described in 1857 by the Scottish paleontologist, geologist, and botanist Hugh Falconer (1808–1865), who erected the multituberculate genus *Plagiaulax* with two species, *Plagiaulax becklesii* and *P. minor* (now *Plioprion minor*), from the earliest Cretaceous Purbeck Limestone Group, referred to at that time as the Upper Oolite Beds. Falconer regarded *Plagiaulax* as an herbivorous marsupial.

The next step was the monograph by Sir Richard Owen (1871) on all Mesozoic mammals known at that time. Owen (1804–1892) was the greatest authority in paleontology and comparative anatomy of Victorian England; an anti-evolutionist and anti-Darwinist, he was referred to sometimes as the British Cuvier. Owen is best known for his role in founding the Natural History Museum in London (at that time the British Museum [Natural History]), for creating the name "Dinosauria," for his concept of homology, and for his competent description of numerous fossil vertebrates from around the world. With respect to multituberculates, he erected the genus *Bolodon* from the Purbeck of England and, contrary to Falconer, regarded multituberculates as carnivorous marsupials.

A few years later in 1879 the well-known American paleontologist Othniel Charles Marsh (1831–1899) described the first North American multituberculate from the latest Jurassic Morrison Formation of Wyoming, which he dubbed *Ctenacodon*, belonging to the paraphyletic suborder "Plagiaulacida." In 1881, Marsh's rival, the eminent paleontologist Edward Drinker Cope (1840–1897), described the first North American Tertiary multituberculate *Ptilodus*. During the 1880s, Marsh and Cope

described many multituberculate taxa from the Late Jurassic, Cretaceous, and Paleocene of North America. As noted, multituberculates had been described as belonging to marsupials and sometimes to monotremes. For multituberculates, Marsh erected the marsupial suborder Allotheria in 1880, while Cope in 1884 erected the order Multituberculata.

In the second half of the twentieth century, the most important paleontologist working on multituberculates (and other early mammals) in the United States was William A. Clemens. William (Bill) Clemens (Figure 10.1C) was born in 1932 in Berkeley, California. In 1960 he obtained his Ph.D. at the University of California, Berkeley. In 1960/1961 he spent a year at University College London working with Kenneth A. Kermack. From London he moved to the University of Kansas, teaching paleontology and at the same time working as a curator at its Natural History Museum. In 1963 he published the first part, devoted to multituberculates, of his dissertation on the mammalian fauna of the Upper Cretaceous Lance Formation. The following parts, devoted to marsupials and eutherian mammals, were published in 1966 and 1973, respectively. Over the years, prior to his retirement in 2005, he served as the last chair of the Department of Paleontology before it became part of the Department of Integrative Biology; he also served two terms as director of the museum. Starting with his doctoral research on the mammals of the Late Cretaceous Lance Formation, Wyoming, his research interests focused on Mesozoic mammals until 1972. Then, thanks to discoveries in eastern Montana, he expanded his interests to include the mammalian faunas of the earliest Paleocene. His years as professor of paleontology at the University of California at Berkeley gave him the opportunity to serve as major professor for nearly 40 talented graduate students, most of whom are now professors themselves.

We owe the knowledge of Late Cretaceous multituberculates, other mammals, and different Cretaceous tetrapods of western Canada to the work of the American Canadian vertebrate paleontologist Richard (Dick) C. Fox (Figure 10.1F; see, e.g., Fox 1968). Born in 1933 in Lowell, Massachusetts, in the United States, he received a Ph.D. from the University of Kansas in 1965 on the basis of a paper on the Early Permian reptile *Captorhinus*. In September 1965 he was appointed assistant professor in geology and zoology at the University of Alberta in Edmonton, Canada, in order to establish a teaching/research program in vertebrate paleontology. Richard has spent most of his life in Edmonton, retiring there in 1999. He has collected and described various Cretaceous and Paleocene vertebrates from different formations in western Canada (e.g., Fox 1968, 1969, 1970, 1971a, 1971b, 1984, 1991; Johnston and Fox 1984). The fossils collected by Fox in Alberta are often represented by isolated teeth. However, owing to his deep knowledge of anatomy and geology, Fox has been able, on the basis of various single teeth, to draw important conclusions on the relationships of different groups of Cretaceous mammals and their paleogeography. In addition to various groups of mammals, he has described different land vertebrate fossils and fish from the Cretaceous-Paleocene of

Alberta, along with other Cretaceous birds, amphibians, and other fossils. Since 2003, he has been collaborating with Chinese paleontologist Gao Kequin from Peking University on a new Triassic tetrapod from Gansu Province, China.

Until multituberculates from the Gobi Desert had been described (Kielan-Jaworowska 1970, 1971, 1974; Kielan-Jaworowska, Presley, and Poplin 1986; Gambaryan and Kielan-Jaworowska 1997; Kielan-Jaworowska, Hurum, and Lopatin 2005, and references cited therein), the knowledge on multituberculate skulls was based mostly on specimens from the Paleocene (see Broom 1914; Simpson 1937). The multituberculates from the Southern Hemisphere until recently have hardly been known, with information coming from very incomplete specimens: single teeth or teeth with a fragment of mandible (Kielan-Jaworowska and Bonaparte 1996; Kielan-Jaworowska, Ortiz-Jaureguizar, Vieytes, Pascual, and Goin 2007; Rich et al. 2009). Their presence demonstrates that multituberculates in the Mesozoic had a worldwide distribution.

The Multituberculata (from the Latin *multum*, meaning much or numerous, and *tuberculum* or tubercle, in reference to the multicusped molar teeth) are a monophyletic order of Jurassic-Eocene omnivorous or herbivorous mammals, assigned to the subclass Allotheria. Multituberculates embrace two suborders, the earlier paraphyletic "Plagiaulacida," erected by Ameghino (1889), and the advanced Cimolodonta, erected by McKenna (1975). I begin the description of multituberculates by presenting the skull of *Catopsbaatar catopsaloides* (Figure 10.1A), a Late Cretaceous representative of the Cimolodonta family Djadochtatheriidae from the Gobi Desert, set up by Kielan-Jaworowska and Hurum (1997).

Multituberculates are characterized by multicusped premolars and molars covered with longitudinal rows of low cusps. There are two or three upper incisors, and an upper canine is present only in some early taxa. Five upper premolars are present in the "Plagiaulacida," but one to four are present in the Cimolodonta. There is a single lower incisor, one to four lower premolars, and two lower and two upper molars. A new apomorphic feature (a feature that is characteristic only of a given group) of the upper dentition is a lingual shift of M2 with respect to M1. In the structure of the dentary and the arrangement of the dentition (gnawing incisors and a diastema separating them from the premolars), multituberculates have a superficial similarity to rodents. The characteristic feature of most taxa is the structure of the shearing lower premolar (p4), or several lower premolars in most "plagiaulacidans." The multituberculate lower premolars are blade-like, with a serrated upper margin and oblique ridges that extend along the labial and lingual surfaces. The ridges may disappear in some advanced groups. See Figure 10.1A$_3$ and 10.3C, in this volume); see also Kielan-Jaworowska et al. (2004: 265) for different structures of p4.

The multituberculate skull differs from those of most therian mammals in being wide and dorsoventrally rather than laterally compressed; the postorbital process in some groups – for example, in

Djadochtatherioidea – is situated far posteriorly on the parietal bone, rather than on the frontal, as in other mammals. The orbit in these groups is very large, correlated with the posterior position of the postorbital process; the eyes are big and situated to the rear of a long snout. The zygomatic arches are strong and expanded laterally; the glenoid fossa is large, flat, and set off from the braincase. Philip Gingerich demonstrated in 1977 that multituberculates had a backward power stroke, which means that they cut food when the mandible was moving backward, and they shared this character with the Gondwanatheria (see below). The backward power stroke resulted in a more anterior insertion of the masticatory muscles than in any other mammal group, including rodents. The cochlea is not coiled but only slightly bent, and there are three ossicles in the middle ear, as in crown mammals.

Marsupial bones are present, as they are in marsupials, monotremes, various Mesozoic mammals, and some early eutherians. The most important postcranial character is a very narrow pelvis, with its bones (pubes and ischia) fused ventrally to form a keel. A characteristic feature of the ankle joint is the contact between the calcaneus and the fifth metatarsal, abbreviated as MtV. Kielan-Jaworowska and Gambaryan (1994) argued that multituberculates had a sprawling posture and used a saltatory mode of locomotion. Some may have been fossorial, others perhaps scansorial or arboreal, with a squirrel-like, reversible hind foot and a prehensile tail, as suggested by Krause and Jenkins (1983). The multituberculate brain was probably similar to those of other early mammals, apparently having the midbrain exposed on the dorsal side, but in all available endocasts the midbrain and the vermis (the middle part of the cerebellum) are obscured by a cast of a large vessel, called the superior cistern (see Kielan-Jaworowska and Lancaster 2004). A superior cistern also occurs in eutriconodontans and some extant marsupials.

During the nineteenth century, no multituberculate upper and lower dentitions were found in occlusion. The first were discovered in 1909, when James William Gidley described the skull of the Paleocene *Ptilodus* preserved with dentaries. Another skull associated with dentaries belonged to the Paleocene *Taeniolabis* (referred to as *Polymastodon*), described by Robert Broom (1914). These specimens demonstrated that multituberculates were herbivorous, rather than carnivorous. The idea that they represent a separate clade was slowly accepted, mainly due to the work of George Gaylord Simpson in the 1920s. Simpson (1925a) described the skull of a Late Cretaceous multituberculate from Mongolia – *Djadochtatherium* – and among numerous papers that he wrote in the 1920s and 1930s he published an important monograph devoted to the revision of Mesozoic mammals housed in the collections of the Natural History Museum in London (Simpson 1928a). This was followed in 1929 by another monograph revising American Mesozoic mammals (Simpson 1929). Finally, Simpson, in an important work on the classification of mammals (1945), raised Marsh's suborder Allotheria to a subclass of its own.

Although only a few papers on multituberculates were published during World War II, beginning in the late 1950s and early 1960s the scientific world witnessed increased interest in Mesozoic mammals, including multituberculates, related to the development in 1949 of Hibbard's screen-washing technique (see chapter 2). Through the application of the new method, large collections of Mesozoic (especially Cretaceous) mammals were assembled and described by a new generation of paleontologists, especially in the United States and Canada. Prime among those working on multituberculates (cited more or less in chronological order) have been J. David Archibald, William A. Clemens (Figure 10.1C), Richard C. Fox (Figure 10.1F), David W. Krause (Figure 10.1E), Jason A. Lillegraven, Ashok Sahni, Robert E. Sloan, and later their students, for example, Richard L. Cifelli, Jeffrey Eaton, Marisol Montellano, Christine E. Wall, Anne Weil, and others.

David W. Krause (Figure 10.1D) spent the majority of his scientific life working on multituberculates. Born in 1950 in Medicine Hat in Alberta, Canada, Krause received his master of science at the University of Alberta under the supervision of Richard Fox and his Ph.D. from the University of Michigan under Philip Gingerich. Krause is currently Distinguished Service Professor in the Department of Anatomical Sciences and the Department of Geosciences at Stony Brook University (Stony Brook, New York), a research associate at the Field Museum (Chicago, Illinois), and a former president of the Society of Vertebrate Paleontology (1994–1996). Much of his graduate and early professional career was focused on the systematics, functional morphology, paleoecology, biogeography, and biostratigraphy of multituberculates. His interests then broadened to include other clades of Late Mesozoic and Early Cenozoic mammals, in large part the result of a long-term field research program in the Crazy Mountains Basin, Montana. In 1993, Krause launched a reconnaissance expedition to Madagascar in search of Cretaceous mammals and other vertebrates. He and his team, in the initial foray and in subsequent field campaigns to Madagascar in what has become a large ongoing project (the Mahajanga Basin Project), have discovered a plethora of dinosaurs, crocodyliforms, and other vertebrates, including several species of mammals, one of them represented by a nearly complete, exquisitely preserved skeleton. These discoveries have profound implications for addressing questions related to the timing and sequence of Gondwanan fragmentation during the Mesozoic and the origins of Madagascar's extant fauna. Krause is also the founder of the Madagascar Ankizy Fund, whose mission is to provide education and health care to children (*ankizy*, in the Malagasy language) living in remote areas of Madagascar, one of the poorest countries in the world.

At the same time in Europe, Walter G. Kühne (see chapter 5, for his earlier work in Great Britain) intensively searched for Mesozoic mammals and discovered the Kimmeridgian Guimarota fauna in Portugal, which requires special attention (see below). I refer the reader to the description of the dentition and cranial and postcranial anatomy of the

Multituberculata in Clemens (1963) and Hahn and Hahn (1983, 2006, 2007) and the systematics of the suborders "Plagiaulacida" and Cimolodonta to Kielan-Jaworowska et al. (2004). Important sources of information on multituberculates and related forms are three important books by Gerhard Hahn and Renate Hahn (1983, 2006, and 2007), published in the Fossilium Catalogus series.

Gerhard Hahn and his wife Renate (Figure 10.2G) were both born in Berlin in 1933 and 1940, respectively. After the Second World War, Berlin was divided into eastern and western sectors. East Berlin was controlled by Russians, and West Berlin by American, British, and French forces. Gerhard Hahn lived in East Berlin. Until the construction of the Berlin Wall, the inhabitants of both parts of Berlin could freely communicate and travel by train between the two sectors, and Gerhard studied at the Free University in West Berlin. In August 1961, the authorities of the DDR (Deutsche Demokratische Republik) ended unrestricted travel between the two parts of Berlin, and the infamous wall was constructed. In January 1960, Gerhard Hahn, accompanied by his parents, sister, and his fiancée Renate left East Berlin. The journey was risky—no luggage could be taken; the whole group had to pretend that they were going for a visit of a few hours. Gerhard, who studied at the Free University in West Berlin, received permission to remain there, but his fiancée, who had studied paleontology at Humboldt University in East Berlin, had to spend several months in a transition camp. After Renate was released from the camp, the couple was married, and both Gerhard and Renate graduated from the Free University, Berlin.

In 1973 Gerhard won the competition for the professorship of paleontology at Phillips University in Marburg, and the couple moved to Rauschenberg, a small, medieval town near Marburg. The Hahns moved the collection of Guimarota multituberculates to Rauschenberg, which they prepared and studied for many years. Gerhard Hahn continues to be an active paleontologist. He is an author of many scientific articles and eleven books, most co-authored with Renate Hahn. Half of his publications deal with Late Devonian and Carboniferous trilobites, the remainder with Jurassic and Cretaceous multituberculates and haramiyidans, and a few with cynodonts. Owing to his and his wife's work, knowledge of the early evolution of multituberculates and related forms has enormously increased.

In the spring of 1981, I accompanied my husband on a trip to France, where we remained for two years (see below). The main aim of my stay in Paris was to cut two skulls of multituberculate mammals on a special microtome in the laboratory of Armand de Ricqlès (see Plate 5.D) at University of Paris VII. In parallel, the Norwegian anatomist Gisle Fosse described the microstructure of multituberculate tooth enamel, which he photographed during his visit to the Institute of Paleobiology in Warsaw in 1980. During my stay in Paris we completed our paper on the microstructure of tooth enamel in multituberculates (Fosse, Kielan-Jaworowska, and Skaale 1985).

The Guimarota Fauna of Portugal

The Kimmeridgian Guimarota fauna of Portugal, yielding numerous multituberculates, was discovered by the late Walter G. Kühne in 1959. Kühne found the Guimarota locality not by chance but by methodically searching for Mesozoic mammals in Europe. As searching for Mesozoic karst fillings, which he had successfully exploited in Great Britain (see chapter 5), proved unsuccessful in continental Europe, Kühne turned to searching for Mesozoic mammals in lignite, often referred to as brown coals. Mammals and other vertebrates had been found in Eocene brown coals at the well-known locality of Geiseltal near Halle, Germany, so Kühne expected that they might be found in brown coals of Mesozoic age. As large parts of the Iberian Peninsula were not covered by sea during the Late Jurassic and Early Cretaceous, this region seemed to be promising for this type of search, especially since these areas had yielded dinosaurs. As mentioned in chapter 7, in 1959 Walter Kühne, accompanied by the young geologist Wolfgang Frey, went on a field trip to Portugal, during which they learned that in the village of Guimarota near the town of Leiria north of Lisbon there was a small brown coal mine.

This first prospecting visit to Guimarota was a success, with Frey finding a piece of coal containing an incomplete toothless skull of a multituberculate mammal. In the spring of 1960 a larger party from the Free University in Berlin continued searching for fossils in the Guimarota mine, and in the fall of the same year they decided to hire Portuguese women to help them search. In a barracks hall built over the mine, they set up a makeshift laboratory. The Portuguese women sat at a table, splitting coal with small hammers and examining the surface. The specimens found in this way were subsequently examined by the scientists in the same hall under a binocular microscope. In 1961, a still larger group of paleontologists from Berlin collected at Guimarota from March to September, employing more local workers. This was quite successful. The technical leadership was taken over by Siegfried Henkel (1932–1984), an assistant at the Free University in Berlin. After 1961, scientists taking part in the excavations included, among others, Gerhard Hahn and his wife Renate, Helga Northe (later wife of Siegfried Henkel), Georg Krusat, Friedrich Franz Helmdach (who studied the geology of the area), and several other students of geology and paleontology. The crew was also accompanied by Portuguese workers, some of whom were experienced miners. Financial support for the work was provided by the Deutsche Forschungsgemeinschaft (German Science Foundation) and by the Serviços Geológicos de Portugal (Geological Survey of Portugal).

In spite of the great success of these first years of searching, during which 74 upper and lower jaws of various mammals (some with large parts of skulls) and hundreds of isolated teeth were excavated, there were unexpected obstacles that jeopardized further intensive collecting. The mining company went bankrupt, and the mining stopped. In response to this situation, Siegfried Henkel developed a method of chemical treatment and screen washing of the used coal. Known as "Henkel's process"

10.2. A. Reconstruction of the skull of a representative of Paulchoffatiidae, in dorsal (A_1) and palatal (A_2) views. B–F. Morphology of the dentary and teeth in Paulchoffatiidae. B. Comparison of the dentaries in *Paulchoffatia* (B_1) and *Kuehneodon* (B_2) showing the difference in angle between tooth row and dentary, 7° in *Paulchoffatia* and 20° in *Kuehneodon*. C. Right p4 of unidentified paulchoffatiid, with well preserved row of labial cusps in labial (C_1) and posterior (C_2) views. D. Left m2 of unidentified paulchoffatiid in occlusal view. E. Right p3–p4 of *Guimarotodon leiriensis,* in labial view, showing a row of labial cuspules and additional row of cuspules, below it. F. Left m2 of *Xenachoffatia oinopion,* in posterior (F_1) and occlusal (F_2) views. Note the difference between the heights of the cusps. G. Renate Hahn and Gerhard Hahn.

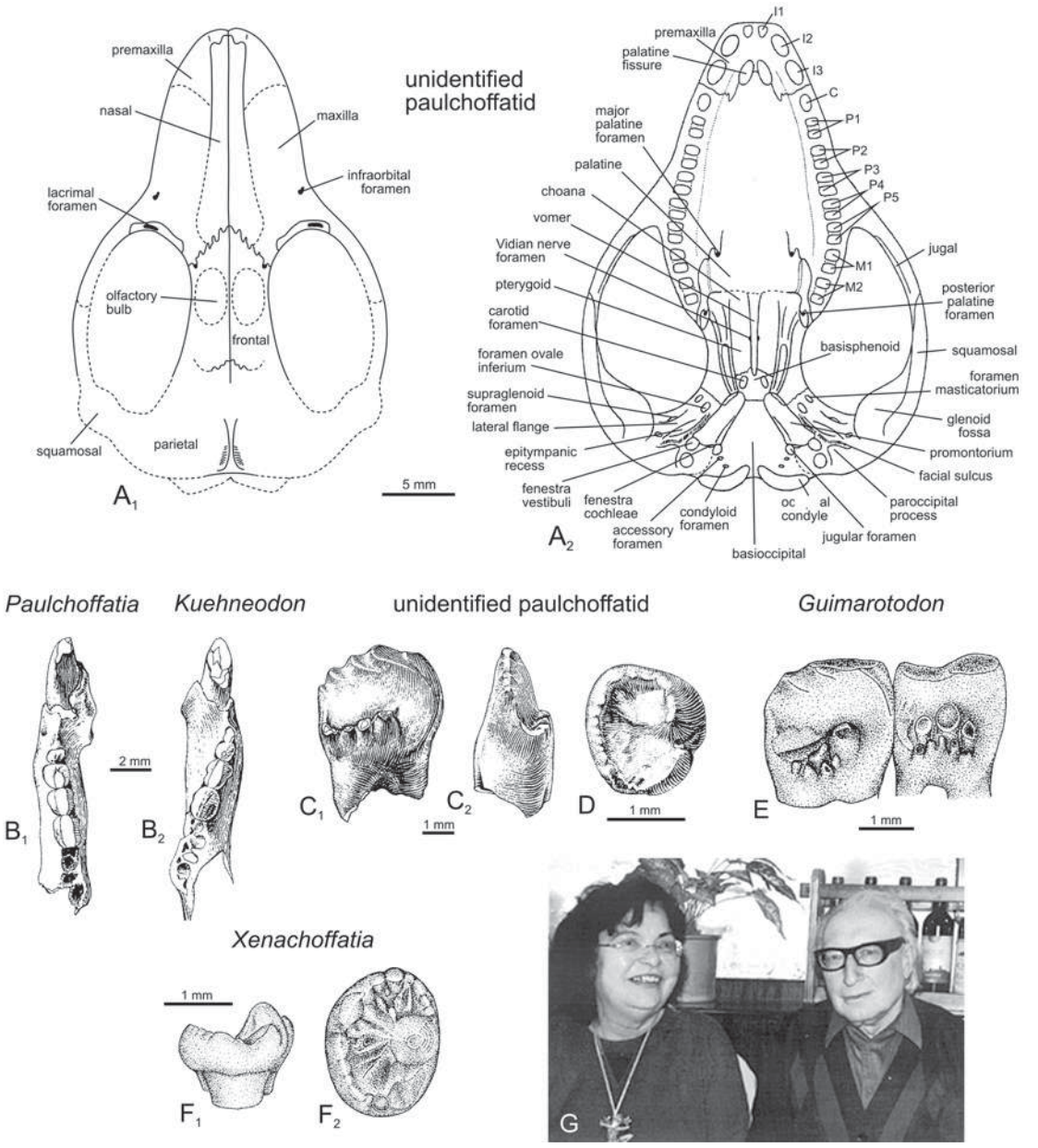
The entire drawing A from Kielan-Jaworowska et al. (2004: figure 8.26). A_1 modified from Hahn (1969); A_2 from Hahn (1988). B–F. From Kielan-Jaworowska et al. (2004: figure 8.27). G. Courtesy of Renate Hahn.

(see Kühne 1971), it recovered isolated teeth but could not supply the most valuable fossils – the jaws and skulls.

Kühne himself lost interest in further exploitation of Guimarota coals and began searching for Mesozoic fossils in other localities in Portugal and in Spain, which, however, did not yield as good results as Guimarota. His co-workers, however, especially Bernard Krebs (1934–2001), Siegfried Henkel (1932–1984), and Georg Krusat (1938–1998), did not give up. In spite of enormous technical difficulties – such as the mine filling with water, which had to be pumped out in order to start new excavations – and a new owner of the land not wanting any coal left on his property, together with the enormous cost of the new endeavor, they managed to obtain financial support from the Deutsche Forschungsgemeinschaft and the Free University at Berlin. After a ten-year break, new excavation started in 1972 and lasted until 1982 (see the beautiful book edited by Tom Martin and Bernard Krebs in 2000, *Guimarota: A Jurassic Ecosystem*). In the final years, the Berlin crew stopped excavating the Guimarota mine because conditions underground had become dangerous and no more funding was available. Even so, the results of this enormous effort exceeded all expectations. The party found more than 1000 jaws with dentition, about 20 skulls, two more or less complete skeletons, and more than 10,000 isolated teeth of mammals, as well as numerous, not yet completely prepared skulls and bones of other vertebrates, plant remains, and invertebrates. The scientific description of the collected materials published to date exceeds 100 papers and monographs, but work on this unusual material is still going on.

The first reports on the discovery of Guimarota fauna were in three papers published by Kühne: one in German (Kühne 1961b); a second, shorter one in *Nature* in English (Kühne 1961a); and the third one in Portuguese (not cited herein). In the first of these papers, which appeared in *Neues Jahrbuch für Geologie und Paläeontologie, Monatshefte*, Kühne erected a new genus and species of Guimarota multituberculate, based on an incomplete edentulous skull, which he called *Paulchoffatia delgadoi*, and reconstructed its dental formula on the basis of the alveoli, part of which had been preserved. In spite of these reports and a few other small papers by Kühne, the Guimarota multituberculates were poorly known until 1969, when Gerhard Hahn published the first of his numerous monographs on the Guimarota multituberculates and also another one, by Hahn and Hahn (1999), on early multituberculates from Portugal.

In the spring of 1969 Walter Kühne invited me to the Free University of Berlin to lecture to his students and co-workers on my work on Mesozoic mammals from Mongolia. On this occasion I had an opportunity to learn details about the Guimarota work and to meet Kühne's co-workers. Among others, I met for the first time Gerhard and Renate Hahn. In 1974 I visited the Hahns again, this time in Rauschenberg. I spent some ten days in their hospitable house full of pets. The aim of my visit was an examination of the Guimarota collection (Figure 10.2A–F). Compared with specimens from the Late Cretaceous of the Gobi Desert, which I had



studied, where we found several skulls in association with lower jaws and postcranial skeletons, the fossils from Guimarota seemed to me poorly preserved. They are slightly flattened, and no single bone of the postcranial skeleton of a multituberculate has been found, nor have the upper and lower dentitions been found in occlusion. This indicated a long transport of fossils before they were fossilized in the coal of Guimarota. In Figure 10.2A I present a reconstruction of the skull of an unidentified paulchoffatiid in dorsal (A_1) and ventral (A_2) views.

A characteristic feature of the multituberculate dentition is that the row of lower premolars and molars are arranged obliquely with respect

to the long axis of the dentary. However, in the holotype and other specimens of *Paulchoffatia delgadoi* the tooth row is at an angle of only 7–10° with respect to the anteroposterior axis of the dentary. In contrast, this angle is 20° in *Kuehneodon* from the same beds and varies around 20° in cimolodontans (Figure 10.2B; see also the reconstruction of the skull and head of *Paulchoffatia* sp. in Figure 10.3A).

In spite of the drawback caused by the lack of associated upper and lower dentitions, the Guimarota multituberculate fauna is extremely important in casting new light on the origin of some characters found in multituberculates. Among the reports published by Kühne on the Guimarota mammals, one paper in 1968 illustrated an isolated multituberculate p4 from Guimarota, designated *Paulchoffatia* sp. This is perhaps the most famous multituberculate lower premolar (Figure 10.2C), referred to subsequently by Hahn and Hahn (in their 2006 Fossilium Catalogus paper) as Paulchoffatiidae gen. et sp. indet. This specimen shows how the blade-like p4, characteristic of multituberculates, originated from lower teeth that had the usual two rows of cusps of various early mammals, including multituberculate molars. The tooth is relatively short, with only five apical cusps provided with ridges. It has a blade-like structure, typical for multituberculate lower premolars, but shows on the labial side a row of five prominent, large labial cusps, situated lower than the apical row, interpreted as a remnant of the second row of cusps of an ancestral form, with two longitudinal rows of cusps. In Figure 10.2E, I demonstrate that in some paulchoffatiid genera (in this case, *Guimarotodon*) there may occur two rows of cuspules placed on the labial side of the teeth, one below the other.

Gerhard Hahn demonstrated in his first monograph (1969) and in several later papers that members of the Paulchoffatiidae, to which the bulk of the Guimarota multituberculates belong, are specialized, especially in having the second lower molar (m2) basin-like with only a single cusp (Figure 10.2D), which does not occur in any other multituberculate. Hahn regarded the structure of m2 as an apomorphy of the Paulchoffatiidae, which excluded them from the ancestry of the Cimolodonta. The Paulchoffatiidae show numerous plesiomorphic features, which help us to understand how some characters, typical of later multituberculates, developed. One of the multituberculate characteristics is the equality of height of multicusped upper premolars. The Paulchoffatiidae (and the Pinheirodontidae) are exceptions in this respect in having cusps of different heights (Figure 10.2F). Another plesiomorphy is retention of the coronoid bone, which is not present in later multituberculates.

In the whole collection of various mammals from Guimarota (docodontans, multituberculates, dryolestid, and paurodontid "eupantotherians"), and a representative of the "stem-lineage of Zatheria," there are only two specimens with partial postcranial skeletons preserved. One of these belongs to the "eupantotherian" *Henkelotherium*, described by Krebs (1991), and the other to a docodontan, *Haldanodon*, preliminarily described by Krusat (1991) and redescribed by Martin (2005).

For many years the Guimarota fauna contained the oldest-known uncontested multituberculates. In 2005, however, Percy M. Butler and Jeremy J. Hooker described a collection, originally assembled and described by Kenneth A. Kermack et al. (1998), of haramiyidan and multituberculate teeth from Kirtlington in England, which is of Bathonian age. The Bathonian multituberculates are some 13 million years older than the multituberculates from Guimarota. But while in the Guimarota collection there are parts of jaws with teeth and skull fragments, which make possible at least a partial reconstruction of the skull, the Kirtlington material consists of only isolated teeth.

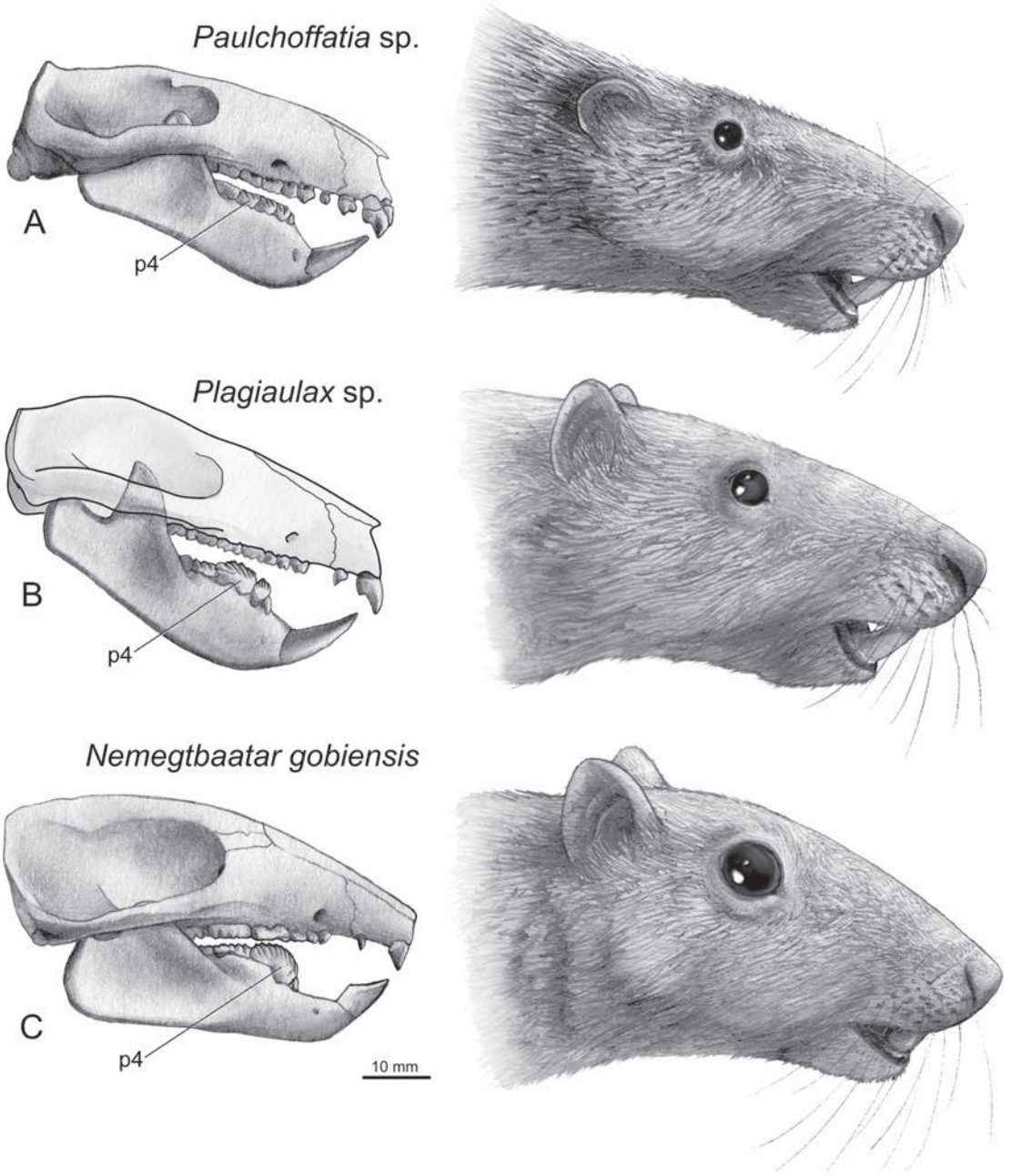
Other "Plagiaulacidan" Multituberculates and Relationships within Them

The latest Jurassic multituberculates are best known from the North American Morrison Formation, distributed over three states (Wyoming, Colorado, and Utah) and numerous localities yielding mammals. Simpson (1929) offered a very thorough analysis of mammals of the Morrison Formation known at that time and cited long lists of nineteenth-century papers by Marsh, Cope, Osborn, and numerous others, which I will not cite here, referring readers instead to Simpson's great opuses. Much has changed in the taxonomy of Jurassic mammals since Simpson's time, as numerous forms assigned by Simpson to mammals are now classified as cynodonts.

The Morrison Formation multituberculate fauna embraces several genera, known either from dentaries with dentition or from upper jaws with incomplete dentition, described as early as the nineteenth century. Of the taxa described from lower dentitions, the most complete is *Plagiaulax* (Figure 10.3B), while among species described from upper dentitions, the most complete is *Bolodon osborni*. The multituberculate assemblage from the Purbeck Limestone Group of England, now regarded as being of the earliest Cretaceous age (Berriasian), is in many respects similar to that from the Morrison Formation. There occur members of Plagiaulacoidea and Allodontoidea, although rare members of the Paulchoffatioidea are also present.

Other Early Cretaceous multituberculates are known from the Berriasian of Porto Pinheiro in Portugal, represented exclusively by isolated teeth (250 in number), described by Hahn and Hahn (1999). In this impressive monograph the authors introduced a method of numbering the cusps on the teeth of multituberculates. For this fauna they erected five new genera with several species and established the new family Pinheirodontidae (assigned to Paulchoffatioidea). In addition, they assigned to the Pinheirodontidae the genus *Lavocatia*, earlier known from the Early Cretaceous (Barremian) of Spain. They also described Early Cretaceous teeth from Spain in several papers.

Very important Early Cretaceous multituberculates are those from Aptian or Albian Höövör beds at the Guchin Us locality in the Gobi Desert. The locality was discovered by the Soviet-Mongolian Paleontological Expedition in 1969, members of which used the screen-washing



technique. Their work continued for several years, and the material, now housed in the Paleontological Institute in Moscow, consists of several hundred specimens. As is usual with materials acquired by using the screen-washing technique, the collection consists mostly of isolated teeth and jaws with teeth, as well as fragments of skulls and upper dentitions. The late Mongolian paleontologist Demberlyin Dashzeveg, a specialist on Cretaceous and Paleocene mammals, also collected at this locality and assembled an important collection of mammals, now part of

the treasures of the Geological Institute of the Mongolian Academy of Sciences in Ulaanbaatar.

The first report on Höövör multituberculates was published by the late Russian paleontologist Boris A. Trofimov (1980). In this brief paper he named and described the peculiar, highly specialized multituberculate *Arginbaatar dimitrievae*, together with new "symmetrodontans."

Because the Höövör multituberculates of the PIN and Geological Institute collections complement each other, Boris Trofimov and Demberlyin Dashzeveg decided to describe the two collections together and invited me to collaborate with them. There were 68 multituberculate specimens in the two collections. I borrowed these specimens and returned to Warsaw. When I went to Paris in 1982 (see below), I took the collection with me. During my two-year stay in Paris I worked primarily on the skull structure of multituberculates, but I also spent some time completing the paper on enamel microstructure of Late Cretaceous multituberculates with Gisle Fosse (Fosse et al. 1985) and on Höövör multituberculates. After my return to Poland in the fall of 1984, the descriptions and comparisons were finalized, and our paper on the Höövör multituberculates was published in *Acta Palaeontologica Polonica* (Kielan-Jaworowska, Dashzeveg, and Trofimov 1987b).

The Höövör multituberculates include numerous specimens of *Arginbaatar*, assigned now to a separate superfamily Arginbaataroidea. *Arginbaatar* has three lower premolars, of which the p4 is very large and highly vaulted. I noted that the p4 rotated during ontogeny over the smaller p3, which became resorbed. From an evolutionary point of view, the more interesting genus is *Eobaatar* (for which the family Eobaataridae was erected), represented by the two species *E. magnus* and *E. minor*. *Eobaatar* is similar to members of the Plagiaulacidae in having a rectangular (in lateral view) p4, but it differs from them in having a single posterolabial cusp, rather than a row of posterobasal cusps, and a smaller p3 and p2. Early Cretaceous multituberculates have been found in recent years in Japan, increasing our knowledge of this poorly known period of multituberculate evolution. The strongly specialized *Arginbaatar* or its relatives, which occur in Mongolia, have not been found in Japan. The most active Japanese multituberculate specialist was Nao Kusuhashi (Figure 3.5C), who, after earning his Ph.D. in Japan, received a postdoctoral fellowship at IVPP in Beijing. In collaboration with Chinese colleagues, he also described Early Cretaceous multituberculates from China (Kusuhashi et al. 2010).

In our Höövör multituberculate paper (Kielan-Jaworowska et al. 1987b), in addition to Asian species we published several SEM micrographs of plagiaulacidan multituberculates from the Purbeck Limestone Group of England for comparison with the Mongolian material. We made SEM micrographs of the casts of the specimens housed in the Natural History Museum in London, kindly sent to me by Jeremy Hooker from that museum.

10.3. Reconstructed skulls and heads of three multituberculates of different age. A. *Paulchoffatia* from the Kimmeridgian of Portugal. B. *Plagiaulax* from the Purbeck (regarded now as the earliest Cretaceous) of Great Britain (also known from Morrison Formation). C. *Nemegtbaatar* from the Late Cretaceous of the Gobi Desert (Mongolia). Note changes in the dentition, especially increasing the size of p4.

All original drawings by Oscar Sanisidro. Skulls modified from various sources; heads original artwork by Oscar Sanisidro.

Later on, during my stay in Norway (1987–1995) as a professor of paleontology at the University of Oslo, I had an opportunity to work with Paul C. Ensom, at that time with the Dorset County Museum (later at the Natural History Museum in London), on the multituberculates from the Purbeck Limestone Group, based on a collection of isolated teeth he had collected from several localities in the Dorset area. Paul had excavated several tons of matrix, which he screen washed in the Dorset Museum using a processing machine constructed by David Ward. Ensom recovered a great number of isolated teeth belonging to various early mammals. He described the multituberculates with me (Kielan-Jaworowksa and Ensom 1992, 1994) and other mammals with me and Denise Sigogneau-Russell (see Sigogneau-Russell and Kielan-Jaworowska 2002). Of the several papers that I published with Paul, the two most important were by Kielan-Jaworowska and Ensom (1992, 1994). In the first of these we also redescribed some of the Purbeck mammals housed in the Natural History Museum in London. In the second, we established a new monotypic family of multituberculates, the Albionbaatariidae for *Albionbaatar denisae*, a tiny multicusped taxon, based on several isolated teeth which we assigned to Plagiaulacoidea and which Hahn and Hahn (2006) reassigned to Paulchoffatioidea.

Early Cretaceous multituberculates are also known from the famous Jehol Biota of China, represented there by the single species *Sinobaatar lingyuaensis* (assigned to the Eobaataridae), represented by the holotype alone, consisting of a skull with dentaries and parts of the postcranial skeleton. Kielan-Jaworowska and Hurum (2001), Kielan-Jaworowska et al. (2004), and Hahn and Hahn (2006) discussed the relationships among the members of the "Plagiaulacida." The question that arises is which group (family) is most plesiomorphic (primitive). The "Plagiaulacida" were regarded by Kielan-Jaworowska et al. (2004) as a grade that now consists of nine families grouped into four superfamilies. I follow Hahn and Hahn (2006) in excluding the Hahnodontidae from Multituberculata and assigning them to the Haramiyida.

The two families Allodontidae and Paulchoffatiidae are candidates for being the most primitive "plagiaulacidans." It is difficult to decide which family is more plesiomorphic since different combinations of primitive and derived features characterize both. The Allodontidae retain a plesiomorphic structure of the lower molars, with two rows of well-separated cusps, and smooth enamel (lack of grooves and ribbing on the molars). Both the Allodontidae and Paulchoffatiidae retain five upper and four lower premolars; Allodontidae are, however, more advanced than members of the paulchoffatiids in the structure of the lower premolars and in having a larger angle between the tooth row and the longitudinal axis of the dentary (as seen in dorsal view), which is very low (7°) in at least one paulchoffatiid genus, *Paulchoffatia*, as discussed earlier and illustrated in Figure 10.2B. The Paulchoffatiidae appear in the Kimmeridgian, while the Allodontidae are younger, appearing in the late Tithonian. As demonstrated by Gerhard Hahn, beginning with his 1969 monograph,

the Paulchoffatiidae are a blind line. They did not apparently give rise to other multituberculates.

More similar to the Cimolodonta are the Plagiaulacidae, which are ancestral to the Eobaataridae, the latter being very close to the ancestors of the Cimolodonta. Origins of the Plagiaulacidae are, however, uncertain. Kielan-Jaworowska and Hurum (2001), followed by Kielan-Jaworowska et al. (2004), argue that the Plagiaulacidae share more characters with the Paulchoffatiidae than with the Allodontidae, but the intermediate forms are yet to be found.

The most important Early Cretaceous locality yielding mammals are the Jehol Biota from northeastern China, which yielded unusually well preserved specimens of early mammals, preserved often with soft parts. The only multituberculate so far found in the Jehol Biota is *Sinobaatar lingyuanensis*, described by Hu and Wang (2002) and assigned to the Eobaataridae.

Late Cretaceous Multituberculates from the Gobi Desert

The Late Cretaceous multituberculate mammals that we collected first during the 1964 and 1965 Polish-Mongolian Expeditions to the Gobi Desert, for the most part, consisted of the rostral parts of skulls, often associated with partial dentaries. Some almost complete skulls associated with postcranial skeleton have also been found (see Plate $4B_1$–B_2). In 1965 my late friend Halszka Osmólska, during our search at Bayan Zag at the locality that we called the Ruins, discovered a complete skull of a mammal, associated with both lower jaws, and small fragments of the postcranial skeleton (see below).

In 1967 two technical assistants of the Institute of Paleobiology, Maciej Kuczyński and Wojciech Skarżyński, visited Mongolia under the terms of an agreement on the exchange between our two academies. Accompanied by Mongolian geologist Ceveg, they spent 2 weeks at Bayan Zag searching for mammals and lizards on the surface of the outcrops. They brought back to Warsaw several specimens, including an exquisitely preserved skull of a juvenile multituberculate lacking the dentaries, of which only parts of the zygomatic arches were missing. In 1970, I briefly described these two well-preserved skulls, along with some other less-complete multituberculate material, and designated the one from the Ruins *Sloanbaatar mirabilis*, in honor of Robert E. Sloan, from the University of Minnesota in Minneapolis, a known multituberculate specialist. The other I named *Kamptobaatar kuczynskii*, after Maciej Kuczyński, who found the holotype specimen and skillfully prepared it, removing it delicately from the matrix.

During the summers of 1970 and 1971, we conducted large-scale Polish-Mongolian expeditions in Mongolia, during which time we assembled a large collection of Late Cretaceous mammals from the Baruungoyot Formation and its stratigraphic equivalents – from the localities of Khulsan and Nemegt in the Nemegt Valley and in Hermiin Tsav. The age of the Baruungoyot Formation, which conformably underlies the Nemegt

Formation, has been tentatively assigned as late Campanian (Gradziński et al. 1977). It might be younger than the Djadokhta Formation, which may be of early Campanian age (Kielan-Jaworowska 1974).

In 1982, as mentioned in the introduction, my husband Zbigniew received an invitation from the Centre d'Etudes Nucléaires in Fontenay-aux-Roses near Paris to come for a year to study the history of the contamination of the French population by heavy metals and radioactive elements. I took a 1-year leave from the Institute of Paleobiology and joined him. We prolonged our stay in Paris until August 1984.

In Paris, the director of the Institute de Paléontologie at the Museum National d'Histoire Naturelle, my colleague and friend Philippe Taquet, offered me an office and facilities, including technical help. As Cécile Poplin (Plate 5C, on the right) from the same institute had used the Jung microtome to study the cranial anatomy of fossil fishes for her Ph.D. thesis, I invited her to join me in my work. I knew that Armand de Ricqlès (Plate 5D) at the University of Paris VII had used the Jung microtome, a special German microtome originally designed as a machine for cutting metals, for cutting undecalcified fossil bones. De Ricqlès, a world-famous paleohistologist, conducted histological studies of the bones of dinosaurs and other fossil vertebrates, including early mammals. He kindly allowed me to use his microtome for sectioning two multituberculate skulls in his laboratory and offered the help of his technical assistant, Françoise Alizard (Plate 5B). This sectioning helped a lot in reconstructing cranial vessels and nerves and in examining the internal cranial anatomy of the multituberculates being studied.

The experience of Cecile Poplin in this work was invaluable. We embedded the two well-preserved multituberculate skulls from the Upper Cretaceous of the Gobi Desert belonging to *Nemegtbaatar gobiensis* (Plate 5A) and *Chulsanbaatar vulgaris* in epoxy resin, and I spent three full months at Armand's laboratory cutting the skulls. The *Nemegtbaatar* skull yielded 1370 sections, each 25 µm thick. From the smaller *Chulsanbaatar* skull (not figured here), the preserved part of which measured 17.7 mm in length, I obtained 885 sections 20 µm thick.

Further work on the cut skull of *Nemegtbaatar* included photographing each fifth section and magnifying it 16 times. The enlarged photographs were redrawn on transparent thin paper, on which I marked the corresponding elements in the same color. On this basis of each drawing, we made a wax plate 2 mm thick, cut according to the drawing. These plates glued together made the model of the endocranial cavity. This model illustrated the structure of the endocranial cavity, housing the brain, cranial nerves, and vessels of the multituberculate skull (Plate 5C).

For interpreting the structures of the model, I needed the help of an anatomist who had expertise in the skull structure of modern mammals and its embryological development. I invited Bob Presley from the Department of Anatomy, University of Cardiff, to work with us, and he accepted. During my stay in Paris, Bob visited us three times, and once Cécile traveled to Cardiff. Based upon cranial sections of the two

skulls, as well as on other multituberculate skulls from the Gobi Desert and isolated petrosals from the Bug Creek Formation in Montana, we published a monograph (Kielan-Jaworowska, Presley, and Poplin 1986). In our monograph, we did not include all available information on the skull structure contained in those serial sections. So, subsequently, during my stay in Norway (see below) as a professor at the University of Oslo, I handed over the sections to my Ph.D. student Jørn H. Hurum (Figure 1.4C), who described the osteology of these skulls in full detail in his Ph.D. thesis.

In 1930, the great British anatomist Edwin Stephen Goodrich (1868–1946) published an important book in which he drew transverse sections of skulls of reptiles and mammals in the orbitotemporal region (facsimile edition, Goodrich 1986). This drawing demonstrated that an extracranial space in reptiles containing some nerves and vessels, the cavum epiptericum, in mammals had been incorporated into the cranial cavity, being separated from it only by a membrane wall. In multituberculates, in the posterior part of the brain cavity the cavum epiptericum is separated from the primitive braincase by a thick bony wall, unlike the membranous wall of other mammals (Plate 5B).

Beginning in 1990, new exploration of the Mongolian part of the Gobi Desert began, this time conducted by researchers from the Mongolian Academy of Sciences and the American Museum of Natural History (see chapters 1–3 for details). Of the enormous number of mammals they collected at the Late Cretaceous Ukhaa Tolgod locality in the Gobi Desert, only a part has been studied so far. The multituberculates have been described mostly by Guillermo W. Rougier, John R. Wible, and Michael J. Novacek, who in 1996 described the ear ossicles in the multituberculate *Kryptobaatar*. Ear ossicles are rarely found as fossils. Rougier, Novacek, and Dashzeveg (1997) described a new multituberculate genus *Tombaatar*, while Wible and Rougier (2000) redescribed the skull of *Kryptobaatar* based on more complete material than was previously known from the Djadokhta Formation.

At the same time, Novacek, Rougier, and Wible, working with Jim Hopson, now professor emeritus at the University of Chicago, reconstructed the braincase and cranial vasculature of cynodonts and several groups of early mammals, including multituberculates, and published in different configurations several papers on this subject (see, for example, Wible et al. 2007, 2009).

Description of all the collections from Ukhaa Tolgod, housed temporarily in the American Museum of Natural History in New York, will certainly increase our knowledge of multituberculate anatomy and their true relationships to other mammals. The fossils from the Chinese part of the Gobi Desert (from Inner Mongolia) have not been described to the same extent of those from the Mongolian Republic. In the early 1990s, reports were published on Cretaceous mammals found by the Sino-Canadian Dinosaur Expedition in the Bayan Mandahu region of northern China, close to the boundary with Mongolia (see Jerzykiewicz et al. [1993] for a

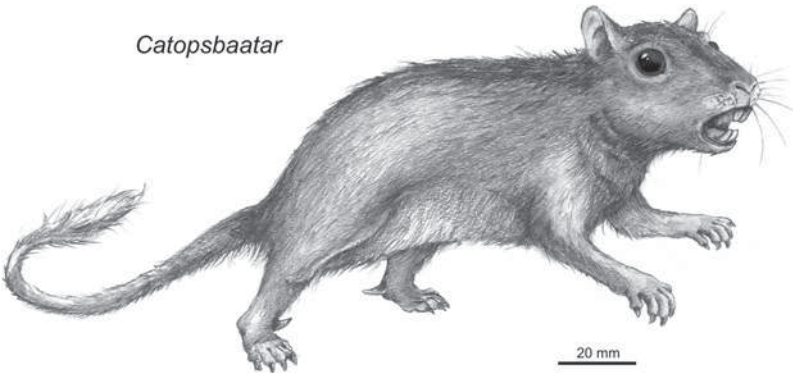
review). These reported mammals, presumably of an age equivalent to that of the Djadokhta Formation, have not as yet been described. The Belgian paleontologist Thierry Smith, in cooperation with Chinese colleagues Dian-Yong Guo and Yan Sun (2001), described two skulls of a new species of *Kryptobaatar*, designated *Kryptobaatar mandahuensis*, housed at the Inner Mongolian Museum in Hohhot in China, which came from the Bayan Mandahu red beds and were found by members of the Sino-Belgian Expeditions in 1996. Other multituberculate specimens found by the same expeditions in 1995 and 1999 await description.

Important information on the evolution of Tertiary multituberculates may be found in the article by Weil and Krause (2008) – "Multituberculata," which was published as chapter 2 of the book edited by Janis et al., *Evolution of Tertiary Mammals of North America*, volume 2.

The Multituberculate Postcranial Skeleton

Postcranial skeletons of early mammals are rarely preserved and are seldom found articulated as in life. However, during the 1965 Polish-Mongolian Expedition, at the Bayan Zag locality I discovered the skull of the most common Late Cretaceous Gobi Desert multituberculate, *Kryptobaatar dashzevegi*, associated with a large part of the postcranial skeleton, which consisted of a fragmentary scapula, part of the lumbar and caudal vertebrae, and a complete pelvis in anatomical arrangement with left and right, nearly complete hind limbs (Plate $4B_1$). While preparing the pelvis, I found the epipubic (marsupial) bones, so well known in marsupials and monotremes. They were preserved in situ on both sides. These bones were previously unknown in multituberculates, and in 1969 I published a short note about this find in *Nature* (Kielan-Jaworowska 1969a). Many years later, working with my former student Jørn H. Hurum on the postcranial skeleton of a relatively large multituberculate from the Gobi Desert, *Catopsbaatar* (Figure 10.4), we discovered in its tarsus the presence of the os calcaris, related probably to a venomous spur unknown previously in multituberculates (Hurum and Kielan-Jaworowska 2008). I discuss this issue in chapter 15; see also Hurum et al. (2006).

Isolated bones of the multituberculate postcranial skeleton had been described beginning with nineteenth-century papers by Cope and Marsh. During the 1970 and 1971 expeditions, we found several almost complete skeletons in the Barungoyot Formation and its equivalents (for example, see Plate 5E), but preparation of this material required time. The first work describing an entire multituberculate skeleton is the monograph by Krause and Jenkins, published in 1983, which includes a description of a fairly complete skeleton of the Paleocene *Ptilodus*, as well as a comprehensive review of the literature on multituberculate postcranial material. While reading the literature on postcranial anatomy of extant mammals, I came across papers by Petr P. Gambaryan (Figure 10.1D), an Armenian Russian zoologist who lived for many years in St. Petersburg, and I was impressed by their excellence. I decided that in order to describe the



10.4. Reconstruction of *Catopsbaatar catopsaloides* ready for an attack.

From Kielan-Jaworowska and Hurum (2006). Artwork by Bogusłasw Waksymundzki, emended by Aleksandra Hołda-Michalska.

postcranial skeleton of multituberculates, I would need to collaborate with a zoologist who was familiar with the skeletons and musculature of small present-day mammals. So I made contact with Gambaryan ("PP" to his friends), and in 1979, he came to Warsaw for a month-long visit. This was how our work together began.

However, political and personal events intervened. In December 1980 martial law was imposed in Poland, and in 1982 I joined my husband for a two-year stay in Paris (see above). This delayed our cooperation. During the years 1984–1987, the financial situation for Polish science was far from flourishing, and I could not secure financial support for inviting PP to Warsaw. In 1987 I got a position as professor of paleontology at the University of Oslo (Figure 1.4), and my husband and I spent the next 8 years working in Norway. Here our financial situation was much better. I received grants from the Norwegian Science Foundation, which enabled me to invite Petr P. Gambaryan to Oslo. During my stay in Oslo, PP visited me five times, beginning in 1991, twice accompanied by his late wife Anna, who helped us in technical work. Once I visited them in St. Petersburg.

Petr P. Gambaryan was born in 1925 in Paris. In the second half of the 1920s, the Soviet government encouraged his parents to return to the Soviet Union, and in 1929 the Gambaryan family arrived in Yerevan. Petr studied at the University of Yerevan, and in 1949 he was granted the degree of Candidat of Sciences (equivalent to a Ph.D.) on the basis of a thesis devoted to burrowing mammals. In 1961 he moved to St. Petersburg, where he got a position as an assistant professor and, subsequently, full professor at the Institute of Zoology of the Russian Academy of Sciences. He is the author of the book, originally published in Russian and translated into English, *How Mammals Run* (1974) and more than 100 scientific papers.

At the end of 1993, we submitted our monograph (Kielan-Jaworowska and Gambaryan 1994) to the Scandinavian series Fossils and Strata. This monograph described the postcranial anatomy of several partial skeletons of Late Cretaceous multituberculates from the Mongolian part of the Gobi Desert, reconstructed their musculature, and interpreted these animals as having a sprawling posture. We based our

conclusions mostly on the structure of the pelvic girdle and hind limbs, demonstrating that in multituberculates the pelvis was relatively deeper than the pelvis of extant placental mammals of similar size, which have parasagittal posture. Another character suggestive of a sprawling stance was the structure of the tibia. In multituberculates, the mediolateral diameter of the tibia is greater than the craniocaudal, while in animals with parasagittal limbs these proportions are just the opposite (Kummer 1959). The third character supporting a sprawling stance was the position of the fifth metatarsal, which articulates with the peroneal groove on the calcaneus and is not aligned with the axis of the tuber calcanei. In mammals with parasagittal limbs, all the metatarsals are aligned with the axis of the tuber calcanei.

Our conclusions supporting a sprawling stance for multituberculates were questioned, first by Sereno and McKenna in a paper published in *Nature* (1995), and more recently by Sereno (2006) in a chapter of the book *Amniote Paleobiology*, published in honor of James A. Hopson. Sereno and McKenna advocated a parasagittal posture for multituberculate mammals, based on an excellently preserved shoulder girdle and forelimbs found of the Late Cretaceous *Kryptobaatar* from the Gobi Desert. The authors, however, neglected the evidence from the hind limbs and misinterpreted the structure of the multituberculate humerus. Sereno also challenged the conclusions of Hu et al. (1998), concerning the sprawling forelimb posture in the "symmetrodontan" *Zhangheotherium*, and of Ji et al. (1999), related to such posture in the eutriconodontan *Jeholodens*. A reconstruction of *Zhangheotherium quiquecuspidens* by Mark Klingler appears in the beautiful book *The Jehol Biota* edited by Chang et al. (2003: 157).

After the paper by Sereno and McKenna (1995) was published, I returned to Poland and again invited Petr P. Gambaryan to Warsaw. During his stay we responded to Sereno and McKenna's paper. In our response (Gambaryan and Kielan-Jaworowska 1997), we argued, among other things, that in all known multituberculate humeri, the distal extremity has a condylar structure characteristic of vertebrates with a primarily sprawling stance, lacking any trace of a trochlea, a feature characteristic of mammals with parasagittal stance. I discuss very important taphonomic evidence on the sprawling posture in multituberculates in chapter 15.

Among the earliest mammals, the tarsal spur has not been found as yet in the Morganucodonta, the tarsus of which is only incompletely known (Jenkins and Parrington 1976). Similarly, the spur is not known in several other poorly known groups such as the haramiyidans and gondwanatherians, as none of the postcranial skeletons for those groups has been discovered. Kielan-Jaworowska and Hurum (2006) hypothesized that mammaliaforms originally had a sprawling stance and probably a spur, which played an important role as a defensive weapon in a world inhabited by dinosaurs and other serious predators (of course, only small dinosaurs could feed on tiny mammaliamorphs). The parasagittal stance appears to have been acquired in the evolution of mammals only in

tribosphenidans. In the only known skeletons of this group – for example, those from the Late Cretaceous of the Gobi Desert – no spur has been found. It remains an open question whether the spur disappeared in tribosphenidan mammals as a consequence of their acquisition of a parasagittal stance. Perhaps the greater ability to escape predation with agility and speed with an upright stance meant that there was no longer selection for preserving a spur.

After our postcranial skeleton monograph, Petr Gambaryan and I published a paper on the reconstruction of the masticatory musculature of multituberculates (Gambaryan and Kielan-Jaworowska 1995). In this paper (see especially figure 11), we demonstrated, among other things, that the multituberculates, which are unique among mammals in having a backward power stroke (as demonstrated by Gingerich 1977), are characterized by a more anterior insertion of the masticatory muscles than any other group of mammals, even including rodents. This is important and might have implications for interpretation of haramiyidan and multituberculate relationships, as discussed in chapter 6.

Gondwanatherians

MAMMALIA *INCERTAE SEDIS*: SUBORDER GONDWANATHERIA MONES, 1987 (KRAUSE AND BONAPARTE, 1990)

Gondwanatherians are a group of poorly known, small mammals, found exclusively in the Late Cretaceous and Early Paleocene of Gondwana. Bonaparte (1986: figure 10.15), described the m2 of a brachyodont genus dubbed *Ferugliotherium* from the Late Cretaceous of Southern Patagonia, Argentina, and erected for it the new family Ferugliotheriidae.

The two South American genera of the family Sudamericidae – the Late Cretaceous *Gondwanatherium* and the Paleocene *Sudamerica* – were originally assigned to the Edentata. However, Krause and Bonaparte (1990, 1993) set up the order Gondwanatheria, placing it within Multituberculata. The multituberculate affinity of the Gondwanatheria was challenged by Pascual et al. (1999), who described a dentary of *Sudamerica* with two molariform, hypsodont teeth and two more molar loci posterior to them (Figure 10.5A). The question of affinities of the Gondwanatheria remains open until more material is found.

José F. Bonaparte

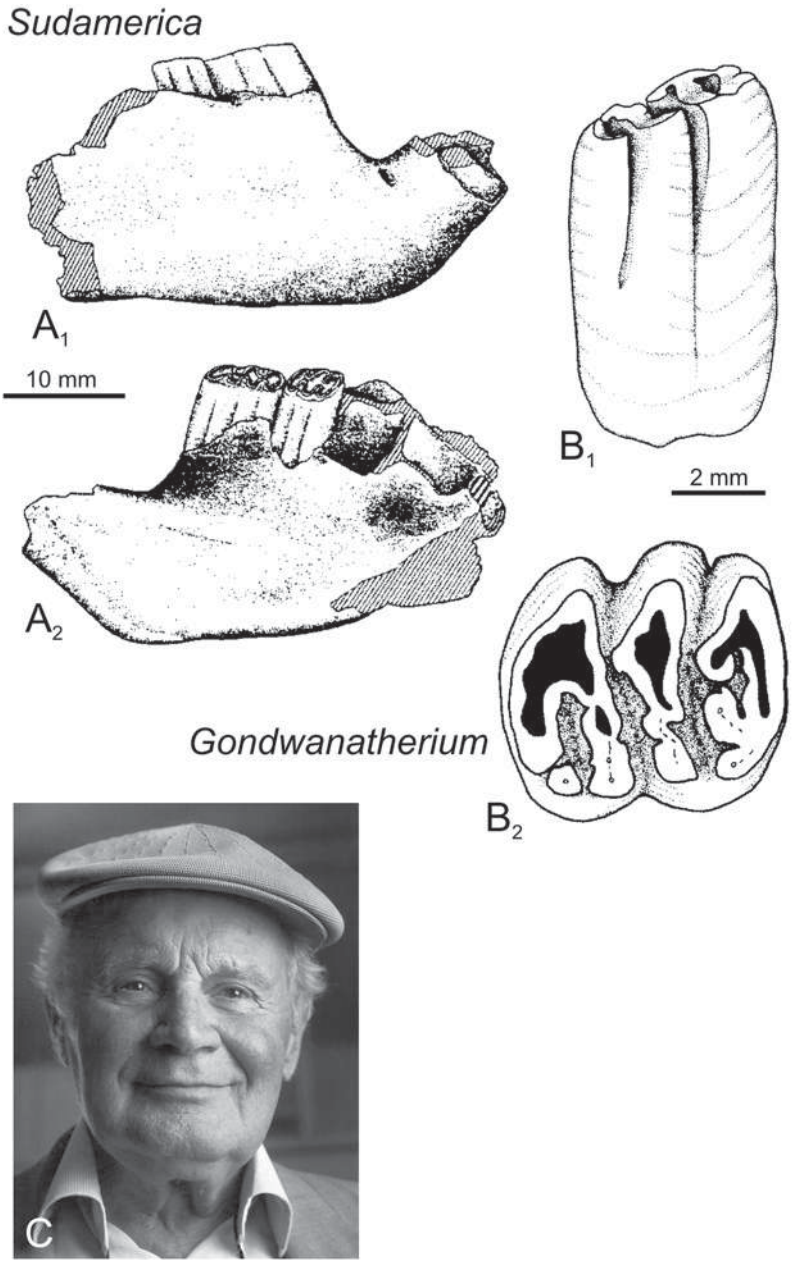
José F. Bonaparte (Figure 10.5C) was born in Argentina in 1928. He had no formal education, but gained recognition for his especially prolific discoveries in paleontology. In 1974 he was granted the title of doctor honoris causa at the National University of Tucumán in Argentina. He spent two seasons at Harvard University, in Cambridge, Massachusetts, studying under Professors A. S. Romer and A. W. Crompton. Between 1963 and 2003 he worked as a qualified scientist at the National Research Council of Argentina. In 1975 José was appointed full professor of vertebrate palaeontology at National University of Tucumán and he

worked there until 1982. Bonaparte published 150 scientific articles on Mesozoic continental vertebrates from South America and four books on this subject. He and his assistants discovered and published on the Late Cretaceous assemblage of nontribosphenic mammals from Los Alamitos Formation in Argentina. They also found and described several skulls and bones of the postcranial skeleton of the Early Cretaceous pretribosphenic mammal *Vincelestes neuquenianus*. Bonaparte discovered and described many advanced cynodonts and archosaurs from the Triassic, and several dinosaurs from the Jurassic and Cretaceous of Argentina and Brazil. He recognized the endemic character of the Laurasian and Gondwanan continental tetrapods after long isolation caused by the Tethys Sea during most of the Jurassic and Cretaceous. His last research dealt with small, derived cynodonts from the Late Triassic of Southern Brazil, which show transitional anatomical characters between mammal-like reptiles and the Morganucodonta.

The Ferugliotheriidae is a poorly known family of Gondwanatheria, represented by isolated fragmentary upper and lower incisors (tentatively assigned), lower molars, and M1. The m1 and m2 show similar occlusal morphology and are apparently congeneric (belonging to the same genus). They share with some Multituberculata (e.g., Plagiaulacidae, Eobaataridae, and the *Paracimexomys* group), a tendency of molar cusps to coalesce in peripheral aspect and ornamentation of grooves and pits on the molars. They share with numerous multituberculates – but also with numerous eutherian mammals – lower incisors with limited enamel bands. They differ from the Sudamericidae in having brachyodont, rather than hypsodont, molars, but they share with them the occlusal morphology of the molars and other characters of the suborder.

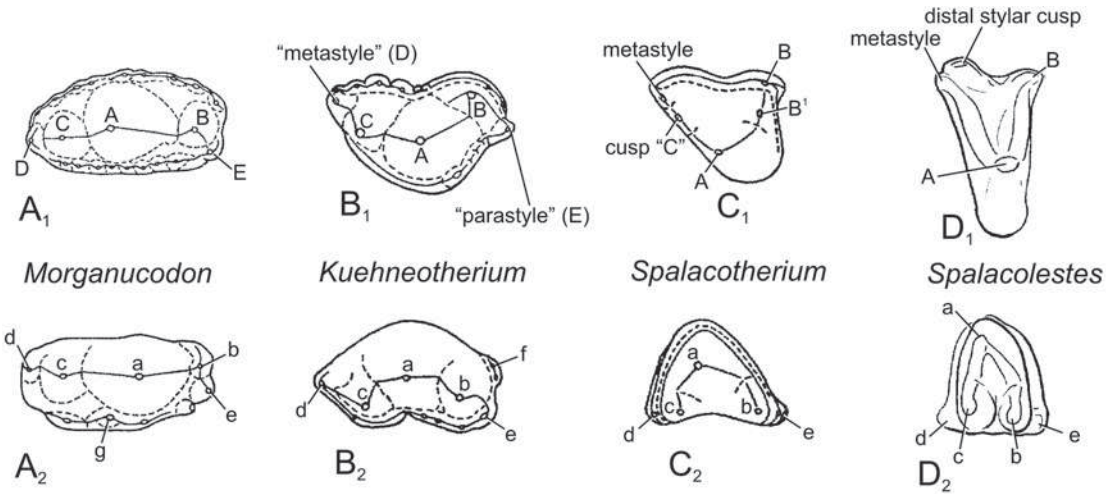
The second family of Gondwanatheria – the Sudamericidae erected by Scillato-Yané and Pascual (1984), differs from the Ferugliotheriidae in being much larger and in possessing large, hypsodont molars, each supported by a massive root covered with cement. The coronal pattern of ridges and furrows on molars is generally more complex than in Ferugliotheriidae. The lifestyle of *Sudamerica* may have been semiaquatic and or possibly burrowing, similar to that of living beavers (Koenigsvald et al. 1999).

Kielan-Jaworowska et al. (2004: 517) wrote that "we accept the assignment of Pascual et al. (1999), but we exclude from the Ferugliotheriidae the dentary with the blade-like p4 and upper premolars of multituberculate pattern, tentatively assigned, respectively by Kielan-Jaworowska and Bonaparte (1996) and by Krause et al. (1992: figure 2C–F) to *Ferugliotherium*." Kielan-Jaworowska et al. (2004) described these fossils under Multituberculata *incertae sedis* and figured them in their figure 8.44. I follow this opinion.



10.5. Representatives of Gondwanatheria. A. *Sudamerica ameghinoi,* right dentary bearing the root of the incisor, separated by a large diastema from two molariform cheek teeth, and alveoli for two cheek teeth distally, in labial (A_1) and lingual (A_2) views. B. *Gondwanatherium patagonicum,* postcanine tooth, presumed labial (B_1) and occlusal (B_2) view (in B_2 presumed labial side down). C. Jose Bonaparte.

A, B. From Kielan-Jaworowska et al. (2004: figure 14.2), emended. C. Courtesy of José Bonaparte.



11.1. A–D. Composite drawings showing the occlusal surfaces of the upper and lower molar teeth in *Morganucodon, Kuehneotherium, Spalacotherium,* and *Spalacolestes.* Upper (A_1–D_1) and lower (A_2–D_2) teeth.

From Kielan-Jaworowska et al. (2004: figure 9.1, emended).

"Symmetrodontans" 11

IN JURASSIC AND EARLY CRETACEOUS ROCKS ONE MAY FIND MINUTE mammal jaws with teeth, both upper and lower, as well as the isolated molar teeth of the same type. These teeth differ from those of cynodonts and from the primitive mammals earlier referred to as "triconodontans" (now assigned to morganucodontans and eutriconodontans; see chapter 5) in that they have three main cusps arranged not anteroposteriorly but as on angles of a triangle. In lower teeth, the medial and the highest cusp is situated lingually, and in upper teeth, labially. In lower molariform teeth of these tiny mammals the talonid is weakly developed or absent. The upper and lower molar cusps are arranged relative to one another as reversed triangles.

The Teeth and Dentaries of "Symmetrodontans"

The minute teeth of "symmetrodontans" have been known since the time of Richard Owen. As early as 1854, Owen formally described the first representative of this type of dentary with teeth, which he named *Spalacotherium*. During the first hundred years after Owen's discovery, "symmetrodontans" were further described or discussed by Richard Owen, then Othniel C. Marsh, Bryan Patterson, George G. Simpson, Percy M. Butler, J R. E. Mills, F. R. Parrington, Doris M. Kermack, Kenneth A. Kermack, Richard C. Fox, Alfred W. Crompton, and many others. Simpson (1925c, 1925b) erected for mammals of this type a new order, the "Symmetrodonta."

Until 1997 "symmetrodontan" mammals were known only from incomplete dentaries with teeth or isolated teeth. The schematic drawings of upper and lower molars in occlusal view of *Morganucodon* (figure 11.1A), with main cusps arranged in anteroposterior line, and "symmetrodontans" (figure 11.1B–D) show the differentiation of the cusp position from an obtuse angle (for example, in *Kuehneotherium* and *Spalacotherium*) to an acute angle (for example, in *Spalacolestes*). The cusps on the upper teeth are denoted with uppercase characters, and those in the lower teeth with lowercase characters, as proposed by Crompton and Jenkins (1968).

Kielan-Jaworowska et al. (2004: 343–344) offered this description of "Symmetrodontans" (emended and abbreviated):

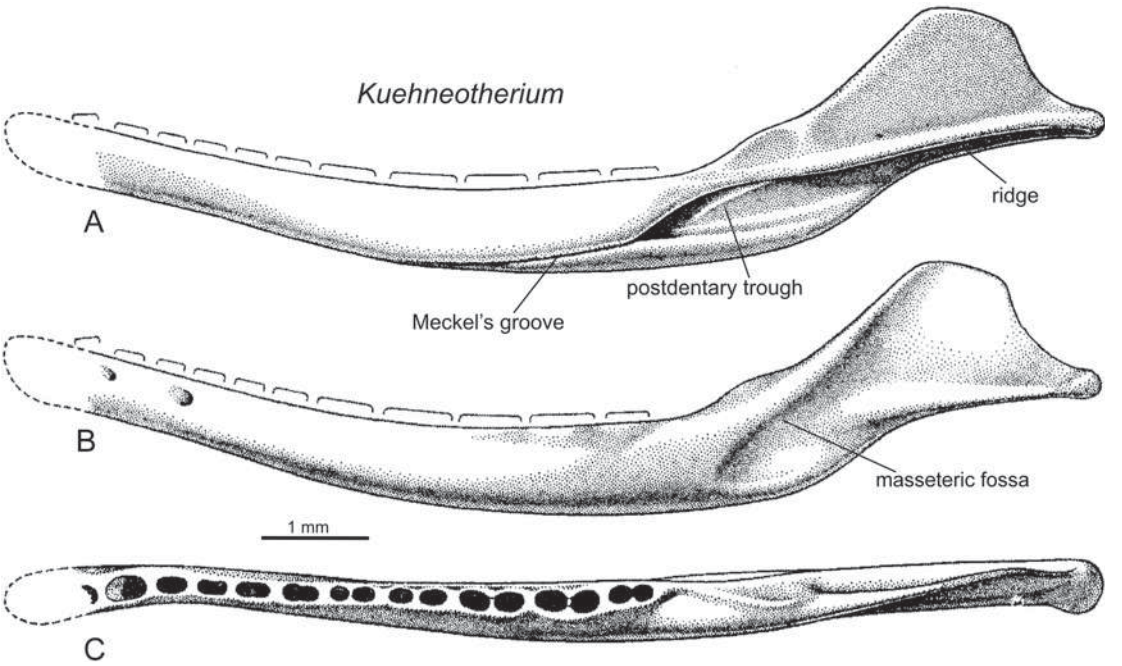
> Mostly small mammals with common possession of a reversed-triangle molar pattern, and little development of a talonid on the lower molars (plesiomorphy). Dental formula ranges as follows: Upper dentition: I3 (known at that time for *Zhangheotherium* only, see below), C1, P2–5 or

6?, M4 or 5?–7 (number of upper premolars and molars inferred from the lowers). Lower dentition: 3.1.2–5 or 6?; 4–7; canines generally small with these and anterior premolars that may be single or double-rooted; teeth at premolar loci may be retained through life or shed ontogenetically, with subsequent "plugging" of alveoli; premolars with second, permanent replacement set (diphyodont) in *Zhangheotherium*, although in alternating sequence as in *Dryolestes* and different from the sequential premolar replacement as in extant placentals. Angulation of molar cusps varies from negligible to acute; within the series, angulation generally becomes progressively more acute posteriorly. Molar cingula/cingulids may be complete, incomplete, or lacking entirely. Lower molar cusps d and e are usually present, with cusp f present in some taxa, except for the invariably tall paraconid. Dentary is long and slender, with an unfused, subhorizontal symphysis; angular process is uniformly lacking; pterygoid crest (medially) and flaring of the inferior margin of the masseteric fossa (laterally) are common but not universally present. There is a postdentary trough, overlying ridge, and scars indicative of the presence of attached postdentary elements. Meckel's groove and scars for the coronoid and/or splenial also are variable, or may be altogether absent in some taxa; cochlea of known forms is probably uncoiled.

The dentary in "symmetrodontans" is slender and lacks an angular process. A postdentary trough, an overlying ridge, and scars indicating the presence of attached postdentary elements may be present. The Meckel's groove and scars for the coronoid and/or splenial are variable in their development and expression, or may be altogether lacking in some taxa. It has been demonstrated that the "symmetrodontan" type of molars appeared iteratively many times. The category "Symmetrodonta" is not a clade, but a grade. The oldest molars with triangular arrangement of three main cusps belong to *Kuehneotherium precursoris* (figure 11.2), described by Doris M. Kermack and colleagues (1968) from the Late Triassic fissure fillings of Wales. The material includes an edentulous lower jaw (figure 11.2) and several isolated upper and lower molars. Cusps on the lower molars are higher than on the uppers, forming obtuse angles. The lower jaw of *Kuehneotherium* (figure 11.2A) is characterized by a wide postdentary trough in medial aspect, apparently housing the reptilian bones and a deep masseteric fossa in outer aspect (figure 11.2B). Figure 11.2C shows the same dentary in dorsal view with numerous alveoli for a canine and cheek teeth.

The Skulls and Skeletons of "Symmetrodontans" and the Issue of Holotheria

By 1971, the symmetrodontan skeleton was known only from *Zhangheotherium* (figure 11.3A), which shows a mosaic of primitive and derived features, including unfused ribs on postaxial cervical vertebrae, interclavicle present but with mobile clavicular joint, strong supraspinous fossa on scapula; humerus with at least 30° of torsion, lesser tubercle large relative to greater tubercle, incipient ulnar trochlea and vestigial ulnar condyle; the epipubic bones present in the pelvis. The tarsal spur, found only in the holotype of *Zhangeotherium*, has been preserved as an imprint of the



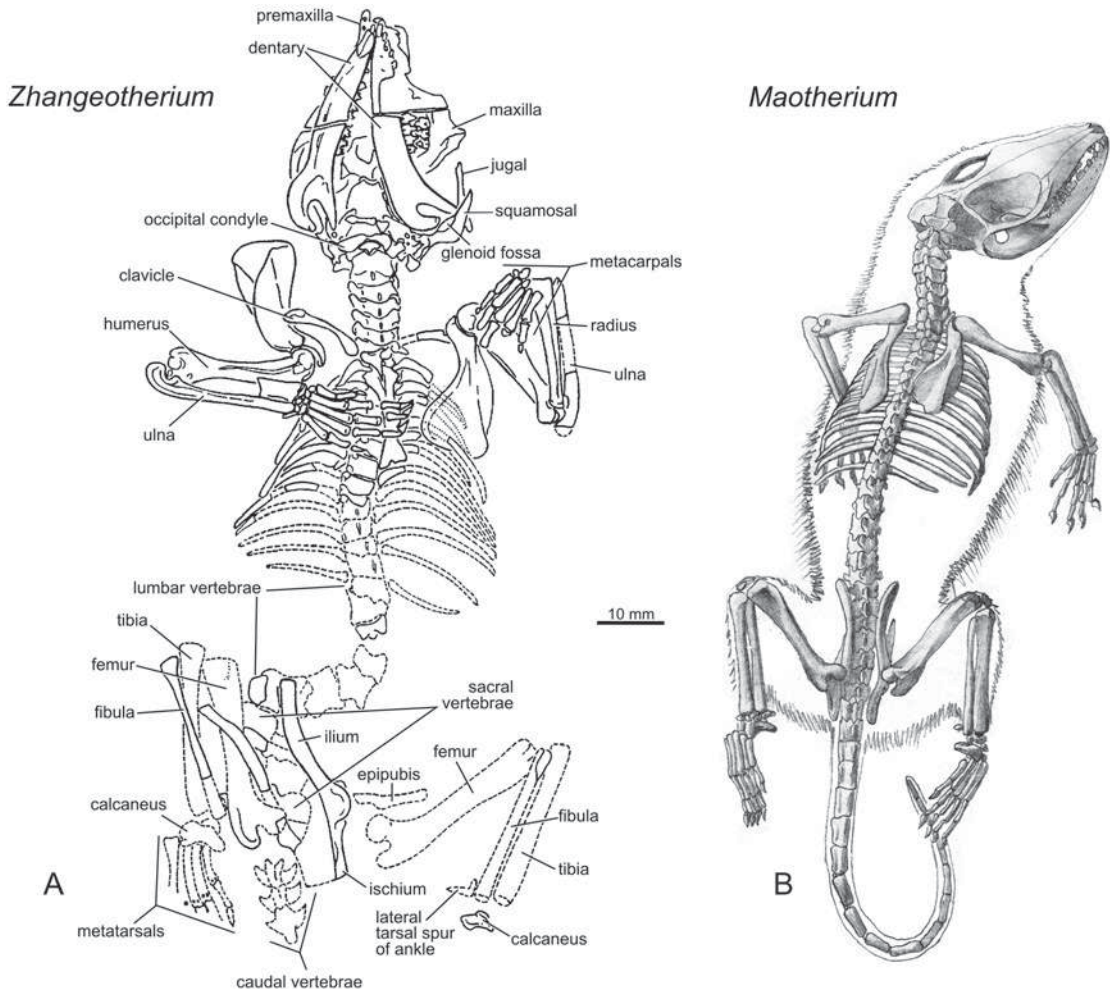
11.2. A–C Reconstruction of the right edentulous dentary of *Kuehenotherium praecursoris,* in medial view (A); the left dentary of the same, in outer (B) and dorsal (C) views.

From Kielan-Jaworowska et al. (2004: figure 9.3.A_1–A_3).

bone on the right side of the skeleton, but the bone itself has not been found (see Hurum et al. 2006: figure 7).

Until 1997, "symmetrodontans" were known only from teeth and jaw fragments. In 1997, Hu, Wang, Luo, and Li described the first "symmetrodontan" mammal preserved with a skull and almost complete postcranial skeleton, named *Zhangheotherium qinquecuspidens*. The specimen came from the Jianshangou Beds, which form the lowest lacustrine intercalation in the volcanic beds of the Yixian Formation, from Liaoning Province in northeastern China (see Chang et al. 2003). The Jianshangou beds are either of the latest Jurassic age or near the Jurassic-Cretaceous boundary.

The holotype specimen of *Zhangeotherium qinquecuspidens*, housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica in Beijing, consists of a nearly complete skeleton, dorsoventrally compressed and exposed in ventral view (figure 11.3A). The authors figured a stereophotograph of the specimen, accompanied by an explanatory drawing when first published. The authors of *Zhangeotherium* noted in the figure of the skeleton an imprint of a bone, which they identified as extratarsal spur, but they did not discuss its importance. Hurum et al. (2006: figure 7) illustrated the silicone cast of the tarsus of the holotype specimen of *Zhangheotherium quinquecuspidens*, which has an L-shaped structure. In the other specimen of *Zhangheotherium* housed in IVPP and described by Luo and Ji (2005), no trace of extratarsal spur has been preserved. It cannot be excluded that this other specimen belongs to a female, which in extant monotremes does not have a spur.



11.3. A. The skeleton of *Zhangeotherium quinquecuspidens,* exposed in ventral view, from the Jianshangou Beds, Liaoning Province, northeastern China. B. *Maotherium sinense* Rougier, Ji, and Novacek, 2003, from the Yixian Formation, reconstruction of the skeleton in dorsal view, showing the outline of the fur.

A. Modified from Hu et al. (1997), by Kielan-Jaworowska et al. (2004: figure 9.2) and redrawn from the latter.
B. Modified from Rougier et al. (2003).

The next new report on the structure of "symmetrodontans" was by Richard L. Cifelli, who published (in cooperation with various colleagues, in particular with Scott K. Madsen from Dinosaur National Monument in Jensen, Utah) a series of papers on Early and Late Cretaceous "symmetrodontans" recovered from Utah. Possibly the most important paper is by Cifelli and Madsen (1999), in which the authors established a new genus *Spalacolestes*, with two new species, and a new species of the genus *Spalacotheridium*.

The next skeleton, named *Maotherium sinense*, was discovered four years later in 2003 and reported by Rougier, Ji, and Novacek in *Acta Geologica Sinica* (2003). The specimen (figure 11.3B) was discovered in the same Yixian Formation, as was *Zhangheotherium*, and assigned to a new family, Zhangheotheriidae, erected by Rougier et al. in the same paper. *Maotherium* differs from *Zhangheotherium* in its state of preservation, being completely covered with fur.

Rougier et al. (2003) diagnosed the Zhangheotheriidae as follows:

11.4. *Akidolestes cifellii,* set up by Li and Luo (2006), from the Yixian Formation of northeastern China. A. Reconstruction of the skeleton in dorsal view, with outline of the fur. B. Life reconstruction of the animal in dorsal view.

Original artwork by Oscar Sanisidro.

Zhangheotheriids (including *Zhangheotherium* and *Maotherium*) are medium–sized symmetrodonts. Their last upper and lower premolars are molariform. They have at least five cusps forming a very broad angle, unlike the more acute trigon/trigonid of the molars. The upper canines are double rooted, reduced in size and not trenchant. The upper molariforms and last premolar have a well-developed, cuspidate, lingual cingulum in *Maotherium* but shorter in *Zhangheotherium.* The coronoid process in *Maotherium sinense* (see Rougier et al. 2003) is elongate and narrow, inclining posteriorly, and slightly downwards; the condylar process is long and dorsally directed, separated from the coronoid by a deep notch.

The next important contribution on "symmetrodontans" involved yet another discovery from Northeastern China and came again from Yao-Ming Hu, this time with R. C. Fox, Y.-Q Wang, and C.-K. Li as co-authors (2005a). The authors set up a new genus and species of an acute-angled spalacotheriid symmetrodontan, *Heishanlestes changi* (not figured in this volume), assigning it to a specialized subfamily Spalacolestinae, known previously only from North America. Knowledge of the anatomy of symmetrodontans and their interrelationships increased considerably as a result of these discoveries, but several questions remain concerning the relationships of the "symmetrodontans" to other early mammals.

The third fairly complete skeleton of a "symmetrodontan" from the Jehol Biota of China belongs to the genus *Akidolestes* (figure 11.4), set up by Li and Luo (2006).

Some Problems of Classification of the "Symmetrodontans" and Their Paleobiology

After Simpson (1925c) established the order Symmetrodonta, numerous authors followed him, tacitly accepting that *Kuehneotherium* was the oldest-known "symmetrodontan" and consequently seemed to have accepted the possible monophyly of the "Symmetrodonta" (for example, Crompton and Jenkins 1968; Crompton 1971; Cassiliano and Clemens 1979; Rowe 1988, 1993; and McKenna and Bell 1997). Hopson (1994) informally introduced the term Holotheria to replace the old term "Theria" *sensu lato*, the largest clade of mammals, characterized by molars with a reversed triangle molar pattern. The next year Wible et al. (1995) formalized the term Holotheria as a clade to include the last common ancestor of *Kuehneotherium*, living Theria, and all descendants.

Luo et al. (2002) argued that obtuse-angle symmetrodontans were paraphyletic. I agree, based on my own experience showing that the molars with obtuse-angle cusp pattern might have originated from the eutriconodontans (in addition to the origin from the morganucodontans) several times independently. When Demberlyin Dashzeveg and I described the Early Cretaceous amphilestid "triconodontans" from Mongolia, we noted that the main cusps in the upper molars in two species of *Gobiconodon*—for example, M3–M5 of *Gobiconodon hoburensis*—reflected an incipient triangulation, while the cusps in lower molars were aligned (Kielan-Jaworowska and Dashzeveg 1998: figure 11). In contrast, in most "symmetrodontans" the cusps in both upper and lower molars are triangulated. The "symmetrodontan" species from Mongolia *Gobiotheriodon* was subsequently revised by Averianov (2002), who also proposed a new systematics of "Symmetrodonta."

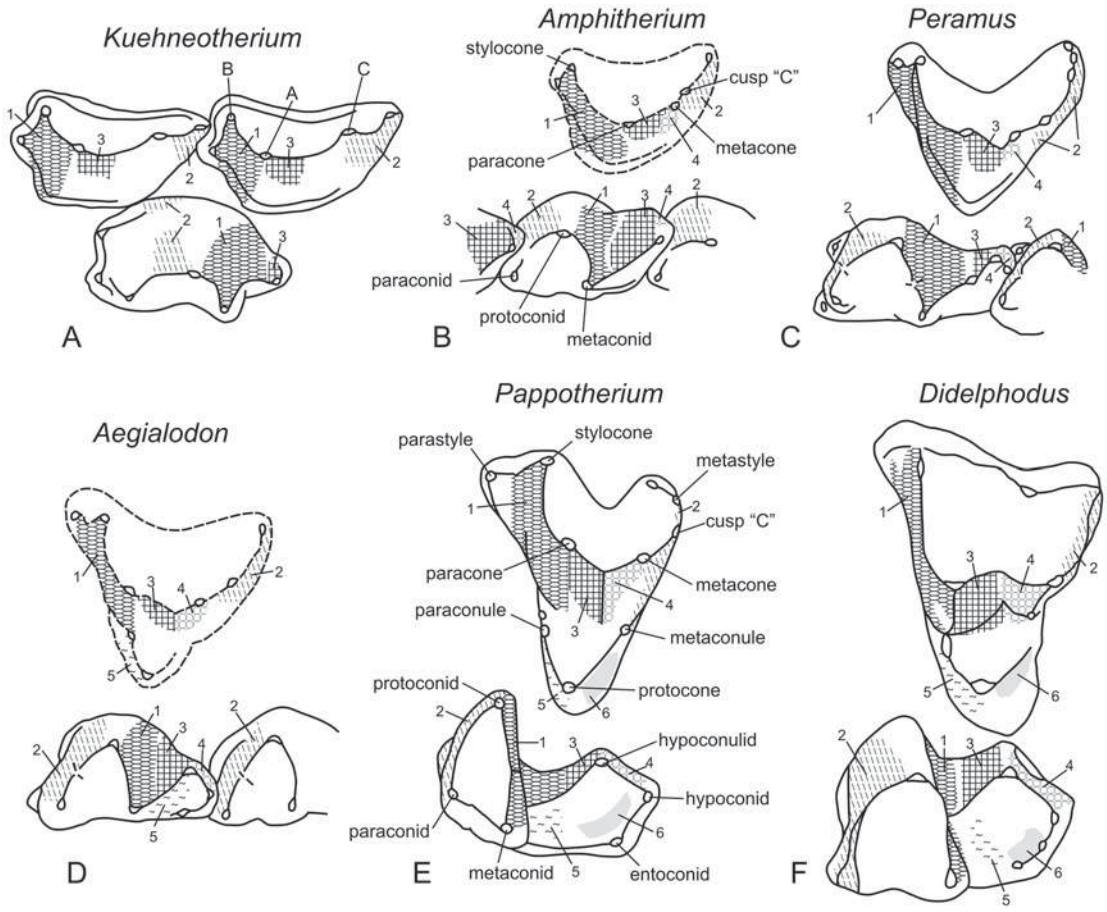
Kielan-Jaworowska et al. (2004) followed Luo, Kielan-Jaworowska, and Cifelli (2002) in rejecting the notion of the Holotheria. They argued that

> the definition and practical utilization of the Holotheria is problematic (see Luo et al. 2002). For example, *Kuehneotherium* (a taxon critical for the definition of the group) is poorly known. The phylogenetic position of *Kuehneotherium* is uncertain, so, leading to similar instability in makeup of Holotheria. Significantly, however, recent studies now place Monotremata within Holotheria, as defined on the basis of *Kuehneotherium* (see review by Cifelli 2001). And recent analyses also suggest that the diagnostic character for Holotheria, molars of reversed-triangle pattern, appears to have evolved iteratively within the group; the pattern is lacking in some apparent members of Holotheria, such as Eutriconodonta (Luo et al. 2002, see also Chapter 7 herein). With these fundamental issues on the table, at present we see no practical utility in the use of the term Holotheria: as its contents are uncertain, it does not serve the purpose for which it was intended, and it is diagnosed by a single character that is of dubious value. (Kielan-Jaworowska et al. 2004: 356)

Other papers (not discussed in this volume) describe isolated "symmetrodontan" teeth or jaws with teeth. Many of the authors of the relevant papers offer their own systematics of "Symmetrodonta," which differ from one another in details. But because the group as a whole is very poorly known, I prefer to avoid discussion of the systematic position of particular taxa assigned to it and the relationships among them.

There are many questions concerning origins of "symmetrodontans" and their relations to eutriconodontans and to the more advanced "therians," especially the "eupantotherians" (see also chapters 12 and 13). The question of the origin of "Symmetrodontans" requires further consideration.

In spite of three skeletons found in Jehol Biota, knowledge of the biology of "symmetrodontans" is limited. The structure of the postcranial skeleton, its state of preservation (see chapter 15), and presence of the spur indicate that they had a sprawling posture. The spur has not been found in all three skeletons, but as in the modern platypus it occurs only in males, it might be possible that their absence in several specimens is due to sexual dimorphism. A reconstruction of *Zhangheotherium* rendered by Mark A. Klingler was published in the Jehol Biota book (Chang et al. 2003).



12.1. Diagrammatic drawings showing important stages in the evolution of tribosphenic molars, as demonstrated by Crompton (1971). The molars are shown in coronal view; for each pair the upper teeth are above and lower below. Designation of wear facets (shaded in gray, numbers 1–6 indicate particular shearing surfaces) as introduced by Crompton (1971). A. *Kuehneotherium,* a Rhaeto-Liassic "symmetrodontan." B. *Amphitherium,* a Middle Jurassic "eupantotherian," with upper molar reconstructed. C. *Peramus,* an Early Cretaceous "eupantotherian." D. *Aegialodon,* an Early Cretaceous "tribotherian," with upper molar reconstructed. E. *Pappotherium,* Early Cretaceous "eupantotherian." F. *Didelphodus,* a Paleocene eutherian. D, E, and F are tribosphenic molars. There are only three shearing surfaces in *Kuehneotherium,* four surfaces in "eupanthotherians" (*Amphitherium* and *Peramus*), five in primitive tribosphenic mammals, known only from a single, lower tooth (*Aegialodon,* the upper tooth was reconstructed by Crompton). In fully developed tribosphenic mammals (*Pappotherium* and *Didelphodus*), there are six shearing surfaces. Not to scale.

Modified from Crompton (1971) by Kielan-Jaworowska et al. (2004: figure 11.3) and redrawn from the latter.

"Eupantotherians" and the Origin of Tribosphenic and Pseudotribosphenic Molars

12

The Origin of Tribosphenic Molars

"EUPANTOTHERIANS" ARE AN IMPORTANT GROUP OF SMALL MAMmals of the Mesozoic, intermediate between the "symmetrodontans" and the tribosphenidans. The term "Eupantotheria" has a long history. Marsh (1880) erected the order Pantotheria, and in a later paper (1887), he included four families: the Dryolestidae, Paurodontidae, Diplocynodontidae (now assigned to the Docodonta), and Dromatheriidae (now considered to be nonmammalian cynodonts).

Osborn (1888) coined the descriptive term "trituberculate molars" and later (1893) used "trituberculates" as an informal unit in reference to some Late Cretaceous eutherians and marsupials with true tribosphenic molars (the term did not exist in Osborn's time but was introduced later by Simpson in 1936). In 1893 the famous German invertebrate paleontologist Karl von Zittel published a multi-volume textbook of paleontology, in which he used the formal taxon "Trituberculata," mistakenly attributing it to Osborn. The textbook popularized the taxon Trituberculata, and, in spite of criticism by Simpson (1928a), it was used as late as the last half of the twentieth century in the textbooks of Romer (1966) and Carroll (1988) as an infraclass, encompassing the Symmetrodonta and Pantotheria.

Simpson (1925b) erected the order Symmetrodonta for part of Marsh's Pantotheria, and later he set up two separate orders, Symmetrodonta and Pantotheria (Simpson 1928a, 1929). Simpson (1931) formally proposed the infraclass Pantotheria to include the orders Symmetrodonta erected by Simpson (1925b) and Pantotheria erected by Marsh (1880). In his classification of mammals, Simpson (1945) noted that the use of this confusing classification was inappropriate, but in spite of this statement, he continued to use it. In order to avoid further confusion by using the same name for two different taxa, Kermack and Mussett (1958) erected the order Eupantotheria to replace the ordinal name Pantotheria, while retaining the term Pantotheria as the name of the infraclass. Several years later, Simpson (1971) attempted to address the same problem by erecting the infraclass Patriotheria as a replacement for Pantotheria *sensu lato*, including the orders Symmetrodonta and Pantotheria, but his proposal was not followed by subsequent authors. I follow Kermack and Mussett (1958) and Kielan-Jaworowska et al. (2004) in using the order name "Eupantotheria."

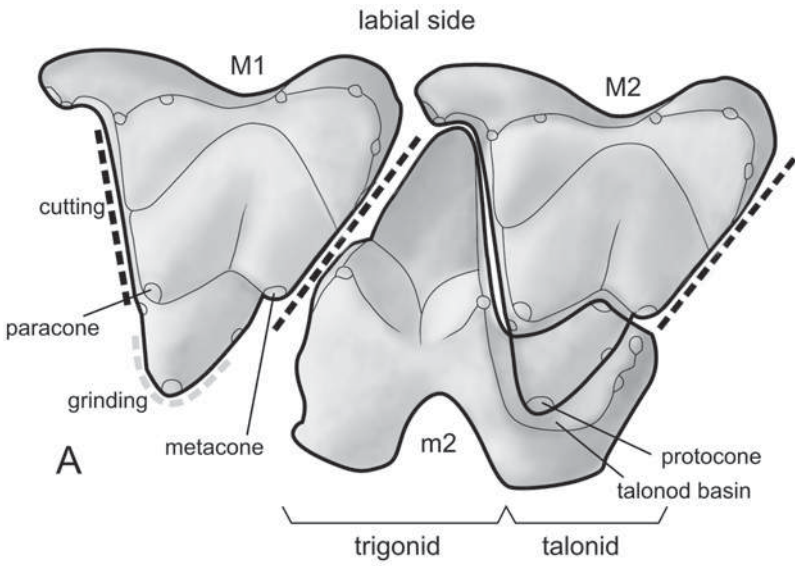
"Eupantotherians" differ from "symmetrodontans" in having upper molars that are wider than the lowers, rather than being of equal width; in having an incipient talonid in lower molars (in "symmetrodontans" there may occur only a single cusp in place of the future talonid); and,

finally, in having an angular process on the dentary, a character shared with Tribosphenida. The "eupantotherians" differ from the tribosphenidans in lacking tribosphenic molars – that is, in lacking the protocone on upper molars and the talonid basin on the lowers. In the structure of the molar teeth, the "eupantotherians" lie intermediate between "symmetrodontans" and tribosphenidans. The upper molars of "eupantotherians" are elongate transversely, roughly triangular in occlusal view, and remind one of tribosphenic molars (see below). Even early students of "eupantotherians" – for example, Butler (1939) and Patterson (1956) – realized that the cusps on "eupantotherian" upper molars were differently arranged than those of tribosphenic mammals and that a protocone does not occur in "eupantotherians." The issue was demonstrated in detail by Crompton (1971). In that paper Crompton offered an analysis of the change in orientation of wear facets in the evolution leading to tribosphenic molars. The cusp homology in "eupantotherians" and the tribosphenic molar is a fairly complex issue, and rather than discuss it here, I refer interested readers to the discussion in Kielan-Jaworowska et al. (2004: 373–375).

One should remember that when Crompton (figure 12.2B) did his important study on the origin of tribosphenic molars (1971), knowledge of most fossil therian mammals and their tribosphenic ancestors was limited to Laurasia. The morphological line studied by Crompton was relatively simple. It extended from a primitive symmetrodontan *Kuehneotherium*, through the "eupantotherians" *Amphitherium* and *Peramus*, to the primitive tribosphenic mammal *Aegialodon* (in which the upper molar was reconstructed) and *Pappotherium*, and then to a eutherian *Didelphodus*, with fully developed tribosphenic molars (figure 12.1).

Alfred Walter Crompton

Alfred Walter ("Fuzz") Crompton, paleontologist and functional anatomist, was born in 1927 at Durban, South Africa. In 1952 he was granted a doctor of science by Stellenbosch University. He then studied under Rex Parrington at Cambridge University and obtained a Ph.D. for his thesis on Triassic Cynodonts from Tanganyika in 1954. During 1956–1964, he was the director of the South African Museum at Cape Town and a lecturer at the University of Cape Town. In 1964 he was appointed director of the Peabody Museum at Yale University, with a joint professorship of biology and geology. In 1970 he was appointed professor of biology and director of the Museum of Comparative Zoology at Harvard. He served as director until 1982 and as the Fisher Professor of Natural History until 2001. While in South Africa, Crompton worked mostly in paleontology, describing mammal-like reptiles, early mammals, and dinosaurs from southern Africa. In 1964 he participated in a joint British, South African, and American expedition that found the first Triassic mammals and early ornithischian dinosaurs in South Africa and Basutoland (now Lesotho). At Yale and Harvard, in collaboration with British anatomist Karen Hiiemae and British neurophysiologist Alan Thexton, Crompton used



12.2. A. Diagrammatic model of tribosphenic molars. B. Alfred W. Crompton.

A. Original artwork by Oscar Sanisidro. B. Courtesy of A. W. Crompton.

cineradiography to study mastication, food transport, and swallowing in primitive extant mammals. Working with Farish A. Jenkins Jr., James A. Hopson, Ailin Sun, and Zhe-Xi Luo, he studied anatomical changes at the synapsid/mammalian boundary. With Zofia Kielan-Jaworowska, he explored the structure-function relationships of the molars of Cretaceous therian mammals. His current research deals with functional anatomy, neural control, and evolution of feeding in placental and marsupial mammals.

An important part of Crompton's work was reconstruction of the shearing surfaces in all the discussed forms (figure 12.1) and then mapping their pattern of evolution. Figure 12.2A offers a three-dimensional scheme showing how tribosphenic molars work. Upper teeth (M1 and M2) have three main cusps each and are triangular in coronal view; this view is named a trigon. The lower tooth (m2) consists of an anterior triangular, high trigonid that enters between the two upper teeth. The

boundaries of the trigon form sharp edges that cut the food when moving against the boundaries of the trigonid. The posterior part of the lower tooth forms a basin-like talonid. The lingual cusp of the upper tooth – the protocone – enters the talonid and works like a mortar and pestle, grinding the food. The tooth M2 is drawn as transparent in order to show the talonid basin in which it enters to grind the food. Cutting surfaces working between the trigons of the upper teeth and the trigonid of the lower are shown by thick broken lines.

Crompton recognized in *Didelphodus* six shearing surfaces and demonstrated that only three of them were present in *Kuehneotherium*. The evolutionarily advanced shearing facets appeared in the intermediate forms in phylogeny – for example, *Peramus*, – before modern eutherians or metatherians originated. Crompton (1971) made a seminal contribution in demonstrating how a complex structure, such as the tribosphenic molar, could have been assembled by evolution.

Among the taxa assigned to "eupantotherians," of special interest is the Late Jurassic genus *Peramus*, first named in 1871 by Owen. The material of *Peramus tenuirostris* for many years consisted of only lower jaws with teeth, and the authors studying them suggested that the number of molars was either three or four. The material gradually increased and now consists of a number of dentaries and maxillae with teeth, but never found in occlusion, all housed in the Natural History Museum in London. *Peramus* has been studied or commented on by numerous paleontologists. Prime among them are Simpson (1928a), Butler (1939), Mills (1964), Clemens and Mills (1971), Crompton (1971), Prothero (1981), McKenna and Bell (1997), Sigogneau-Russell (1999); Butler and Clemens (2001), and Kielan-Jaworowska et al. (2004). Clemens and Mills (1971), who had at their disposal a new maxilla with teeth, some of which were unknown previously, suggested that in *Peramus temuirostris* there were four premolars and four molars.

In *Kuehneotherium*, upper and lower teeth are of approximately the same width (as in all "symmetrodontans"), and the lower jaw moved dorsomedially during occlusion. During the evolution toward the tribosphenic molar from the *Kuehneotherium* pattern, there was an increase in the transverse component of the lower jaw movement, producing new shearing surfaces on the lingual side of the upper molar and in the talonid part of the lower. This resulted in an increase in the width of the upper molar, with new cusps appearing in the lingual region and with enlargement of the talonid, which in "symmetrodontans" had a single cingulid cusp (hypoconulid, or cusp d), to a broadened talonid bearing a grinding basin rimmed with additional neomorphic cusps.

For some 20 years after the publication of the *Early Mammals* volume in which it appeared (Kermack and Kermack 1971), the paper by Crompton (1971) was generally regarded as a lasting contribution to studies of early mammals. However, with an increase in the number of specimens of Mesozoic mammals, it became evident that *Kuehneotherium* did not belong to the line leading to true tribosphenic mammals and that

the patterns of tribosphenic molar evolution proposed by Crompton are likely to have occurred more than once, in a more complex evolutionary tree of early mammals, as evidenced by the many fossils discovered since the 1970s. For example, molars of pseudotribosphenic structure (Chow and Rich 1982), and the forms with tribosphenic molars from the Early Cretaceous of Australia (Rich et al. 1997) and other mammals from Gondwanan continents were not known at that time.

Denise Sigogneau-Russell (1999) described several new genera belonging or related to the Peramura from the Early Cretaceous of Britain and Morocco, and re-described several genera erected by Dashzeveg from the Early Cretaceous of Mongolia, clarifying and expanding our knowledge of these early mammals.

In 1975 Malcolm C. McKenna published his first cladistic analysis for the entire class Mammalia, in which he introduced 20 new high-ranking taxa and assigned a new rank to numerous existing taxa. In his classification, the taxa were diagnosed only by the lower-rank taxa nested in them. Twenty-two years later, in collaboration with Susan Bell, he published his comprehensive, excellent book *Classification of Mammals above the Species Level* (1997). During the years that separated these publications, much changed in our understanding of the systematics and phylogenetic relationships of mammals. Numerous papers, including phylogenetic analyses of various groups of mammals, appeared, and the information from these studies was incorporated by McKenna and Bell into their book. They used Linnean taxa, increasing the number of ranks above the species level category in mammals to 25, in contrast to the 14 proposed by Simpson in his classification of mammals (1945). McKenna and Bell (1997) also incorporated rarely used ranks such as parvorder, mirorder, grandorder, magnorder, and several others.

In 1975 McKenna introduced several high-rank taxa for various groups of mammals. Among them was the taxon Cladotheria. As described by Kielan-Jaworowska et al. (2004: 371), "Cladotheria McKenna, 1975 is a stem-based clade defined by the common ancestor of the boreosphenidans [now tribosphenidans, see Chapter 9 and below] (including marsupials and placentals) and the fossil taxa more closely related to Crown Theria than to the more plesiomorphous Spalacotheriidae. By current, prevailing hypotheses of cladistic relationships from the best available evidence, these groups are stem taxa more closely related to extant marsupials and placentals, which form a clade of Cladotheria McKenna, 1975, than to the more plesiomorphous symmetrodontans." Peramurids, dryolestoids, and amphitheriids are the stem clades nested within the monophyletic Cladotheria. These are related to tribosphenidans in a successively more distant order but do not form a natural group by themselves.

The main new idea that arose about that time was the notion of a phylocode, introduced by the proponents of phylogenetic systematics (for example, de Queiroz and Gauthier 1990; and many others), who argued that Linnaean systems cannot work with cladistic phylogenies. As a result,

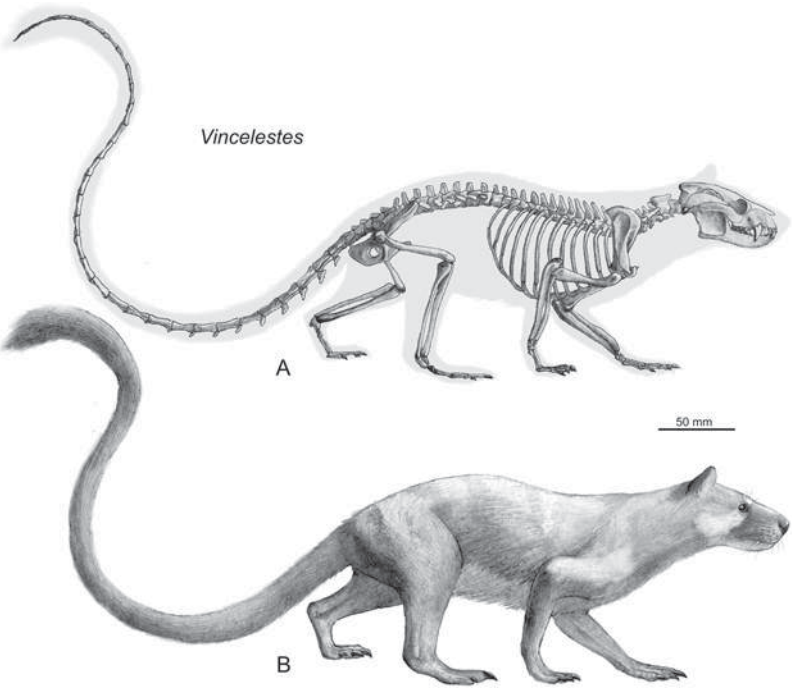
the advocates of the phylocode system do not use Linnean ranks, instead using only high-rank taxa without providing the values of the ranks. The literature concerning the issue of the phylocode is enormous, published mostly in journals such as *Taxon*, *Cladistics*, and *Systematic Biology*. It is beyond the scope of the present book to refer to all of them. Instead, I refer the reader to two review articles in *Acta Palaeontologica Polonica*, one by Lee and Skinner (2007), who advocate for the phylocode idea, and the other, a critique by Benton (2007).

One might note, however, that Malcolm C. McKenna, who repeatedly argued that cladistic (phylogenetic) analysis was obligatory in papers dealing with the systematics, completely ignored the phylocode idea (McKenna and Bell 1997). McKenna and Bell rejected the paraphyletic taxa, and after McKenna's (1975) paper, he did even not mention such taxa as "Pantotheria" or "Eupantotheria." McKenna has been followed in this respect by his student Donald Prothero (1981), who described several pre-tribosphenic taxa from the Jurassic of Como Bluff in Wyoming. Instead, McKenna (1975) not only used Linnean taxa but increased their number in systematics of mammals above the species level, as mentioned above, to 25.

By contrast, Kielan-Jaworowska et al. (2004) used the paraphyletic taxon "Eupantotheria" (in quotation marks, as adopted for paraphyletic taxa), which McKenna (1975) replaced partly by the legion Cladotheria. Kielan-Jaworowska et al. (2004: tables 10.1 and 10.2) list 37 "eupantotherian" genera. Adoption of both cladistic and Linnean classifications in that book reflects the compromise of the authors with respect to the current conflict between advocates of the phylocode idea and proponents of the traditional Linnean classification.

Despite as many as 37 genera of "eupantotherian" mammals being known in 2004, the details of their anatomy are limited. The first skull fragments and fragments of the postcranial skeleton were described by Bernard Krebs (1991), who named them *Henkelotherium guimarotae* (see also Vázquez-Molinero et al. 2001). Krebs offered (1991: 1) a very good reconstruction of *Henkelotherium* walking on a ginkgo tree (with artwork by Elke Gröning). Elements of the skull are also known for *Dryolestes* and have been recently redescribed by Thomas Martin (1999a) in one of his meticulous monographs of the "eupantotherian" Guimarota faunas (Martin 1995, 1997, 1998, 1999b, 2002).

In January 1987 I was invited by José Bonaparte (figure 10.5C) to visit Buenos Aires and take part in an expedition organized by him to the outcrops of the late Hauterivian or early Barremian La Amarga Formation in southern Neuquén Province, Patagonia, Argentina, where a few years earlier he and his crew discovered the best preserved skulls of a "eupantotherian" called *Vincelestes neuquenianus*. *Vincelestes* was also known from numerous skeletal elements, described by Rougier (1993) in his Ph.D. thesis. Reconstruction of the skull of *Vincelestes* was first published by Bonaparte and Rougier (1987). The outcrops yielded a rich selection of *Vincelestes*, excavated from a single pocket in the basal unit of the La



12.3. *Vincelestes neuquenianus.* A. Reconstruction of the skeleton. B. Life reconstruction of walking animal.

Both drawings based on a reconstruction made by Guillermo Rougier in his Ph.D. thesis (1993, unpublished), modified by Oscar Sanisidro and Aleksandra Hołda-Michalska.

Amarga Formation. At least nine individuals had been found, represented by six complete skulls, 17 lower jaws, and numerous isolated bones of the postcranial skeleton, all excavated in previous years. McKenna and Bell (1997) assigned *Vincelestes* to sublegion Zatheria McKenna, 1975. (See figure 12.3 for a reconstruction of *Vincelestes neuquenianus.*)

The week I spent in Buenos Aires was most interesting and charming. It was the beginning of the Southern Hemisphere summer, and the weather was mild. My hotel was in the center of the town, at a street allowed only for pedestrians. During the evening, out my open window, I could hear street bands passing by, composed of several men playing guitar and singing a tango. Otherwise, I spent whole days at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," examining the collections assembled by José and his crew and meeting his co-workers. The most impressive was the meeting with Guillermo Rougier, a young Ph.D. student at that time, beginning his work on early mammals.

One day, Juan C. Quiroga, a Ph.D. student from La Plata Museum, arrived in Buenos Aires to meet me. Discussion with him was also most interesting. I knew Juan from correspondence and from his papers on the endocranial casts of cynodonts (Quiroga 1979, 1980, 1984), which he published in the *Journal für Hirnforschung.* Juan was interested in studying endocranial casts of Mesozoic mammals, and I had written a supporting letter for his application to the Guggenheim Foundation for a grant to visit North American and European museums. Unfortunately this project was never realized, as Juan died prematurely of leukemia in 1989.

During my stay in Buenos Aires, we wrote a short paper with José Bonaparte, comparing dinosaurs and Mesozoic mammals of Laurasia

12.4. Dental, mandibular, and postcranial anatomy of *Pseudotribos robustus* from the Middle Jurassic of Inner Mongolia (China). A. Upper molar (M2) in occlusal view. B. Lower molar in labial view. C. Reconstruction of the upper molars (M2 and M3) in occlusion with lower m2 and m3. D. Composite restoration of the upper dentition and mandible with dentition. E–F. Skeletal reconstruction and life restoration.

A–D. Redrawn and simplified from Luo et al. (2007b: figure 2). E–F. Modified by Aleksandra Hołda-Michalska from the unpublished drawings by Oscar Sanisidro, based on data from Luo et al. (2007b).

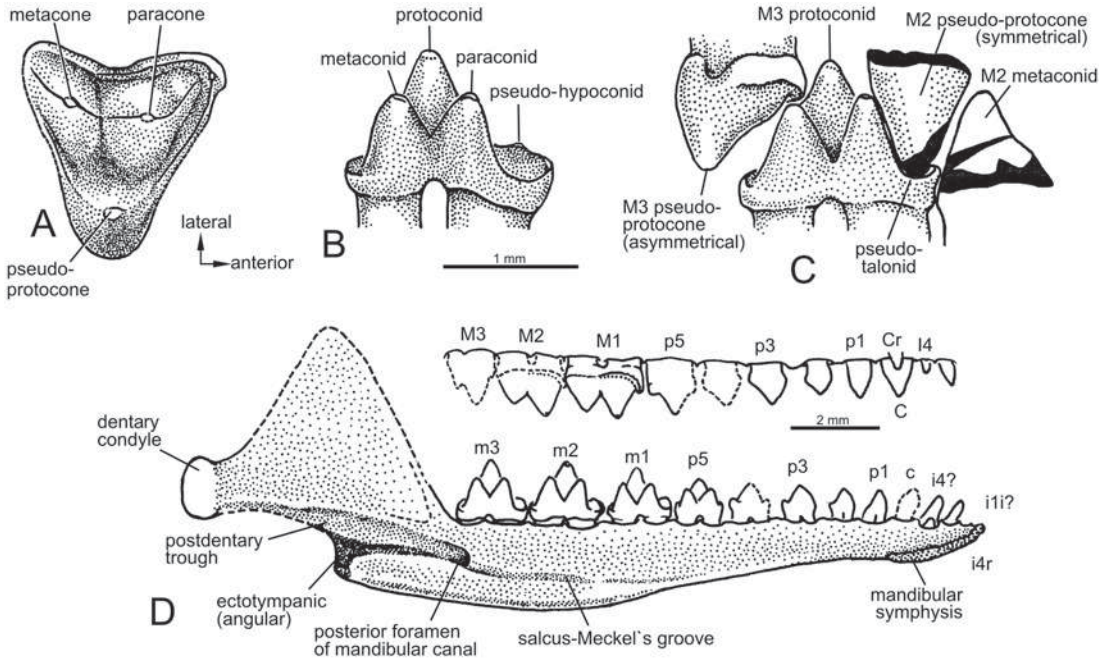
and Gondwana, which we submitted to the Symposium on Mesozoic Terrestrial Ecosystems, to be held in Drumheller, Canada, in August 1987. Our paper was published in the symposium book (Bonaparte and Kielan-Jaworowska 1987), and José attended the symposium.

After one week in Buenos Aires, we headed off to the field. Traveling through Patagonia was quite exotic to me, especially when I saw the South American "ostrich," the rhea, which belongs to the family Rheidae. In several languages rheas are called nandus. Rheas are smaller than African ostriches and are extremely gracile and fast. There are two species of rheas: the greater rhea (*Rhea americana*) and the lesser or Darwin's rhea (*Pterocnemia pennata*). I saw only greater rheas and saw them only twice while in Patagonia. One was a single, apparently young individual, quite skittish, which appeared for a second in our field of vision and ran away from our cars, as fast as it could. My second sighting was a flock of some seven or eight birds of different sizes that crossed the road in front of our cars. I knew that the rhea family (like that of the African ostrich) consisted of a cock and at least three hens, with the cock taller than the hens. The flock we saw ran so fast that it was impossible to recognize who was who!

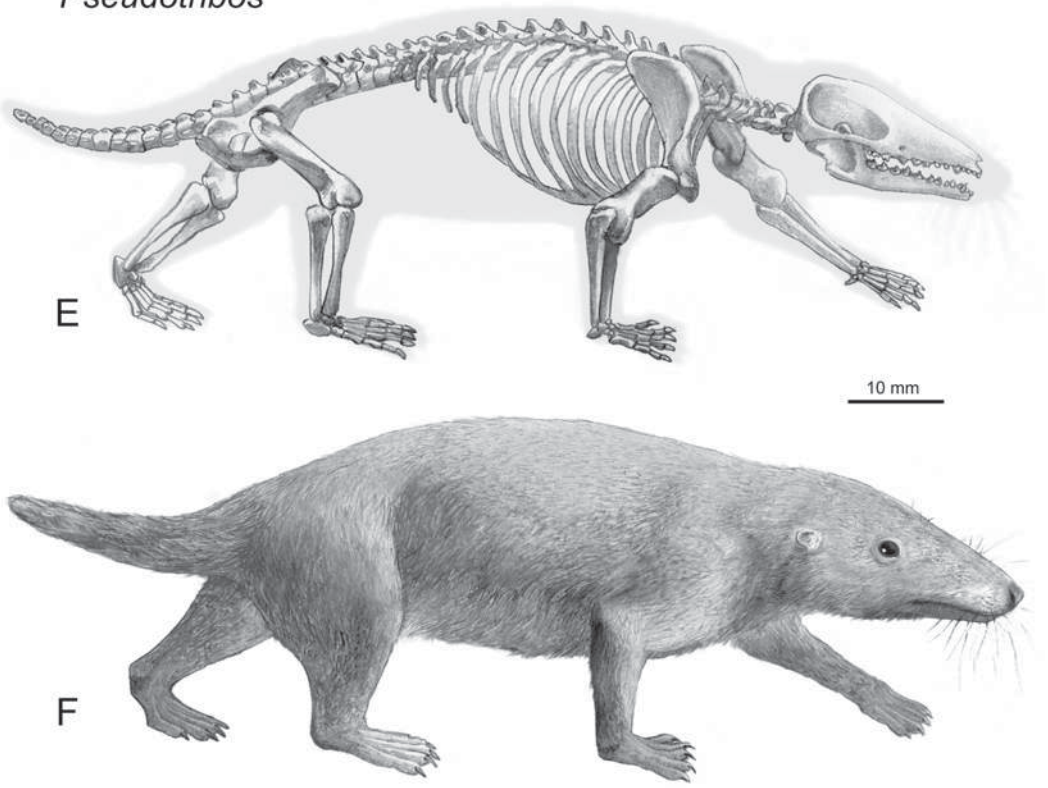
After Guillermo Rougier defended his dissertation on *Vincelestes* in 1993, he visited me in Oslo and brought the 720 page manuscript of his dissertation. He published several papers, often in cooperation with colleagues, on the *Vincelestes* skull structure (for example, see Rougier and Bonaparte 1988; Rougier et al. 1992; and Hopson and Rougier 1993). Although many years have passed since Guillermo's thesis defense, no single paper on the postcranial skeleton of *Vincelestes* has been published in English.

The Issue of Pseudotribosphenic Mammals

In 1982 the eminent, now late Chinese paleontologist Min-Chen Chow, together with Tom Rich, whom I have mentioned several times in this book, described a mammal dentary from the Jurassic of Sichuan Province of China. In that mammal, the last three teeth, which I regard as molars, have talonids. But these talonids are situated, not behind the trigonids, as is characteristic of previously known tribosphenic molars but in front of the trigonids. The authors designated this tooth structure the pseudotribosphenic type and named the new fossil of dentary with teeth *Shuotherium dongi*. In the same paper, Chow and Rich (1982) erected the legion Yinotheria and the family Shuotheriidae for the new genus and species and placed all these units within the superlegion Trechnotheria McKenna, 1975. They also published a hypothetical drawing of the upper molar of *Shuotherium*, with a pseudoprotocone that would enter the pseudotalonid of the lower molar. Many years later, at the end of 2010, Tom Rich and Pat Vickers-Rich published a paper reviewing the notion of pseudotribospheny in *Vertebrata PalAsiatica*. They described in detail the history of the term and showed that it was often used in a way departing from its original, and more restrictive, meaning.



Pseudotribos

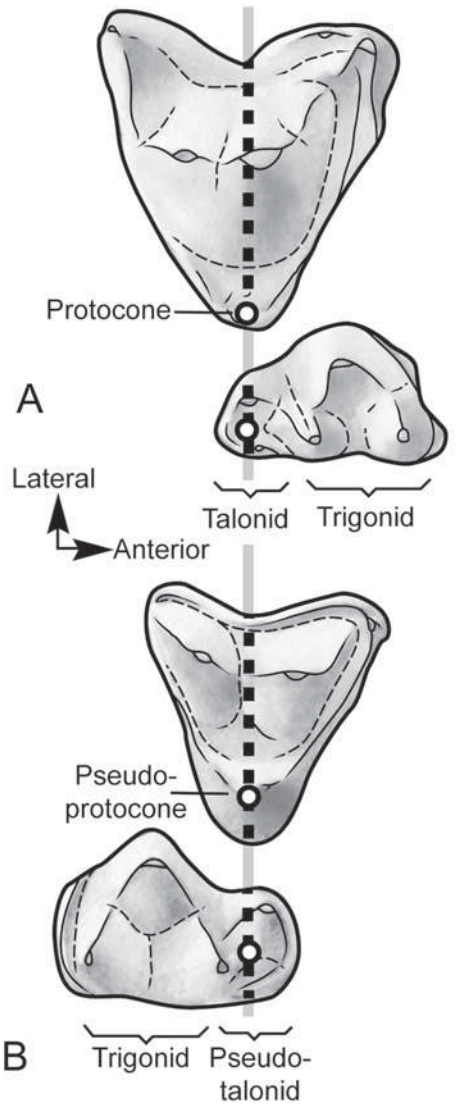


In 1998 Sigogneau-Russell described some isolated upper and lower molars from the Bathonian of England, assigning two of the lower teeth to *Shuotherium dongi* and the remainder to a new species, *Shuotherium kermacki*, and to *Shuotherium* sp. In the same year, Wang et al. (1998) described an upper molar of *Shuotherium* deriving from the same locality as the holotype of *Shuotherium dongi*. This tooth, however, could not be a counterpart of the holotype specimen of Chow and Rich, being too large, and the authors set up for it a new species, *Shuotherium shilongi*. Wang and colleagues (1998) regarded the Yinotheria as a sister taxon to Cladotheria McKenna, 1975, which is more or less congruent with the systematics of McKenna and Bell (1997), in which the Shuotheriidae are placed within the Superlegion Trechnotheria McKenna, Legion Symmetrodonta, along with the Legion Cladotheria McKenna, 1975.

The next paper on *Shuotherium* came from Richard L. Cifelli, Zhe-Xi Luo, and myself (Kielan-Jaworowska et al. 2002), in which we made an attempt to show some similarity between its lower jaw and dentition with that of the Australian *Ausktribosphenos*. This was confirmed by a new, very important find from China of an incomplete skeleton of a mammal with pseudotribosphenic dentition described by Luo, Ji, and Yuan (2007b), who named it *Pseudotribos robustus*. The authors stated, "Our analysis of an improved data set from the new *Pseudotribos* excludes an affinity of Shuotheriids to symmetrodonts, or to the clade of *Peramus* and more derived lineages. Shuotheriids are more closely related to the australosphenidan clade than other Mesozoic mammal groups" (Luo et al. 2007b: 97).

The holotype, the only specimen of *Pseudotribos robustus* (see figure 12.4), was found at the Daohugou locality, in Ningheng County, the Inner Mongolia region of China, in rocks of the Middle Jurassic Juilongshan Formation, and is housed at the Chinese Academy of Geological Sciences. The same formation yielded earlier a docodont, *Castorocauda*, described and reconstructed in chapter 7, and *Volaticotherium*, described in chapter 8.

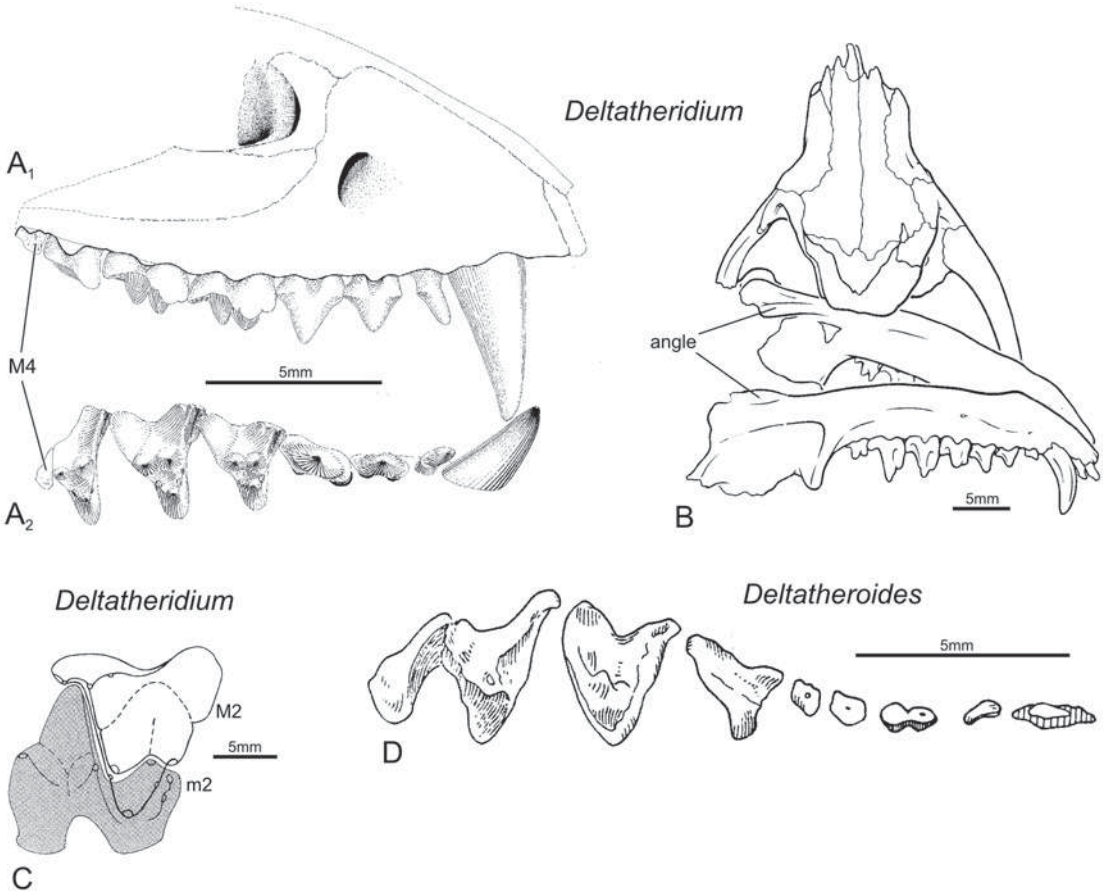
Pseudotribos, as preserved, appears to have 22 thoracolumbar vertebrae, of which 12 are connected by costal cartilages with sternebra, and a mandible with a well-developed dentary condyle, but at the same time with a dental trough for the postdentary bones. Because the middle ear bones are not preserved, it was impossible to state whether the lower jaw suspensorium was built by a single articulation between the dentary and squamosal bone or whether some old "reptilian" bones still participated in its structure and, so, whether the joint was single or double. Luo et al. (2007b) reconstructed the high coronoid process. The angular process of the dentary is distinct, as is the condylar process. This clarifies the key mammalian features that were not preserved in the *Shuotherium dongi* specimen. The dentary is low in the region of mandibular symphysis but more robust and deeper in the region of the molar teeth.



12.5. Comparison of tribosphenic and pseudotribosphenic molars. A. Tribosphenidan *Kielantherium,* as an example of the ancestral tribosphenic pattern. B. Shuotheriids as an example of pseudotribosphenic molars (based on *Pseudotribos*). Thick dashed line shows the protocone-talonid occlusion and the pseudo-protocone-pseudotalonid occlusion.

From Luo et al. (2007b: figures 3c, e).

In the same paper, Luo et al. (2007b) provided a comparison of the work of tribosphenic and pseudotribosphenic molars, summarized in their figure 3 and a part of it redrawn in this volume as figure 12.5. They concluded: "The new fossil of *Pseudotribos* adds to the inference that both the upper molar protocone and lower molar talonid could have undergone convergent evolution, and that there is more than one pathway to combine slicing and crushing functions in a single jaw motion for more effective faunivory and omnivory in early mammalian history" (Luo et al. 2007b: 97).



13.1. Skulls and teeth of selected deltatheridiids. A–C. *Deltatheridium pretrituberculare.* A. Reconstruction of the rostrum. A_1. Lateral view. A_2. Left upper dentition of the same in coronal view. Please note the extremely small size of M4. B. Anterior part of the skull of the same species in dorsal view, associated with both overturned dentaries. C. Oblique view of M2 and m3 in occlusion. D. *Deltatheroides cretacicus,* upper dentition in coronal view.

Modified from various sources by Kielan-Jaworowska et al. (2004: figure 12.4) and redrawn from the latter.

Tribotheria, Metatheria, and the Issue of the Deltatheroida

13

Tribotherians and Deltatheroids

THE EARLY MEMBERS OF THE METATHERIA (INCLUDING MARSUPIALIA) and Eutheria (including Placentalia) had tribosphenic molars. In addition, there are isolated tribosphenic molars in Early and Late Cretaceous rocks that, because of the incompleteness of the data, cannot be assigned to either Metatheria or Eutheria. Patterson (1956) described Early Cretaceous (Albian) isolated tribosphenic molars from Texas, naming them "Theria of metatherian-eutherian grade." This terminology remained in the literature for more than 20 years. Butler (1978) studied the collection of teeth from the Albian of Texas and set up within the subclass Theria a new infraclass, Tribotheria. Kielan-Jaworowska et al. (2004: 411) assigned to the Tribotheria 16 genera, of which one – *Kielantherium* – was represented by a dentary with four molars and possibly four or five double-rooted premolars (with alveoli preserved). Four teeth were also preserved together in a dentary fragment in *Slaugtheria* from the Albian of Texas. All other tribotherians are represented only by isolated teeth (see Kielan-Jaworowska et al. 2004: chapter 11).

The Central Asiatic Expeditions mounted by the American Museum of Natural History (see chapter 2), conducted fieldwork in Mongolia and China in the 1920s and assembled a modest collection of Late Cretaceous mammal skulls from the Djadokhta Formation cropping out at the locality of Bayan Zag (referred to earlier as Bayn Dzak, and sometimes also as Shabarkh Usu) in Mongolia. The skulls were poorly preserved, as apparently they had been lying for a long time on the surface of outcrops exposed to considerable weathering. Seven skulls (or fragments) were collected, and their short descriptions published, by Simpson (1925a, 1928b) and Gregory and Simpson (1926). Six new genera and species were described; one of these was *Djadochtatherium matthewi*, erected by Simpson (1925a) – a multituberculate. Three taxa were assigned to the family Deltatheridiidae and classified as belonging to the Insectivora; all three taxa, as well as the family, were erected by Gregory and Simpson (1926). These were *Deltatheridium pretrituberculare*, *Deltatheroides cretacicus*, and *Hyotheridium dobsoni*, the last regarded by subsequent authors as a *nomen dubium*. The last group included two species in the genus *Zalambdalestes*, assigned to the family Zalambdalestidae, erected by Gregory and Simpson (1926).

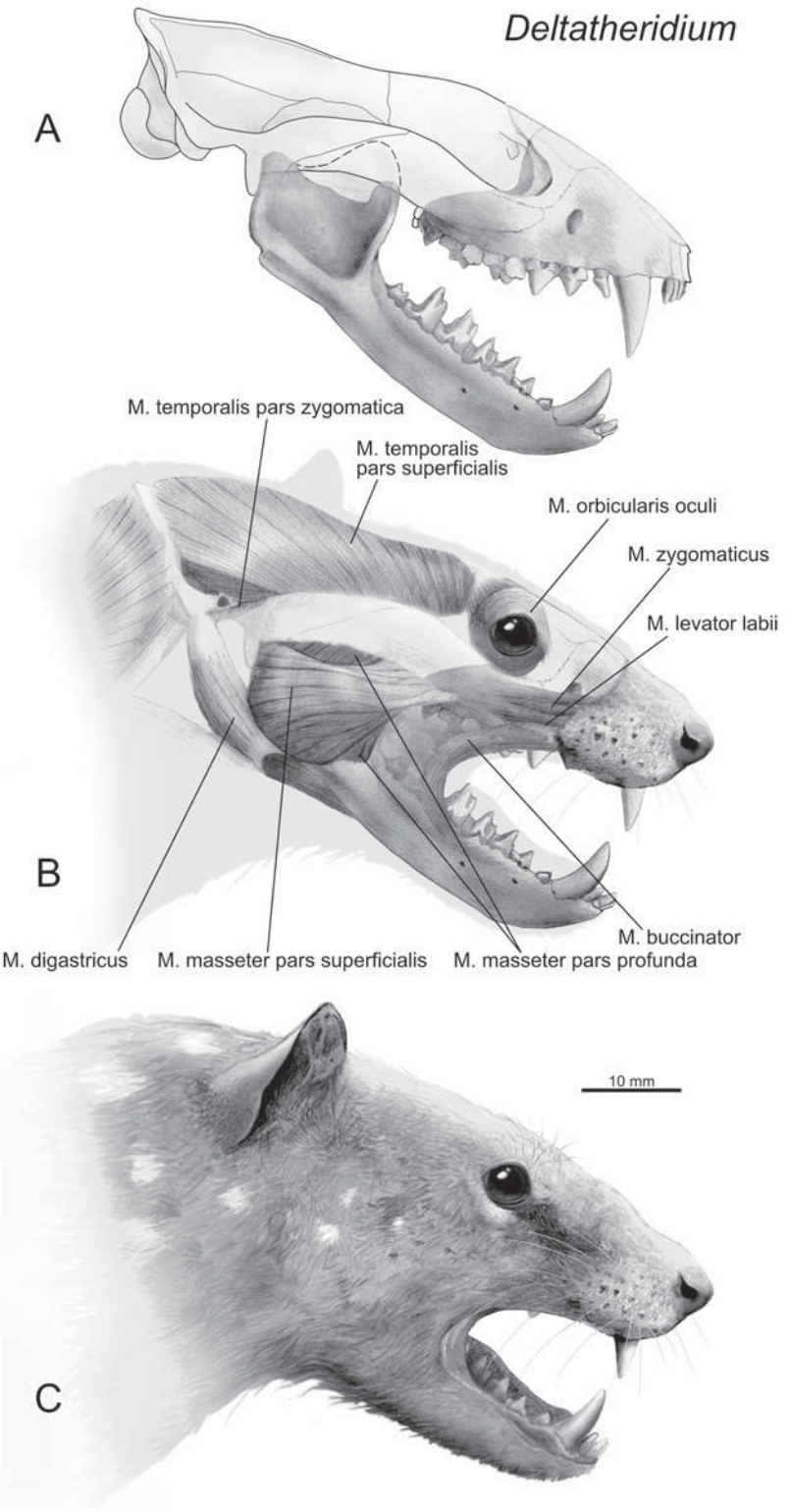
In 1966 Leigh Van Valen published a comprehensive monograph on the deltatheridiids, in which he treated the Deltatheridiidae as the central group in the evolution of placental mammals. Later, he abandoned the name Deltatheridia, using Hyenodonta instead. The Polish-Mongolian

Expeditions in 1970 and 1971 collected a few more, incomplete skulls of *Deltatheridium* in rocks of the Baruungoyot Formation. In 1973, when I was working on a description of therian mammals from the Baruungoyot Formation, Percy M. Butler, a great scholar and a specialist on early mammals, arrived in Warsaw to see our new collection of Cretaceous mammals from the Gobi Desert. I spent some time with Percy discussing the unresolved issue of the dental formula of the Deltatheridiidae, and we wrote a short paper that was published in *Nature* (Butler and Kielan-Jaworowska 1973). In that paper we argued that the dental formula of *Deltatheridium* (with four molars) is more similar to that of marsupials than to that of eutherians. In 1975, I published a paper in *Palaeontologia Polonica* (Kielan-Jaworowska 1975a) describing all the material of deltatheridiids collected by the Polish-Mongolian Expeditions and erected the two subspecies of *Deltatheridium pretrituberculare*. The best specimen was a skull rostrum from the Baruungoyot Formation that had only three molar teeth preserved on each side. Subsequently, I established the metatherian order Deltatheroida for the Deltatheridiidae (Kielan-Jaworowska 1982).

The late Russian paleontologist Lev A. Nessov began publishing in 1982 on his discoveries of Cretaceous mammals in the republics of Uzbekistan, Kazakhstan, Kyrgyzstan, and Tajikistan, all belonging at that time to the Soviet Union and referred to in the Soviet and Russian literature as "*Srednaya Asia*." Soviet and Russian scientists often referred to this region in English as "Middle Asia," a confusing term requiring some explanation. The German naturalist and explorer Alexander von Humboldt (1769–1859), in his great three-volume opus *Asie Centrale*, published in Paris in 1843, introduced the term "Central Asia" to refer to a region, somewhat larger than those four republics, centered in this area. In the present book, I follow Miroschnikov (1992), in Dani and Masson's *History of Civilization in Central Asia*, published by UNESCO, in which "*Srednaya Asia*," – "Central Asia" – includes Mongolia, Tibet, northeast Iran, Afghanistan, northern areas of Pakistan, Kashmir, and Ladakh, central-east Russia south of the Taiga, and the former five Central Asian Soviet Republics, Uzbekistan, Kazakhstan, Kyrgyzstan, Tajikistan, and Turkmenistan.

I had corresponded with Lev Nessov regarding his work on Cretaceous mammals and traveled to Leningrad in the summer of 1988 to examine the collection of Cretaceous mammals he had collected in Uzbekistan and elsewhere in Central Asia. On this occasion, I met Lev Nessov for the first time. In the rich collection of Cretaceous mammals he had assembled, there were specimens of the deltatheroid genus *Sulestes*, erected by Nessov (1985), represented by upper and lower molars. During my short stay we wrote a joint paper that we published in the Scandinavian journal *Lethaia* (Kielan-Jaworowska and Nessov 1990).

In 1998 my Argentinean and American colleagues (Guillermo Rougier, John R. Wible, and Michael J. Novacek), working on the fossils from the Gobi Desert as part of the Mongolian Academy–American Museum



13.2. Reconstruction of the skull and head of *Deltatheridium pretrituberculare.*
A. The skull with the dentary.
B. Musculature of the skull.
C. Life reconstruction of the head.

Original artwork by Oscar Sanisidro.

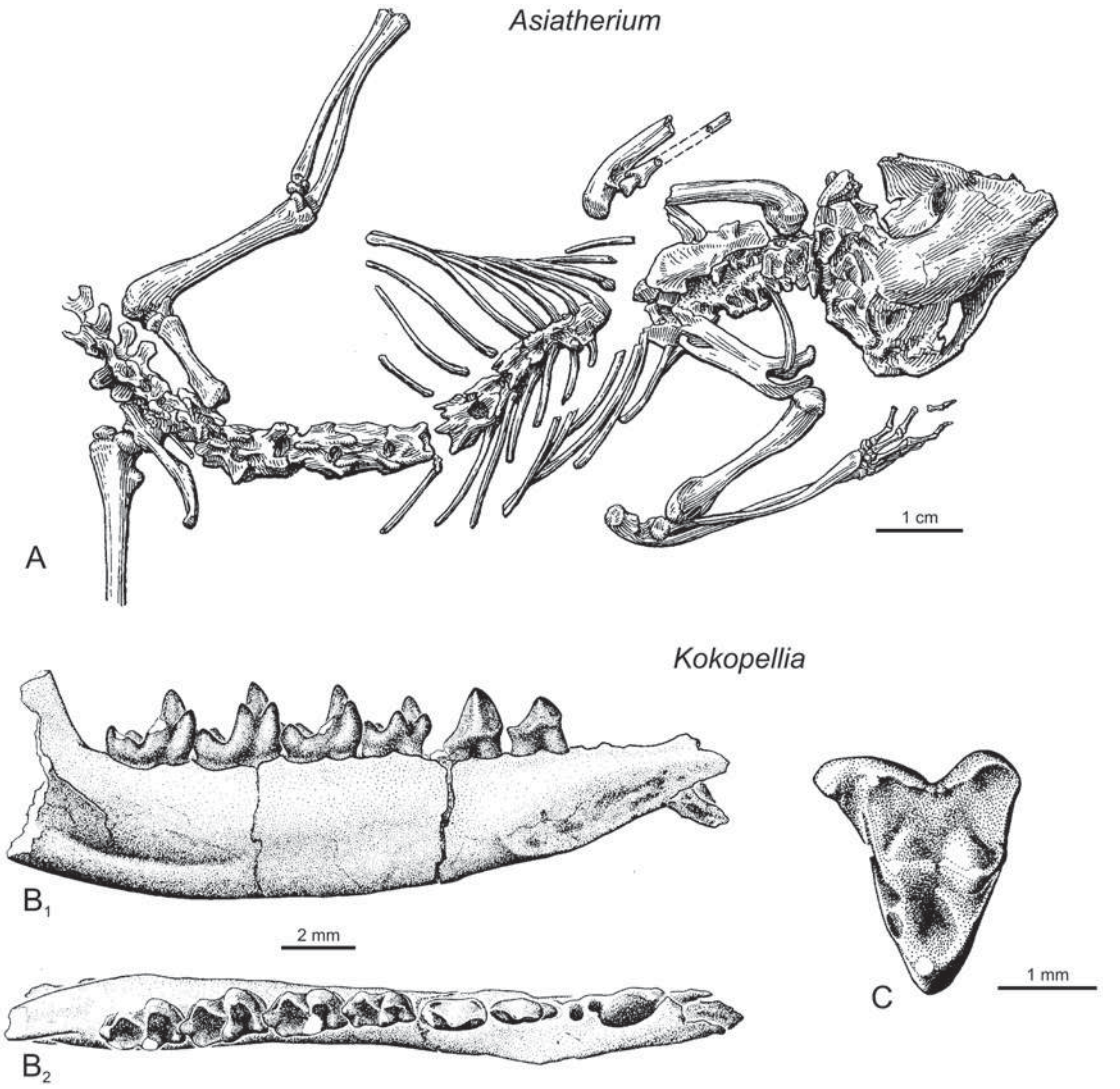
Expeditions project, described in *Nature* new material of *Deltatheridium* from the Ukhaa Tolgod locality, in the Gobi Desert, Mongolia, discovered by these expeditions. They suggested that there was only one species of *Deltatheridium*, *D. pretrituberculare*, and no subspecies (which I erected in Kielan-Jaworowska 1975a). They described two new specimens of *D. pretrituberculare*, better preserved than those hitherto known but still not complete. I accepted their conclusion concerning the lack of subspecies of *D. pretrituberculare*. The better-preserved specimen of *Deltatheridium pretrituberculare* described by Rougier et al. (1998) consists of the rostral part of the skull with four molars on each side (the last one tiny) and complete lower jaws containing four molars and three premolars (figure 13.1A and B, in this volume) displaying the inflected angle forming a shelf-like structure so characteristic of some extant marsupials. Figure 13.2 shows a reconstruction of the skull, musculature, and life appearance of the head of this species.

The structure and degree of wear on the dentition allowed one to conclude that in deltatheroidans only the third premolar has been replaced, as is characteristic of modern marsupials. Another, less complete specimen, consisting of distorted bones of the skull and a well-preserved petrosal bone, reflected features characteristic of marsupials. The Deltatheriidae differ from marsupials in some details of their dentition, for example, in a dramatic reduction of the size of the last upper and lower molars, in having the small protocone narrowed both longitudinally and transversally, and in having generally more slender molar teeth than in early marsupials. Rougier et al. (1998) accepted the conclusion proposed by Kielan-Jaworowska and Nessov (1990) that the Deltatheroidea were a sister group of Marsupialia, nested within Metatheria, and this assignment has been followed by subsequent authors. In 2004 my colleagues and I (Kielan-Jaworowska et al. 2004: table 12.1) divided the infraclass Metatheria into two cohorts, Deltatheroida, which I had erected (Kielan-Jaworowska 1982), and Marsupialia, set up by Illiger (1811). We assigned seven genera to the Deltatheroida and a further nineteen to the Marsupialia.

Marsupialia

It is well known that marsupials and eutherians differ from one another in the method of reproduction and in the structure of reproductive organs. These differences are associated with differences in dental formulae: 4, 1, 3, 4 in both lower and upper jaws of marsupials, and 3–4, 1, 4–5, 3 in early eutherians (see Cifelli 2000). In marsupials, in contrast to eutherians, only the last premolar is replaced. The dentary of marsupials differs from that of Eutheria in possessing the mandibular angle inflected inward, forming a horizontal shelf. This is also characteristic of the deltatheroidans.

In the middle of the twentieth century, the main student of Mesozoic marsupials was William A. Clemens from the University of California, Berkeley, who published in three volumes a description of the Late



13.3. A. Skull and postcranial skeleton of *Asiatherium reshetovi*. B. *Kokopellia juddi*. Left dentary with p2–p3 and m1–m4 in lingual (B_1) and occlusal (B_2) views. C. Left M3 of the same in occlusal view.

A. From Kielan-Jaworowska et al. (2004: figure 12.6.A), redrawn and emended from Trofimov and Szalay (1994). B. From Kielan-Jaworowska et al. (2004), redrawn from Cifelli (1993a). C. From Kielan-Jaworowska et al. (2004: figure 12.6.A_3). All figures slightly emended.

Cretaceous mammals of the Lance Formation, Wyoming, dealing respectively with multituberculates, metatherians, and eutherians (Clemens 1963, 1966, 1973). In addition, he published review articles dealing with the evolution of Marsupialia (Clemens 1968, 1979). He later described isolated bones of the Early Jurassic and Late Triassic of Europe (Clemens 1980, 1986).

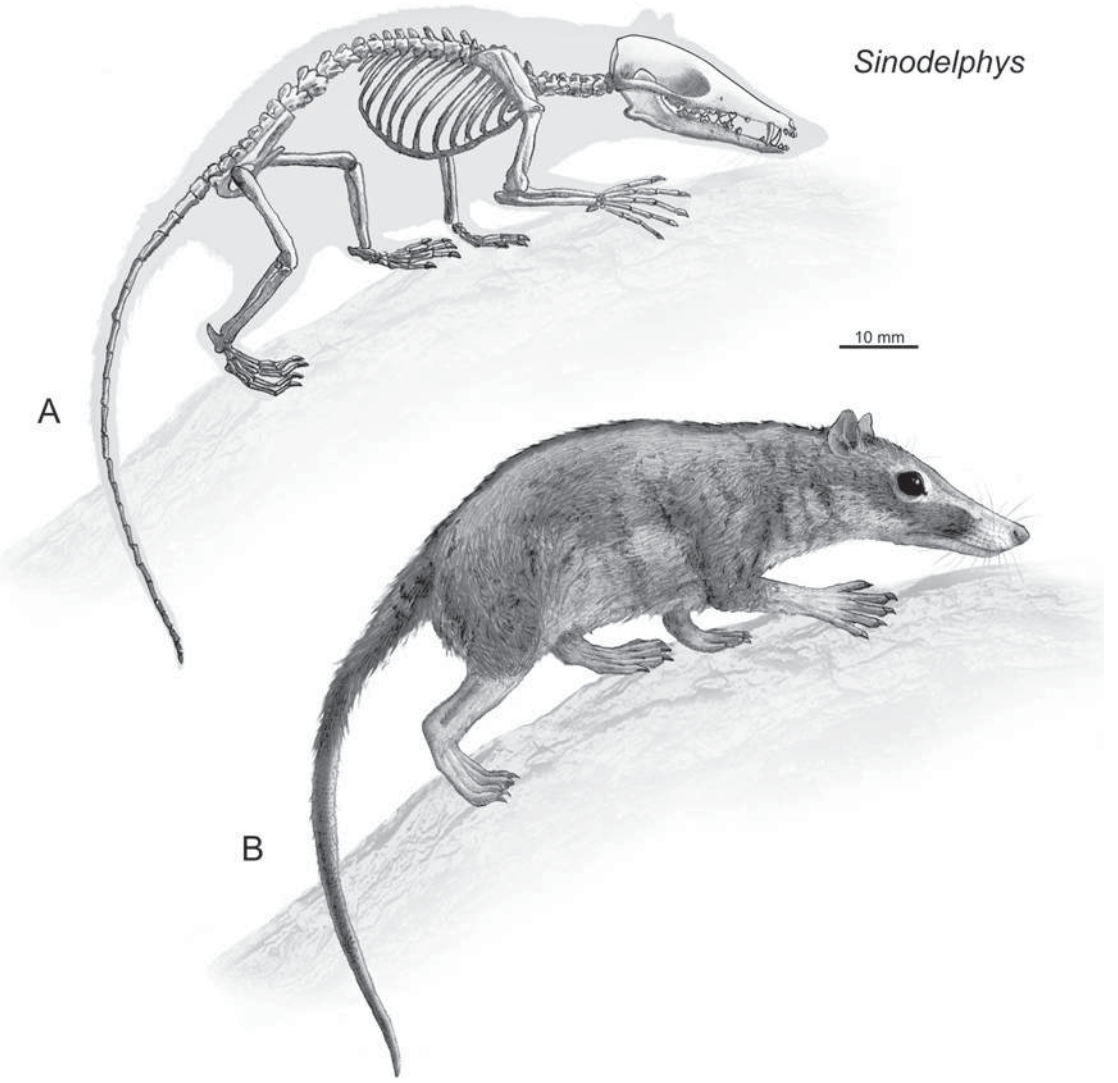
In the last two decades of the twentieth century, Frederick S. Szalay began to publish intensively on Cretaceous marsupials, concentrating especially on an analysis of the postcranial skeleton (see, for example, his well-known book *Evolutionary History of the Marsupials and an Analysis of Osteological Characters*, 1994). Trofimov and Szalay (1994) described the skeleton of a Late Cretaceous marsupial from the Baruungoyot Formation in the Gobi Desert, found several years earlier by the Soviet-Mongolian Expedition. The specimen was a slightly crushed skull

associated with the better part of a postcranial skeleton. They named the specimen *Asiatherium reshetovi* and placed it in a new marsupial order, the Asiadelphia. Two years later, Szalay and Trofimov (1996) published a more detailed analysis of the *Asiatherium* skull and postcranial skeleton (figure 13.3A), including a cladistic analysis of the early Metatheria and the paleogeographic implications of this material.

They also published a photograph of a relatively large, complete skull (without dentaries) of a yet unnamed Late Cretaceous metatherian from Mongolia. The colored photograph of this same skull was published earlier in a leaflet, describing the activities of the Paleontological Institute in Moscow. I refrained from commenting on this skull, leaving the priority to Russian colleagues.

At about the same time, Rich Cifelli carried out intensive fieldwork in the western United States (Utah, Texas, and Oklahoma), as well as in South America. Based on his discoveries, he described several isolated teeth of Cretaceous marsupials (Cifelli 1990a–c; 1993a, b; 1994). Most important was his discovery of a nearly complete dentary containing four molars, two premolars, and alveoli for the first premolar and canine, from the Cedar Mountain Formation (Albian) of Oklahoma (Cifelli 1993a), which he designated the new mammal *Kokopellia juddi* (figure 13.3B, this volume). He assigned *Kokopellia* to the Metatheria, without further qualification. During subsequent years, Cifelli collected more specimens of *Kokopellia* from the medial Cretaceous (Albian, Cenomanian) of central Utah and published another paper on this genus, co-authored with the French paleontologist Christian de Muizon, who had been working for several years in South America (Cifelli and de Muizon 1997). The authors referred to *Kokopellia* as a "primitive marsupial" or a "near marsupial" and argued that the dental formula of this taxon—i4, c1, p3, m4—was primitive with respect to North American marsupials. Other characters of *Kokopellia*, such as the presence of a labial mandibular foramen, an apparently inflected angle, the trace of a Meckel's groove in the dentary, the lack of "staggered" lower incisors, the lack of "twinning" between entoconid and hypoconulid in the lower molars, and the relatively small and mesiodistally narrow upper molar protocone, were all primitive characters for marsupials. During his stay in South America, Christian de Muizon published extensively on early metatherians (especially from the Paleocene of Bolivia), initially in collaboration with Larry Marshall and, later, with Rich Cifelli and other authors.

A most important development for Cretaceous metatherians was the discovery of a nearly complete skeleton with associated skull and fur impressions of the Early Cretaceous *Sinodelphys szalayi*, probably from the Barremian Yixian Formation, part of the Jehol Biota in northeastern China. This unique specimen was described by Luo et al. (2003) in an article published in *Science*. By that time, our book (Kielan-Jaworowska et al. 2004) was already in advanced proofs, and it was impossible to cite Luo et al. (2003) or publish illustrations of *Sinodelphys* (see figure 13.4, in this volume).



13.4. *Sinodelphys szalayi.* A. Reconstruction of the skeleton. B. Reconstruction of the living animal.

A. Modified from Luo et al. (2003: figure 1). B. Original artwork by Oscar Sanisidro, modified by Aleksandra Hołda-Michalska.

During the nineteenth century, and even at the beginning of the twentieth century, Mesozoic mammals were as a rule assigned to Marsupialia (for example, see Owen 1871; Marsh 1887, 1889). By the middle of the twentieth century, the situation had changed dramatically. By 2004, we were able to list (Kielan-Jaworowska et al. 2004: table 13.1) seven genera in the Cohort Deltatheroida: *Deltatheridium*, *Deltatheroides*, *Deltatherus*, *Sulestes*, *Khudukulestes*, *Oxlestes*, and (tentatively assigned) ?*Atokatheridium*, erected by Kielan-Jaworowska and Cifelli (2001). The remaining 19 genera in our table (two of which were only tentatively assigned) were placed in the cohort Marsupialia. As in the case of Deltatheroida, most of these genera are cited without the authors of their names or dates and with complete references only for more important and most completely preserved genera. The list of marsupial genera includes *Anchistodelphys*, *Iugomortiferum*, *Kokopellia*, *Asiatherium*, ?*Marsasia*,

Alphadon, *Aenigmadelphys*, *Albertatherium*, *Protalphadon*, *Turgidodon*, *Varaalphadon*, "*Pediomys*," *Aequiladelphis*, *Iqualadelphis*, *Peradectes*, *Didelphodon*, *Eodelphis*, ?*Pariadens*, and *Glasbius*. Of these, *Asiatherium reshetovi*, erected by Trofimov and Szalay (1994), is the most completely preserved, represented by a skull with dentaries (see figure 13.3, this volume).

As noted above, the most complete Cretaceous marsupial is *Sinodelphys szalayi*, set up by Luo et al. (2003; see figure 13.4, this volume), of which the entire skeleton and a fur halo was preserved. The remaining Cretaceous marsupials named so far are much less complete, in contrast to a rich and diversified fauna of Paleocene marsupials known from Bolivia. Christian de Muizon described several marsupial genera from the Paleocene of Bolivia. In Kielan-Jaworowska et al. (2004), we published as figure 12.1A the exquisitely preserved skull of *Mayulestes ferox*, simplified after Muizon (1998), derived from the Early Paleocene of Bolivia.

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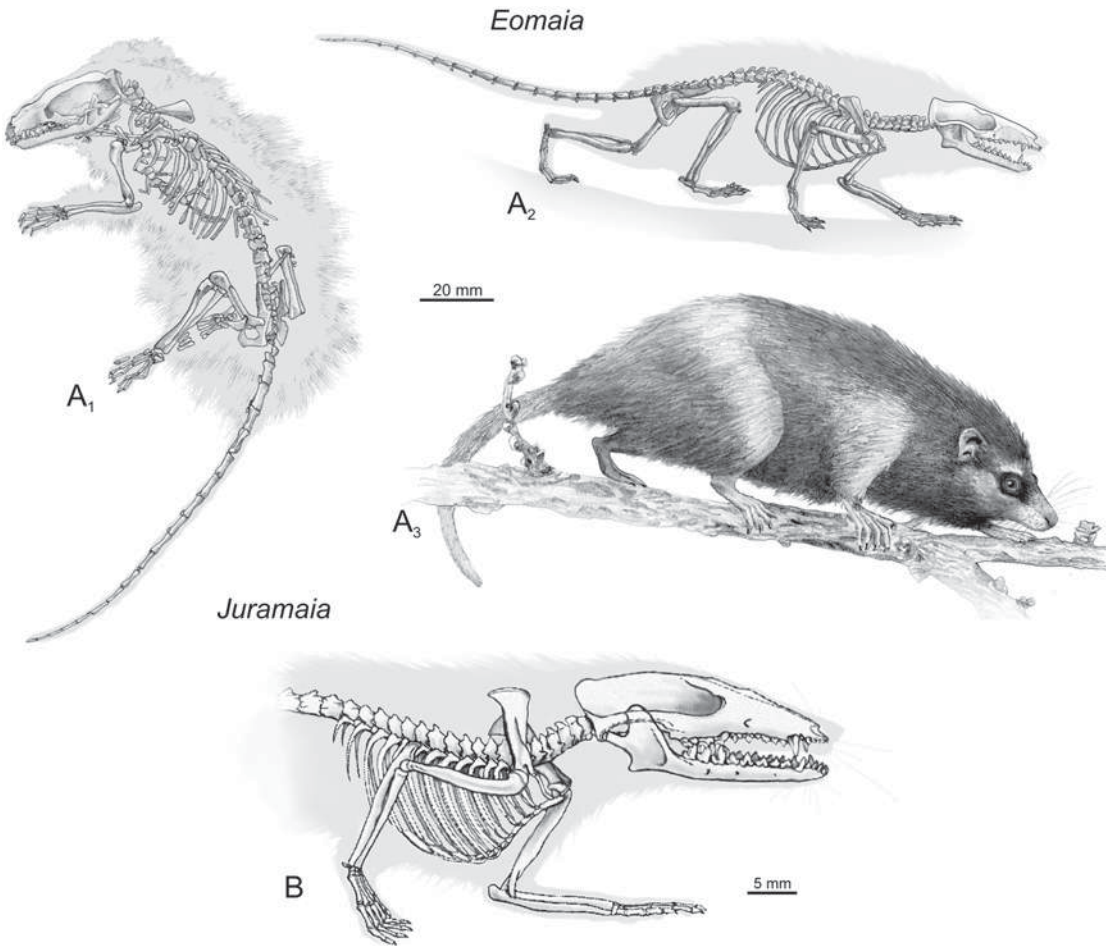


14.1. *Eomaia scansoria,* from the Early Cretaceous (Middle Barremian) of the Yixian Formation, Liaoning Province in northeast China. A. Skeleton. A_1. Nearly complete skeleton with a fur impression, as preserved, holotype. A_2. The skeleton prepared from the rock in walking position. A_3. Life reconstruction of the animal by Marc Klingler. B. Anterior part of the skeleton with skull and forelimbs of *Juramaia windscheffeli,* reversed.

From Ji et al. (2006), emended by Aleksandra Hołda-Michalska.

Eutherian and Placental Mammals

14

The Role of Embryology in Paleontology

THE POSITION OF THE PLACENTALIA AMONG MAMMALS AND THE division of Placentalia into lower rank taxonomic units were for a long time debated. Gill (1872) grouped both marsupials and placentals into the Eutheria, Huxley (1880) limited the scope of Eutheria to Placentalia, and some authors treated Placentalia and Eutheria as synonyms (e.g., Simpson 1945; Kemp 2005). However, most present authors (for example, Wible et al. [2004], largely based on data from Novacek [1999]) limit the Placentalia to crown Eutheria, leaving the Cretaceous Eutheria outside the Placentalia.

The complicated issue of the systematics of Placentalia and Eutheria is perhaps best exemplified in the systematics of primitive therian mammals provided by McKenna and Bell (1997: 43–81). It is beyond the scope of this book to discuss this issue. I refer the readers to an article by Archibald and Rose (2005: table 1.1), which offers a comparison of placental systematics from Linnaeus (1758) to Murphy et al. (2001: summary in table 1.1).

Parker and Haswell (1897) erected the taxon Theria for placental and marsupial mammals, leaving the monotremes in Prototheria, which was established earlier by Gill (1872). McKenna and Bell (1997) assigned to the Theria a new rank of supercohort, in which they placed several poorly known extinct taxa from both Early and Late Cretaceous: the extinct order Deltatheroida erected by Kielan-Jaworowska (1982) and the cohort Marsupialia erected by Illiger (1811), giving to it a new rank.

Members of Eutheria (including living placental mammals) are similar to Metatheria in skeletal anatomy. The most fundamental differences between the two groups lie in the structure of the reproductive tract and the pattern of reproduction. Both marsupials and placentals are viviparous; however, placental mammals differ from marsupials in possessing the unique trophoblastic tissue. The trophoblast forms a barrier between the maternal and embryonic tissues, preventing rejection of the developing embryo. As a result, eutherians undergo a prolonged period of development and morphogenesis in the uterine environment. This permits higher levels of metabolism, more extensive brain development, and a far greater range of morphological divergence as adults (Lillegraven et al. 1987; Kielan-Jaworowska et al. 2004). According to numerous zoologists, there are around 4,630 living mammal species, 4,354 of which belong to placental mammals, which is about 94 percent of all mammals. This indicates the broad radiation of placentals when compared to that of other mammals (marsupials and monotremes). This enormous success

is related, as argued by Lillegraven et al. (1987), to the acquisition of the trophoblast.

Vertebrate paleontologists owe the knowledge of the embryology of therian mammals to Jason A. Lillegraven. For many years, first during 6 years spent at the California State University in San Diego and, later, for some 30 years at the University of Wyoming in Laramie, Lillegraven gave outstanding lectures on embryology, based on his extremely detailed command of the embryological literature. I was greatly impressed when, in the 1970s and beginning of the 1980s, I read numerous papers by Lillegraven on various aspects of embryology (e.g., Lillegraven 1975; and many others). Most interesting were his discussions of the work of the German embryologist Dr. Fabiola Müller.

Between 1967 and 1973 Müller published a series of excellent, meticulously presented papers on the embryology of marsupial and placental mammals, in which she provided detailed comparisons of the two. Written in German, these papers were hardly known outside Germany, but Lillengraven took on the task of reading some 500 pages of her papers in German and summarizing them in English. Lillegraven never met Müller, and I am not sure whether she realized how great a service he had done for her by popularizing her work in English. Probably Lillegraven's best paper about Müller's results was published in 1975 in *Evolution*. In it, he wrote

> Living marsupials are born following a short period of internal gestation at a remarkably immature state of organogenesis. As described by Dr. Fabiola Müller, they have a series of temporary closures for the mouth, eyes, and ears that develop shortly before birth and are functionally significant after birth in attachment to the nipple, development of the secondary jaw joint, and in protecting the eyes and ears against desiccation in the new atmospheric environment. Living eutherians generally have longer periods of internal gestation than do marsupials, and some have greatly lengthened intrauterine development times. Even eutherians that may be born in precocial states intrauterinely form transitory mouth, eye, and ear closures at early stages of development that may be lost well before birth. These closures are today without function in eutherian nidifuges and seem only to be conservative features retained from eutherian ancestors that were, as are marsupials today, in an extreme nidicolous state, following a short period of internal gestation. (Lillegraven 1975: 719)

Lillegraven further argued that

> the "invention" of trophoblastic tissues by primaeval eutherians was probably the single most important evolutionary event in the history of the infraclass. The ability of the trophoblast to protect the embryo from immunological attack and to coordinate the endocrinological events, nutritional sources, and waste removal requirements were key features in the evolution of prolonged internal gestation combined with sustained high rates of organogenesis; the birth of anatomically advanced offspring was thus allowed. Marsupial embryogenesis is rigidly channeled by natural selection in that the new born must be capable of independent travel to and attachment onto the teat. Eutherians, on the other hand, are allowed

> greater flexibility of embryological heterochrony and anatomical "experimentation." This is seen especially clearly in adaptation of forelimbs (with flippers, non-opposable claws, single hooves, etc.), parts of the body critically adapted to specific ways of life in all species. A case is made for the possibility that the immediate common ancestor to marsupials and placentals was viviparous and nidicolous as are the marsupials today. (Lillegraven 1975: 720)

Among the tens of illustrations in Müller's papers, those from her paper of 1972, which illustrate numerous eutherian embryological stages with various closures, are especially interesting. Lillegraven's papers induced me to read Müller's originals. From illustrations in her papers I made slides for my presentations, and I used these important new data on the Eutheria in my lectures.

Foreign Languages and the Spread of Scientific Literature

The case of popularization of Müller's work by Lillegraven is one of many examples showing how important a knowledge of foreign languages is for scientists. A similar case occurred in the 1950s, when the great German entomologist Willy Hennig published his important idea of phylogenetic systematics in German. For many years his ideas were hardly known outside Germany. The situation changed in 1966 when Hennig's book Phylogenetic Systematics was translated into English and published in the United States. Soon after, numerous American and Western European biologists became enthusiasts of Hennig's idea and developed it further. Probably the most tragic history related to the issue of the language barrier in science occurred in the Soviet Union. After the revolution, all the Russian scientific literature (in many disciplines at very high levels) was published only in Russian, with rare quotations of Western literature. Still worse was the situation in Western countries, where Russian literature was quite often completely ignored! For some 80 years there were two separate lines of development in science, which ignored one another. Fortunately, the situation began to change in the second half of the twentieth century, when most important Russian scientific journals began being published in English translation.

In Poland and in many other European countries before the Second World War, German was the main scientific language, especially within the biological sciences. In addition, in Poland for centuries it was regarded as elegant to speak in French. The situation again changed after the Second World War, when all around the world English gradually began to dominate. I have been in a lucky situation as far as reading foreign languages is concerned, as my father, who spent his youth in Russia and then in the Soviet Union and passed extramural high school finals in Russia, knew Russian perfectly. At home he used to sing Russian songs, cite Russian proverbs, and tell Russian jokes. He did not teach us the Russian language, but beginning from my childhood this language was somehow around us, and I never had problems in reading Russian

scientific literature or communicating with Russian colleagues. I learned French in the high school and some German during the war, when Poland was occupied by Germany. But with aversion during the occupation to everything that was German, I did not learn to speak German.

I did not have any contact with English until I was 16. This was during the war, and although the financial situation of our family was difficult, our parents decided that their two daughters should learn English. After having a few English teachers, I finally met Mrs. Górska, an Austrian lady married to a Pole (a professor of mathematics). I do not know how she knew English. I met her around 1943. She had been a widow for several years, and she made her and her son's living by giving English and German lessons. I learned much from her and never had any problems reading and understanding English scientific literature. But I still speak English with a strong Polish accent, and I have had to work hard perfecting my English writing.

Today Polish children are in a much better situation with access to English. It is now taught in many Polish high schools, and several schools have double language classes. In addition there are many English and American schools (beginning with nursery schools). I always have had a feeling of injustice! I believe that our Anglo-Saxon colleagues, who write their scientific papers in their mother tongue, do not realize how easy their life is in comparison with those of their foreign colleagues!

The Oldest Eutherian Mammals and the Matter of Eomaia and Juramaia

According to data available in 2010 and at the beginning of 2011, the oldest eutherian mammal and the oldest marsupial made their appearance at approximately the same time during the Early Cretaceous in the same territory – within the Yixian Formation in northeastern China.

Eomaia scansoria (figure 14.1A), from the Early Cretaceous Middle Barremian Yxian Formation, has for nine years (2002–2011) been cited as the earliest eutherian mammal. Its estimated age is about 125 Ma. It extends the record for the oldest eutherian with skull and skeleton by about 40–50 Ma. The only known specimen has been preserved in the most fossiliferous horizon of the Yixian Formation, with fur impression, and it consists of a skull with nearly complete dentition and nearly complete postcranial skeleton. The structure of the carpus and tarsus of *Eomaia* speaks for the arboreal mode of life, and the arrangement of bones is different than that found in scansorial marsupials, recalling instead the arrangement found in advanced placentals, for example, in some primates.

Eomaia differs from metatherian genera (including marsupials) in having a typical early eutherian dental formula consisting of five upper and four lower incisors, single upper and lower canines, five upper and five lower premolars, and four upper and three lower molars. It differs from metatherians also in several other characters, for example, in having equal distance between the talonid cusps.

Until August 2011 *Eomaia*, was regarded as the oldest eutherian. On 24 August 2011, I read the just-issued online version of the journal *Nature*, in which I found an article by four Chinese paleontologists (Luo, Yuan, Meng, and Ji) announcing the discovery of the oldest eutherian mammal, dubbed *Juramaia sinensis*. *Juramaia* (figure 14.1B) was found in the Jurassic Tiaojishan Formation in Liaoning Province in northeastern China and has been dated at about 160 Ma. The only known skeleton of *Juramaia* is less complete than that of *Eomaia*, with only its anterior part being preserved. The left mandible and the maxilla have survived; the remainder of the skull is badly distorted. The dentition is almost complete, with the same dental formula as *Eomaia*. Similar dental formulae occur in numerous other Cretaceous eutherians (Cifelli 2000). *Juramaia* differs from metatherians in lacking the close approximation of the hypoconulid and the entoconid, characteristic of numerous marsupials. It differs from metatherians (except *Sinodelphys*) in lacking the inflected mandibular angle. *Juramaia* differs from *Eomaia* in having a two-rooted upper canine. *Juramaia* differs from australosphenidans in lacking a continuous mesial cingulid and the wrapping cingulid, and it differs from most australosphenidans in lacking the postdentary trough on the mandible. *Juramaia* differs from all known Cretaceous eutherians in having a deeper ectoflexus on P5–M2. The manual phalanges of *Juramaia* suggest a scansorial adaptation. Luo and colleagues further argued that the oldest-known eutherians, *Juramaia* and *Eomaia*, and the earliest metatherian, *Sinodelphys*, were scansorial and differ from contemporary Mesozoic mammals, most of which were terrestrial (Luo et al. 2011).

The study of Luo et al. (2011) is too technical to be reported here in full detail. They concluded that *Juramaia* is a basal-most eutherian, a Mesozoic relative to Cenozoic placental mammals, more closely related to extant placentals, than to any metatherians, including Cretaceous *Sinodelphys* and *Deltatheridium*.

The Cretaceous Radiation of Eutherian Mammals

Kielan-Jaworowska, Cifelli, and Luo 2004 (table 13.1) listed 40 Cretaceous eutherian genera. Of these, 5 are of Early Cretaceous age, and 35 are Late Cretaceous. The five Early Cretaceous eutherians, cited in alphabetic order, are *Eomaia*, *Montanalestes*, *Murtoilestes*, *Otlestes*, and *Prokennalestes*.

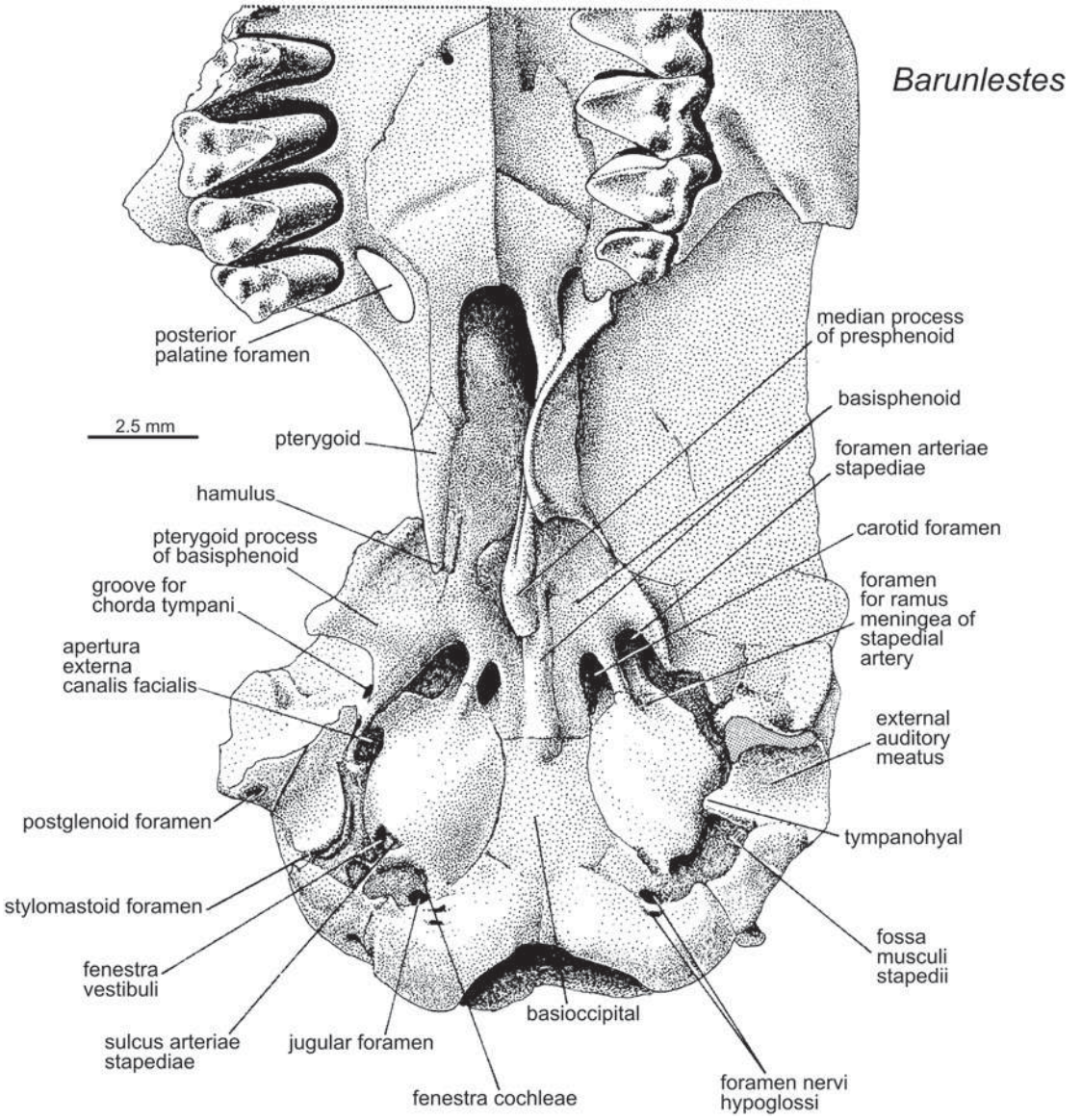
Eomaia scansoria, from the Early Cretaceous Middle Baremian Yixian Formation, until recently had been cited as the earliest eutherian mammal (see Luo et al. 2011). It differs from *Murtoilestes* in having the trigonid shorter anteroposteriorly and a longer talonid basin. It differs from the North American *Montanalestes* erected by Cifelli (1999) in having the paraconid lower than the metaconid. Furthermore, it differs from *Montanalestes* and all the Late Cretaceous eutherians in retaining the Meckel's groove and from most eutherians – except *Prokennalestes*, *Montanalestes*, and several asioryctitherians – in having a slightly in-turned angular process, but this process does not form a horizontal shelf, as it

does in most marsupials. The name *Prokennalestes* was known from the early 1970s. It was introduced as a *nomen nudum* by Belyaeva et al. (1974) and used by other authors.

In 1989 I published a paper with Dashzeveg in which we formally established the genus *Prokennalestes* with two named species, *P. trofimovi* and *P. minor*. The collection we described consisted of 39 specimens, assembled by Dashzeveg and housed at the Institute of Geology of the Mongolian Academy of Sciences in Ulaanbaatar. (A rich collection of mammals from the same locality had been assembled by Russian paleontologists and housed at their Institute of Paleontology in Moscow, but it was not available to us at the time of our writing.) The two species of *Prokennalestes* described by us differ in size, and it cannot be excluded that they could be sexual morphs within the same species. Sigogneau-Russell et al. (1992) described the new dentaries of *Prokennalestes* and argued that the dental formula of I4, C1, P5, M3 was valid for *Prokennalestes*, at least as far as the premolars were concerned. Another taxon similar to *Prokennalestes*, named *Murtoilestes*, is known from apparently somewhat older beds from Russia and described by Averianov and Skutschas (2000, 2001).

Pappotherium and other undescribed taxa from the approximately equivalent Trinity Group of Texas were regarded as eutherians by Slaughter (1971, 1981), but they are poorly known, and this referral was viewed by most researchers with general skepticism (e.g., Butler 1978; Kielan-Jaworowska et al. 1979; Kobayashi et al. 2002; see also chapter 11, in this volume). Similarly, eutherian affinities were suggested for the Australian Early Cretaceous mammals *Ausktribosphenos* and *Bishops* (Rich et al. 1997, 1999, 2001a), but this view has not been widely accepted; for example, see Kielan-Jaworowska et al. (1998), but also see the reply by Rich et al. (1998), and Musser and Archer (1998), Archer et al. (1999), and Luo, Cifelli, and Kielan-Jaworowska (2001a). See also further criticism by Luo et al. (2002), Kielan-Jaworowska et al. (2004), and chapter 6 (in this volume). An early presence of Eutheria in Asia, coupled with the fact that eutherians were the dominant therians in the Late Cretaceous faunas on that continent, led to the view that they arose in Asia, later spreading to North America and elsewhere (Kielan-Jaworowska 1982). The question remains open, however, as a probable eutherian, *Montanalestes*, was described from the Early Cretaceous of North America (Aptian or Albian of Montana), and it might be slightly older even than *Eomaia* (Cifelli 1999).

The list of the Late Cretaceous Eutheria cited by Kielan-Jaworowska et al. (2004: table 13.1) includes 35 genera, which I cite without their authorities and dates. These are: *Bobolestes*, *Eozhelestes*, *Asioryctes*, *Ukhaatherium*, ?*Bulaklestes*, *Kennalestes*, ?*Sailestes*, *Daulestes*, *Zalambdalestes*, *Alymlestes*, *Barunlestes* (see figures 14.2 and 14.3, in this volume, the latter showing four reconstructions of the heads of the Late Cretaceous eutherian genera), *Kulbeckia*, ?*Beleutinus*, *Deccanolestes*, *Gypsonictops*, *Paranyctoides*, *Cimolestes*, *Batodon*, *Procerberus*, *Telacodon*, *Zhelestes*, *Alostera*, *Aspanlestes*, *Avitotherium*, *Eoungulatum*, *Gallolestes*,



14.2. *Barunlestes butleri* Kielan-Jaworowska, 1975a. Ventral view of the braincase and part of the palate.

From Kielan-Jaworowska and Trofimov (1980). Artwork by Jerzy Dzik.

Labes, *Lainodon*, *Parazhelestes*, *Sorlestes*, *Baioconodon*, *Oxyprimus*, *Protungulatum*, "*Mimatuta*," and *Perutherium*.

The best preserved of the Late Cretaceous eutherians are those from the Djadokhta and Baruungoyot formations of the Gobi Desert, represented by partial or complete skulls and often fragments of the postcranial skeleton.

During the Polish-Mongolian Paleontological Expeditions, our first collection of Mesozoic mammals was assembled in 1964 from the Djadokhta Formation at Bayan Zag (at that time referred to as Bayn Dzak)–the locality first discovered by American paleontologists in the 1920s. Our collection of Late Cretaceous mammals collected during the 1964, 1965, and 1967 expeditions numbered 36 specimens, 13 of which

14.3. Skulls and reconstructions of the heads of four taxa from the Late Cretaceous of the Gobi Desert in Mongolia (A–C) and Uzbekistan (D). A. *Zalambdalestes,* from the Djadokhta Formation at Bayan Zag. B. *Barunlestes,* from the Baruungoyot Formation at Khulsan. C. *Asioryctes,* from the Baruungoyot Formation at Khulsan. D. *Uchkudukodon,* from a channel deposited in the Coniacian part of the Bissekty Formation, in Uzbekistan, a juvenile specimen. The arrangement of the skulls and heads does not imply a phylogenetic succession. They are arranged according to the size, all in the same scale.

The skulls in A–C are from Kielan-Jaworowska (1975b), artwork by Krystyna Budzyńska. The skull in D is redrawn and emended from McKenna et al. (2000), artwork by Natalia Florenskaya. Computer adjustments by Aleksandra Hołda-Michalska. Reconstructions of the heads, original artwork by Oscar Sanisidro.

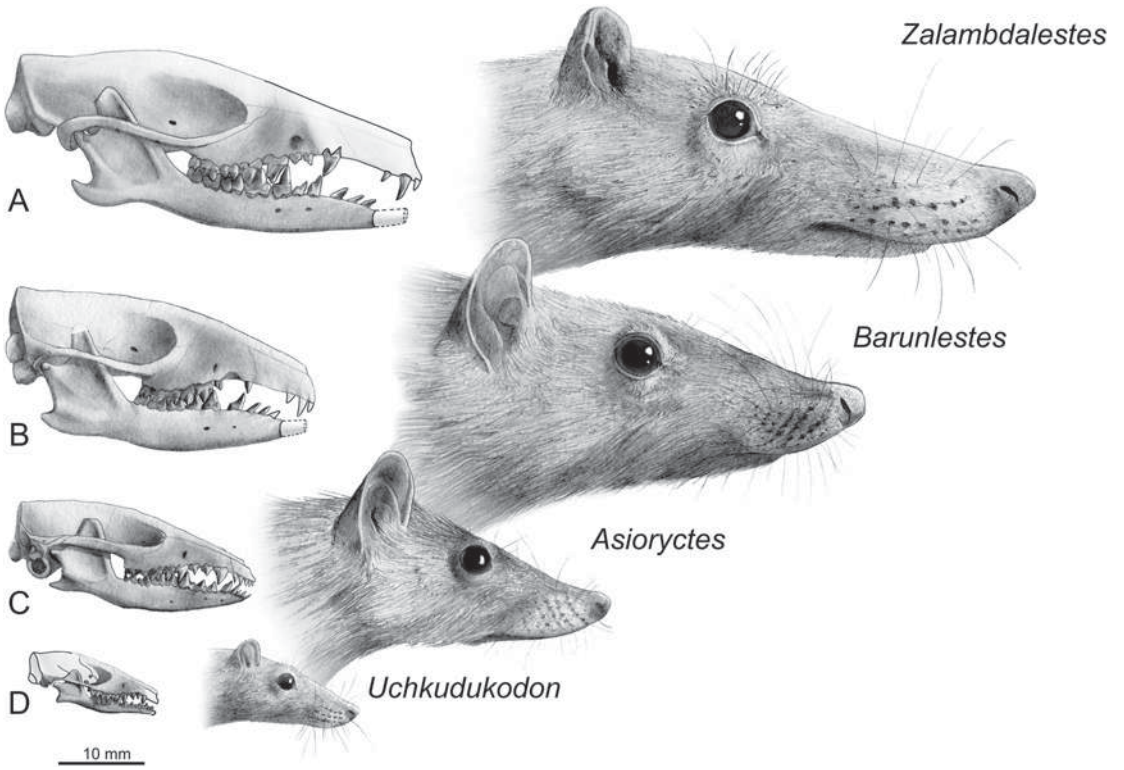
were eutherians, or so—as it seemed to me at that time—and 23 multituberculates. About that time I wrote to Malcolm McKenna telling him about our discoveries. In April 1965, Malcolm first came to Poland to see our modest (at that time) Mesozoic mammal collection.

In 1969 I published a preliminary report (Kielan-Jaworowska 1969c) on our eutherian fauna from Bayan Zag, and I erected the new genus and species *Kennalestes gobiensis*, based on three partial skulls. I also figured two beautifully preserved specimens of *Zalambdalestes.* In addition I noted the presence of a relatively large, incomplete dentary, which I subsequently recognized as belonging to *Deltatheroides.* Of all those specimens, the most intriguing was a tiny skull of a eutherian mammal, associated with two dentaries in occlusion. I referred to this specimen as a "new genus and species . . . represented by a single individual ZPAL MgM-I/1, with lower jaws in occlusion" (Kielan-Jaworowska 1969c: 173). The cranial roof of the skull was partly damaged. I did not think that it belonged to *Kennalestes* because it had a single-rooted upper canine, while in *Kennalestes* the upper canine is double rooted.

The specimen was unusually fragile, and I realized that separation of the lower jaws and removal of the specimen from the matrix would be very difficult. During Malcolm's first visit in Warsaw in 1965, he asked if he could borrow the tiny specimen and have an experienced technician at the American Museum of Natural History in New York prepare it for us. I gratefully accepted his proposal. The difficult preparatory work was carried out by Martin Cassidy in New York. During one of Malcolm's subsequent visits to our institute, he returned the cleaned specimen with separated lower jaws (plate 7). A glance at the dentition of the skull made me realize that, contrary to my previous impression, this specimen was indeed a juvenile individual of *Kennalestes gobiensis.* The single-rooted upper canine was clearly deciduous. I described this specimen and offered an interpretation of its braincase structure in a paper on the skull structure of *Kennalestes* and *Asioryctes* (Kielan-Jaworowska 1981). In that paper I presented photographs of this juvenile *Kennalestes.*

From among 35 genera of the Late Cretaceous mammals listed above, five monotypic taxa come from the Gobi Desert: *Kennalestes*, *Asioryctes*, *Zalambdalestes*, *Barunlestes*, and *Ukhaatherium*. I published (Kielan-Jaworowska 1975b) a preliminary description of *Barunlestes* (see plate 7E) and *Asioryctes*, both from the Baruungoyot Formation. I provisionally assigned them to the Palaeoryctidae, but later on (in Kielan-Jaworowska 1981) I placed them in a new family, the Asioryctidae (figure 14.3C). While working on the postcranial skeleton of the zalambdalestids, I noticed that on the anterior wall of the pubis in the holotype specimen of *Barunlestes* (ZPAL MgM-I/77), there was a small triangular surface that tapered downward. I recognized this triangular surface as an articular area for the marsupial (epipubic) bone (Kielan-Jaworowska 1975b).

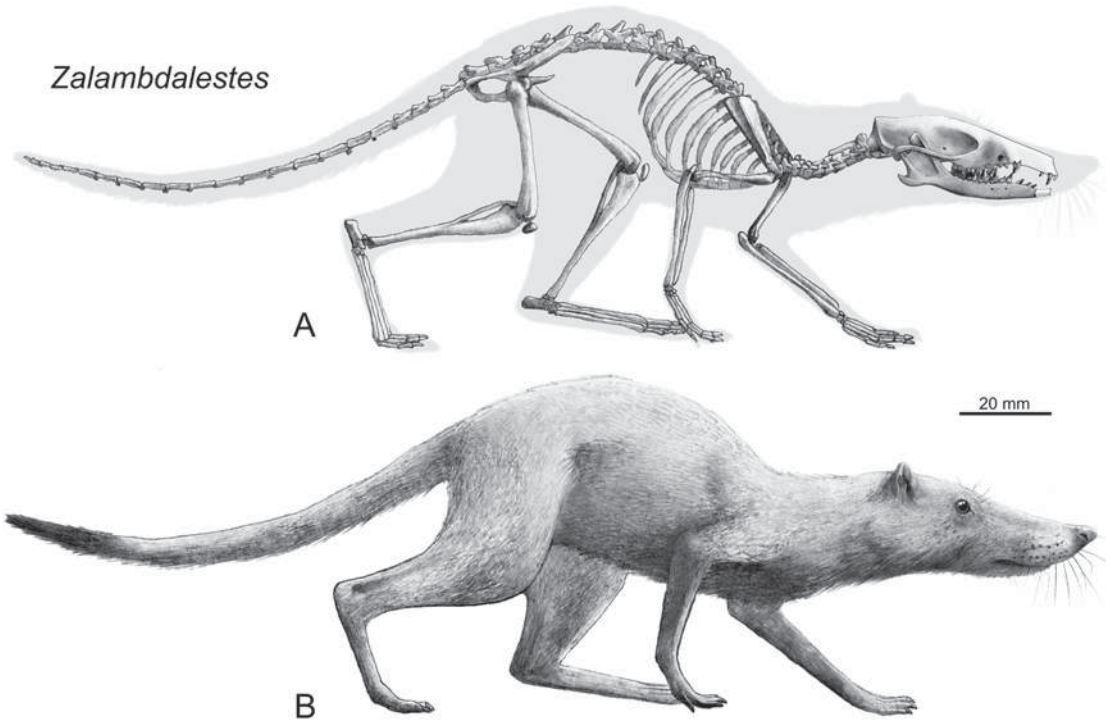
Twenty-two years later, American paleontologists described from the Ukhaa Tolgod locality in the Nemegt Basin a new genus with a single species, *Ukhatherium nessovi*, in which the epipubic bones were preserved



in situ (Novacek et al. 1997). In the same paper they also figured two specimens identified as cf. *Zalambdalestes*, in which the epipubic bones were also preserved. Novacek and colleagues (1997) erected the high-rank taxon Asioryctitheria, to which they assigned *Asioryctes*, *Ukhatherium*, and *Kennalestes*. They concluded:

> Regardless of its implications for reproductive evolution, evidence that Asioryctitheria and Zalambdalestidae retain epipubics refutes a traditional diagnostic feature of the Eutheria. This and other primitive features of Asioryctitheria suggest a basal position for this group among eutherians. Further corroboration of this pattern would provide a useful framework for the difficult problem of higher eutherian phylogeny . . . where the basal branches are, at present, poorly resolved. This pattern raises the possibility that the innovations in the reproductive system diagnosing the crown group Placentalia . . . may not have been present in early members of the Eutheria. (Novacek et al. 1997: 488)

The best known of the Late Cretaceous eutherian genera is *Zalambdalestes*. The four specimens collected by members of the Central Asiatic Expeditions at Bayan Zag were eroded and poorly preserved (Gregory and Simpson 1926). The specimens collected during the Polish-Mongolian Expeditions were somewhat better preserved but did not include complete, undistorted skulls (Kielan-Jaworowska 1969c, 1975a, 1975b, 1978; Crompton and Kielan-Jaworowska 1978). Finally, however, an exquisitely preserved collection of numerous skulls of *Zalambdalestes* was



14.4. *Zalambdalestes lechei.* A. Reconstruction of the skeleton. B. Life reconstruction of the animal.

A. Emended from Kielan-Jaworowska et al. (2004: figure 13.17B). B. Original artwork by Oscar Sanisidro, emended by Aleksandra Hołda-Michalska.

assembled at the famous locality of Ukhaa Tolgod by members of the Mongolian Academy–American Museum Expeditions. These specimens were announced by Wible, Novacek, Rougier, and McKenna (1998) in an abstract (not cited here) and subsequently described in detail in a comprehensive monograph by Wible, Novacek, and Rougier (2004), in which the authors discussed the position of the Zalambdalestidae among the Cretaceous Eutheria. The latter authors noted the remarkable anatomical diversity of the specimens, assigned by them to *Zalambdalestes lechei*, and concluded: "The possibility exists that more than a single species, *Z. lechei*, is represented" (Wible et al. 2004: 3). I agree with their conclusion, for in addition to differences in the skull structure of the Bayan Zag and Ukhaa Tolgod specimens, I noticed an important difference in the robustness of the lower jaw and the size of the first lower incisor, which is distinctly larger in Bayan Zag specimens than in those from Ukhaa Tolgod (figures 14.3A. and 14.4).

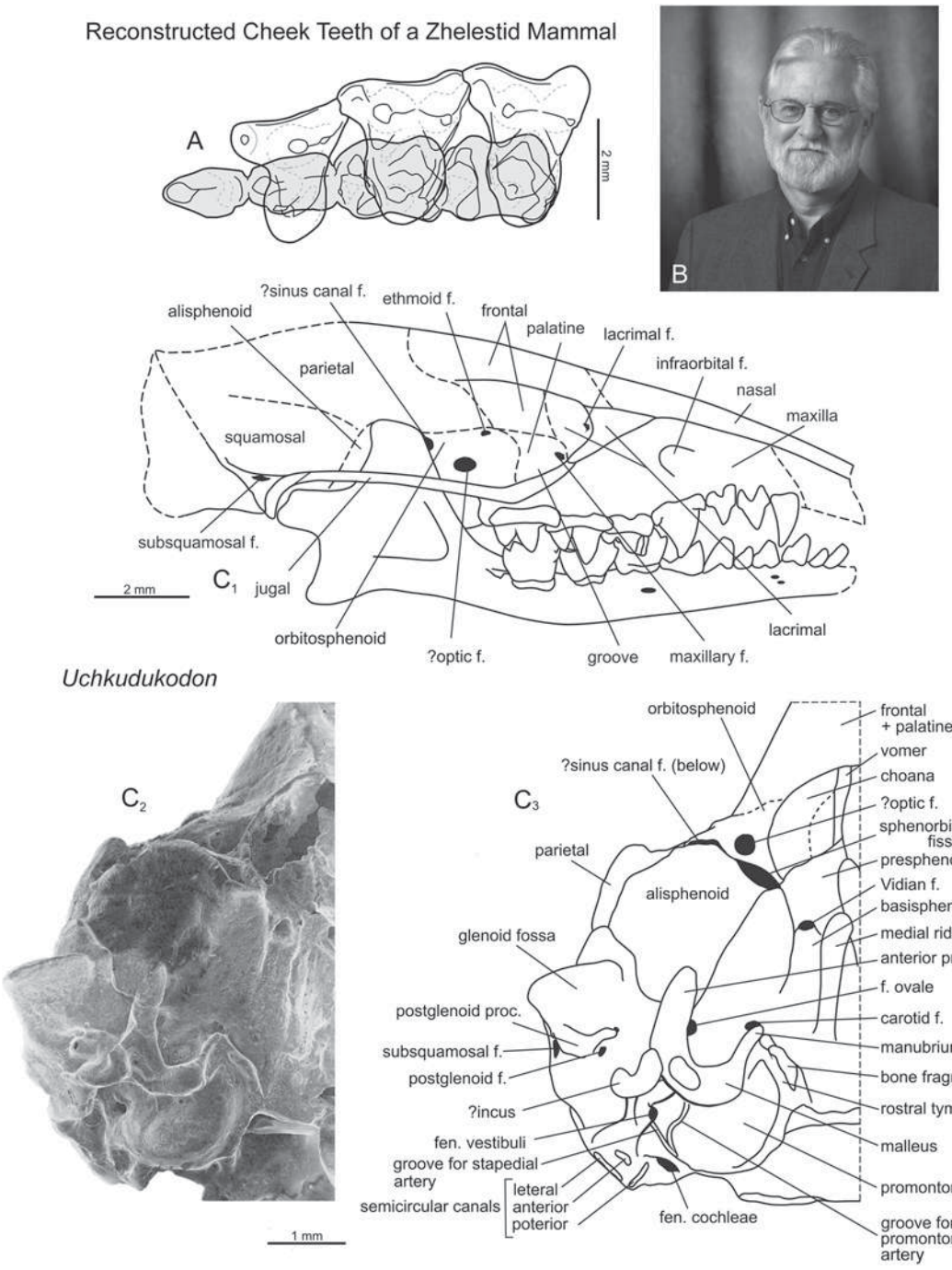
Prior to 1970 we (the members of the Polish-Mongolian Paleontological Expeditions) collected Cretaceous mammals only at Bayn Zag and from its stratigraphic equivalent, the Toogreeg beds. During the 1970 Polish-Mongolian Expedition, we made an important discovery – the first mammals found in the Baruungoyot Formation, which underlies the Nemegt Formation in the Nemegt Basin. During the 1970 and 1971 expeditions, we concentrated our efforts on collecting mammals from various localities within the Baruungoyot Formation and in Red Beds of Hermiin Tsav. After the 1971 expedition, the number of specimens of Cretaceous

mammals from Mongolia housed at the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw numbered some 180 specimens.

A variety of eutherians from the early Late Cretaceous of Central Asia is known owing to the activity of Lev Nessov (figure 3.4). Beginning in 1978, Lev collected Cretaceous mammals and other vertebrates from several localities of the republics of Uzbekistan, Kazakhstan, Kyrgyzstan, and Tajikistan (Kielan-Jaworowska and Nessov 1990, 1992; Nessov and Kielan-Jaworowska 1991; Nessov et al. 1994; Nessov 1997 [published posthumously, and numerous papers cited therein]; Averianov and Kielan-Jaworowska 1999).

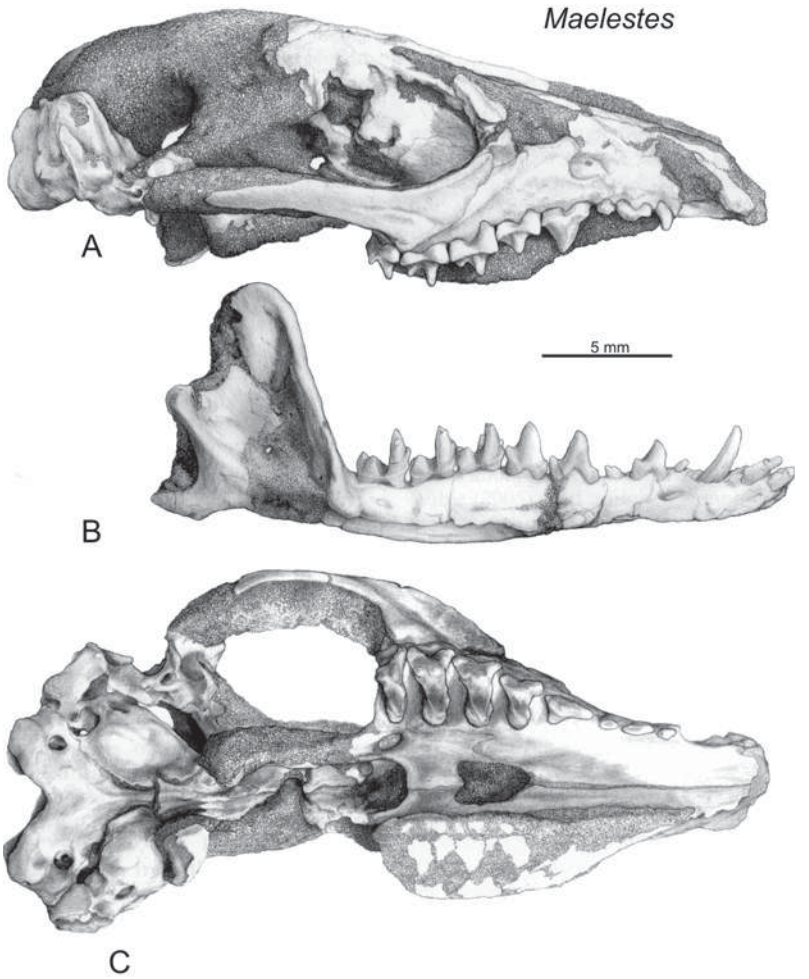
Among the eutherian mammals collected by Nessov in Uzbekistan was one nearly complete Late Cretaceous skull of a juvenile individual, associated with both lower jaws in occlusion. The skull was found in 1989 by Vyacheslav Trikhin, a member of Nessov's crew, in the Bissekty Formation near Dzharakuduk, in the central part of the Kyzylkum Desert of Uzbekistan. In 1990, Lev brought this specimen to Oslo, and we decided to send it to Malcolm McKenna at the American Museum of Natural History, who suggested he might be able to organize its preparation. The specimen was prepared by William Amaral of the Museum of Comparative Zoology at Harvard. Then black-and-white photographs were taken at the Vertebrate Paleontology Department of the American Museum of Natural History. Malcolm invited Jin Meng to assist us in interpretation of the ear region.

When the specimen was sent back to Oslo, I took the SEM micrographs of its ear region (figure 14.5C) with the help of Jørn H. Hurum. In a paper by McKenna, Kielan-Jaworowska, and Meng (2000), we assigned the specimen to Asioryctitheria, family *incertae sedis*, genus *Daulestes*, and dedicated it to Lev A. Nessov, after his tragic death in 1995. After this publication, I returned the specimen we had named *Daulestes nessovi* to the Zoological Museum in St. Petersburg. The Bissekty Formation that yielded this specimen is of Coniacian age, so our specimen was the oldest-known skull of a eutherian mammal at that time. Subsequently, Archibald and Averianov (2006), on the basis of new material of "*Daulestes*" *nessovi* from the Bissekty Formation, withdrew this species from *Daulestes* and erected the new monotypic genus *Uchkudukodon*, containing the single species *Uchkudukodon nessovi*.Most of the eutherian mammals that Lev Nessov found belong to "Zhelestidae," the archaic hoofed mammals known since the time of Cope in 1880s as "condylarths." Nessov originally described representatives of the "Zhelestidae" in several small papers published only in Russian. Beginning in 1990, I invited him several times to Oslo, and we worked together comparing his fossils assembled from Uzbekistan and other Middle Asiatic countries with those of mine from Mongolia. In 1991 Nessov arrived in Oslo to attend the Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota and worked with me on a paper, "Evolution of the Cretaceous Asian Therian Mammals," which we presented at the symposium (Nessov and Kielan-Jaworowska 1991).



14.5. A. Superimposed occlusal outlines of the cheek dentition of the zhelestids *Zhelestes bezelgen* (upper) and *Aspanlestes aptap* (lower). B. J. David Archibald. C. *Uchkudukodon nessovi* from the Bissekty Formation (Coniacian) of Uzbekistan. Reconstruction of the skull and dentary in right lateral view (C_1). SEM micrograph of the ventral view of the right basicranial region (C_2), and explanatory drawing (C_3).

A. From Nessov, Archibald, and Kielan-Jaworowska (1998). B. Credit to J. David Archibald. C. From McKenna et al. (2000), originally assigned to Daulestes. C_1. Artwork by Natalia Florenskaya, modified by Aleksandra Hołda-Michalska. C_2. SEM photograph by Jørn H. Hurum. C_3. Artwork by Z. Kielan-Jaworowska.



14.6. *Maelestes gobiensis.* Incomplete skull in right lateral (A) and ventral (C) views, the left dentary (reversed) in lateral view (B). The holotype specimen (the only one known) is from Ukhaa Tolgod, regarded by the authors as equivalent of the Late Cretaceous Djadokhta Formation, but possibly slightly younger.

From Wible et al. (2007).

Lev also brought to Oslo a collection of his archaic hoofed mammals. I was not familiar with his group, which did not occur in the Cretaceous of Mongolia. I suggested to Lev that we might invite as a co-author of our study a North American early ungulate specialist, J. David Archibald of San Diego State University (figure 14.5B). David accepted our proposal and came to Oslo for the Mesozoic Terrestrial Ecosystems Symposium, where he met Lev. Our collaboration resulted in a paper (Nessov, Archibald, and Kielan-Jaworowska 1998), which Archibald presented at the symposium Dawn of the Age of Mammals in Asia, organized by K. Christopher Beard and Mary Dawson in Pittsburgh in 1998. One drawing of the "zhelestid" mounted from *Zhelestes bezelgen* (upper) and *Aspanlestes aptap* (lower) from our paper is reprinted here as figure 14.5A.

Wible, Rougier, Novacek, and Asher (2007) described one more eutherian skull from the Gobi Desert, designated *Maelestes gobiensis* (figure 14.6). Two years later the same team published a comprehensive monograph on *Maelestes,* which included discussion of the phylogeny of Cretaceous Eutheria (Wible et al. 2009). The phylogenetic analysis

was unusually thorough and significant, including several corrections to previous analyses by the same authors (Wible et al. 2007). The main conclusion was that no Cretaceous eutherians could be identified as members of any known placental group.

In Western Europe, several eutherians are known from the Campanian and Maastrichtian, where they are represented by rare, fragmentary fossils. The best known of these, *Lainodon* and *Labes*, appear to represent a distinctive group related to "zhelestids," suggesting endemism in the latest Cretaceous of Western Europe and a probable earlier continuity with faunas of Asia (see, for example, Gheerbrant and Astibia 1994). The earliest occurrence of the "Zhelestidae" is in the Cenomanian or Turonian of Japan (Setoguchi et al. 1999), demonstrating that the group had a wide distribution. To the east, eutherians are well known from the Campanian of Mongolia, where they are represented by six genera and three families (Asioryctidae, Kennalestidae, and Zalambdalestidae) and one genus assigned to a family *incertae sedis*. The marked compositional difference between the eutherians and other animals of Mongolia and those of Uzbekistan and adjacent countries of the previous Soviet Union (the abundance of multituberculates in Mongolia, replaced ecologically by members of the "Zhelestidae" in Middle Asia), is probably due to differences in habitat and environment (Nessov et al. 1998).

In December of 2007, Luo published a comprehensive article, "Transformation and Diversification in Early Mammal Evolution," in *Nature* (Luo 2007b), in which he presented a broad review of Mesozoic mammal diversification compared to their present-day morphological counterparts. He recognized five distinct "experiments" among Mesozoic mammals that had developed independently from their living morphological counterparts. I discuss this issue in the following chapters.

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15.1. Reconstruction of *Repenomamus robustus,* a carnivorous mammal slightly more than 1 m long, which has just hunted down a juvenile dinosaur, *Psittacosaurus,* and holds it in its mouth.

Original artwork by Aleksandra Hołda-Michalska.

Aspects of Paleobiology of Mammaliaforms and Early Mammals

15

THE LAST TWO DECADES HAVE BROUGHT AN UNUSUAL BLOOMING OF papers that clearly show that Mesozoic mammaliaforms and mammals were much more diversified than had been previously thought. Luo (2007a, b), in his excellent reviews of Mesozoic mammal diversification, recognized five "experiments." In the evolutionary path of early mammals, Luo demonstrated the convergence of new "experiments" with modern mammal morphotypes. Luo challenges

> the traditional assumption that Mesozoic mammals were small animals with generalized feeding and terrestrial habits and had few of the diverse ecomorphotypes of Cenozoic mammals. This hypothesis . . . is now contradicted by recent discoveries of a great range of ecological specializations, such as:
>
> a) the swimming and fish-feeding docodont *Castorocauda* (Ji et al. 2006), and semi-aquatic habits of *Haldanodon* (Martin 2005, 2006);
>
> b) ambulatory carnivory or scavenging (predation or feeding on other vertebrates in large gobiconodontids, see Hu et al. 2005b) and large individuals of *Sinoconodon* (Luo, Crompton, and Sun 2001b);
>
> c) scratch-digging and feeding on colonial insects in *Fruitafossor* (Luo and Wible 2005);
>
> d) scansorial (climbing) limbs characteristic of basal eutherians and metatherians, and their near relatives (Krebs 1991; Ji et al. 2002; Luo et al. 2003);
>
> e) volant (gliding) adaptation in *Volaticotherium* (Meng et al. 2006). (Abridged from Luo 2007a)

To the five types recognized by Luo (2007a) one may add at least two:

f) some multituberculates, resembling some modern rodents in the structure of dentary and arrangement of dentition and, apparently, in the mode of life (see chapter 10); and
g) zalambdalestids, resembling present-day Macroscelididae that are fast-moving, often jumping animals, living in the steppes and savannahs of middle-north Africa. As demonstrated by Kielan-Jaworowska (1978), apparently zalambdalestids had a lifestyle similar to that of macroscelidids (see chapter 14).

As noted in chapter 4, the animals that arose from the therapsids during the Late Triassic, previously assigned to Mammalia, are now more often assigned to the two high-rank taxa, non-mammalian Mammaliaformes

and Mammalia. The main skeletal difference between early mammaliaforms and mammals relates to the structure of the lower jaw and its suspensorium. It is not clear if these differences in anatomy had an effect on their external appearance and mode of life. In the text below I examine some aspects of the supposed physiology of early mammaliaforms and early mammals that might shed light on this question.

Homeothermy of Advanced Mammal-Like Reptiles and Early Mammals, and the Size of Early Mammals

The well-known South African paleontologist Professor A. S. Brink (1924–1991) spent part of his scientific life studying cynodonts and other therapsid reptiles from the Karoo Formation of southern Africa. He described several excellently preserved specimens of the common Early Triassic cynodont *Thrinaxodon liorhinus* including juveniles (Brink 1956, 1980). Brink argued that *Thrinaxodon* probably had a diaphragm, characteristic of mammals, related to the more efficient breathing needed for homeothermic animals. The existence of a diaphragm may be deciphered from the structure of the vertebral column. In the majority of the therapsid reptiles the lumbar ribs exist. However, in some genera of cynodonts, for example, *Thrinaxodon*, the lumbar ribs have been notably shortened (Jenkins 1971), which was regarded as evidence of the presence of a mammalian diaphragm. The lack of lumbar ribs in placental mammals has been preceded by the shortening of them in some cynodonts and mammaliaforms. The mobile and reduced lumbar ribs were found in the following mammaliaforms: in a "symmetrodontan" *Akidolestes* and in a docodontan *Castorocauda*. In addition to the taxa mentioned above, the reduced and mobile lumbar ribs have been also found in many primitive early mammals.

The development of respiratory turbinals, such as those occurring in present-day mammals, also relates to respiration. The complete ossified respiratory turbinals have not been found in mammaliaforms. Hillenius (1994) and Hillenius and Ruben (2004) argued that bony ridges that occur within the nasal cavity of non-mammalian therapsids should be interpreted as attachment sites for turbinals. Kielan-Jaworowska and Trofimov (1980: 175) described the sinuses frontales in the Late Cretaceous eutherian genus *Barunlestes* and stated: "These sinuses evidently contained complicated turbinals," but these structures have not been shown in the illustrations. Lillegraven and Krusat (1991: 67) mentioned the ridge that occurs on the ventral side of the nasal bone of a docodontan *Haldanodon* and stated: "The ridge probably represents the broken base of a nasoturbinal scroll." Presumably the best evidence of the presence of ossified turbinals was found in multituberculates. Hurum (1994), when studying the serial sections of Late Cretaceous multituberculate skulls from Mongolia belonging to *Nemegtbaatar* and *Chulsanbaatar*, found in both of them the crushed remnants of ossified respiratory turbinals, figured in several photographs of the sections.

The secondary palate that enables the animal to breath during eating has been known to be developed in therapsid reptiles for a very long time.

More recent work (see, for example, the articles by Thomason and Russell [1986] and Kemp [2005]) demonstrates that the secondary palate not only was linked with breathing during eating but also enabled suckling and generally strengthened the skull.

Another character related to homeothermy is the development of fur. Years earlier, Brink's supervisor, David M. S. Watson (1931), had interpreted pits on the snout of another therapsid, a bauriamorph, as evidence for the presence of vibrissae, specialized hair, which suggested that ordinary hair must have been present as well (Brink 1956: 86). On this basis, Brink (1956) speculated that the cynodonts might have been homeothermic. One piece of evidence in support of his argument is the curled position of some *Thrinaxodon* skeletons. This position is frequently adopted by mammals as a method of thermoregulation, while being rare in heterothermic animals. The oldest mammaliamorph hairs are those preserved on the body of a Mesozoic docodont, *Castorocauda*, which is 160 Ma old, whereas isolated hairs attributed to mammals are known from Early Cretaceous amber, 100 Ma years old (Vullo et al. 2010).

In his beautifully illustrated article on the evolution of the therapsids published in the South African journal *Optima*, Crompton (1968) presented a process of size reduction during the Permian through Triassic history of this group, in particular in the cynodonts. The article was based on the well-known fossils from the Karoo System in the southern African countries: Lesotho, the Republic of South Africa, Zimbabwe, and adjacent areas. Early and Middle Permian therapsids attained a body length up to 2–3 m, some of them even up to 5 m. The primitive Late Permian cynodont *Procynosuchus* measured 1 m in length, while the well-known Early Triassic *Thrinaxodon* was about 50 cm long. The Middle Triassic *Probainognathus* of South Africa was smaller than a rabbit, while the first Late Triassic mammals, referred to in this book as Mammaliaformes, were smaller than a rat (see the excellent review of the evolution of the therapsids by Tom S. Kemp in *The Origin and Evolution of Mammals* (2005).

The tendency toward reduction in size is rarely observed in the evolution of land vertebrates. Crompton speculated that these changes in therapsid size might have depended on changes in gradual development of homeothermy and simultaneous changes of the climate (Crompton 1968; see also Chinsamy-Turan 2012, and references therein). At the beginning of these physiological changes, therapsids might have been partly endothermic. Their insulation of hair meant that they were able to maintain a relatively constant body temperature, but, during the Late Permian, climate on Earth was generally cold. Near the end of the Permian and during the Triassic, the climate gradually changed, becoming warmer and warmer near the end of the Triassic and into the Jurassic. Large animals, not able to get rid of the extra heat produced by their activity, might have died owing to overheating. So, as argued by Crompton, when the climate became very hot, the only possibility for the first mammals to survive might have been a drastic reduction of their body size and

concentration of their activity to the nighttime. In addition, if cynodonts and early mammals were large, they might easily have been victims of large Triassic reptilian predators, the thecodonts and dinosaurs. As the Mesozoic world was dominated by large reptilian predators, being small might have meant being the fittest!

Several authors regarded an increase of the brain size and an accompanying reduction in the size of the body in mammaliaforms and earliest mammals as related to endothermy (for a review, see Hayes and Garland 1995). Kemp (2009) proposed a correlation of an increase of mammalian brain at the cynodont-mammalian transition with miniaturization. However, the existence of the fox-sized carnivorous mammals with the preserved remnants of juvenile dinosaurs where the alimentary canal would have been points out that the issue is more complicated and requires further study. In addition, the idea presented earlier in this chapter – that reduction in size of cynodonts, mammaliaforms, and the earliest mammals during the Triassic was related mainly to climatic changes that affected forms that were partly homeothermic – appears to me more convincing; see also an interesting article by Pond (1977) on the role of suckling in the evolution of early mammals.

In recent years, studies on the histology of fossil bones have contributed to the discussion on thermal physiology of relevant fossils. In the case of Mesozoic mammals or mammaliaforms these studies are especially difficult, owing to the rarity of available materials. First of all, Mesozoic mammals are rare, as a rule very small, most often represented by teeth, sometimes with fragments of jaws. Postcranial skeletons that might offer the best material for paleohistological studies are extremely rare. No wonder that when Armand de Ricqlès started his pioneering paleohistological studies of fossil bones in the 1960s in France, he began with studies of dinosaurs.

The first publication of the histology of Mesozoic mammals was published by Chinsamy and Hurum (2006). They received the material of isolated bones of the famous Triassic–Early Jurassic mammaliamorph *Morganucodon* from fissure fillings in Wales, offered by Susan Evans from the University College of the University of London. The other material was submitted by me and contained Late Cretaceous multituberculate and eutherian mammals from the Gobi Desert in Mongolia. After their first report in 2006, they worked on the received material further and published an article in the book *Forerunners of Mammals: Radiation, Histology, Biology*, edited by A. Chinsamy-Turan (2012). The main conclusions of Hurum and Chinsamy-Turan (2012) are

- that a determinate growth strategy evolved early in the evolutionary history of the non-mammaliaform therapsids;
- that, based on a small sample of two Late Cretaceous eutherians, the authors suggest a much slower rate of bone deposition than in extant monotremes, marsupials,

and eutherians, as well as in Mesozoic mammals such as multituberculates, *Morganucodon*, and even therapsids;

- that, from their studies, it appears that a flexible growth strategy is plesiomorphic for the mammalian lineage; and
- that the inherent flexible growth strategies of the Mesozoic eutherians may have given them an adaptive advantage at the Cretaceous-Tertiary extinction and after the Cretaceous-Tertiary event.

By invoking sustained (energetically costly) or cyclical (energetically less costly) growth regimes in response to prevailing environmental conditions, the early mammals were thus able to radiate and become dominant mammals (Chinsamy-Turan 2012).

Recent discoveries help us to reconstruct some other physiological issues. The advantages of maintaining high-body temperature by having high levels of resting, or basal, metabolic rates are clear, but not the factors that initiated the evolution of this energy use. The start of endothermy in the ancestors of mammals was proposed as a decrease in body size, as an adaptation to warmer climate, and by a fundamental change in reproduction strategy related to the origin of lactation and elaborate parental care (Hopson 1973). This idea has been confirmed by recent studies, however, with an important modification: the selection for intensified parental care started a self-reinforcing chain of behavioral and morphological adaptations leading to endothermy, not vice versa (Koteja 2000).

As traditionally viewed, Mesozoic mammals were small – somewhere in the range of shrew- to rat-sized. Discoveries of the past few decades call for modification of this concept. Of mammals (sensu Rowe 1988, and as accepted in this book), the largest individuals belong to Eutriconodonta (see chapter 8).

The largest Mesozoic mammals are of the genus *Repenomamus*, represented by two species: *R. robustus* Li, Wang, Wang, and Li, 2000, and *R. giganticus* Hu, Meng, Wang, and Li, 2005. Both were found in Lower Cretaceous beds (about 125 million years old) of the Yixian Formation, in Liaoning Province, northeastern China. *Repenomamus robustus* was initially described as the largest-known Mesozoic mammal, being a carnivore slightly over 1 m long. Now we know that *Repenomamus giganticus*, not as complete as *R. robustus*, was 50 percent larger.

The paper of Hu et al. (2005b), in which *Repenomamus giganticus* was erected, is a very important one, as it also supplies new information on *R. robustus* and addresses the mode of feeding in some early mammals. The authors describe the skeleton of *R. robustus* (previously known only from its skull), giving us a fascinating firsthand glimpse at the diet of this extraordinary mammal: lying within the ribcage, where the stomach would have been situated, is the fragmentary and disarticulated juvenile skeleton of the beaked, bipedal dinosaur *Psittacosaurus*.

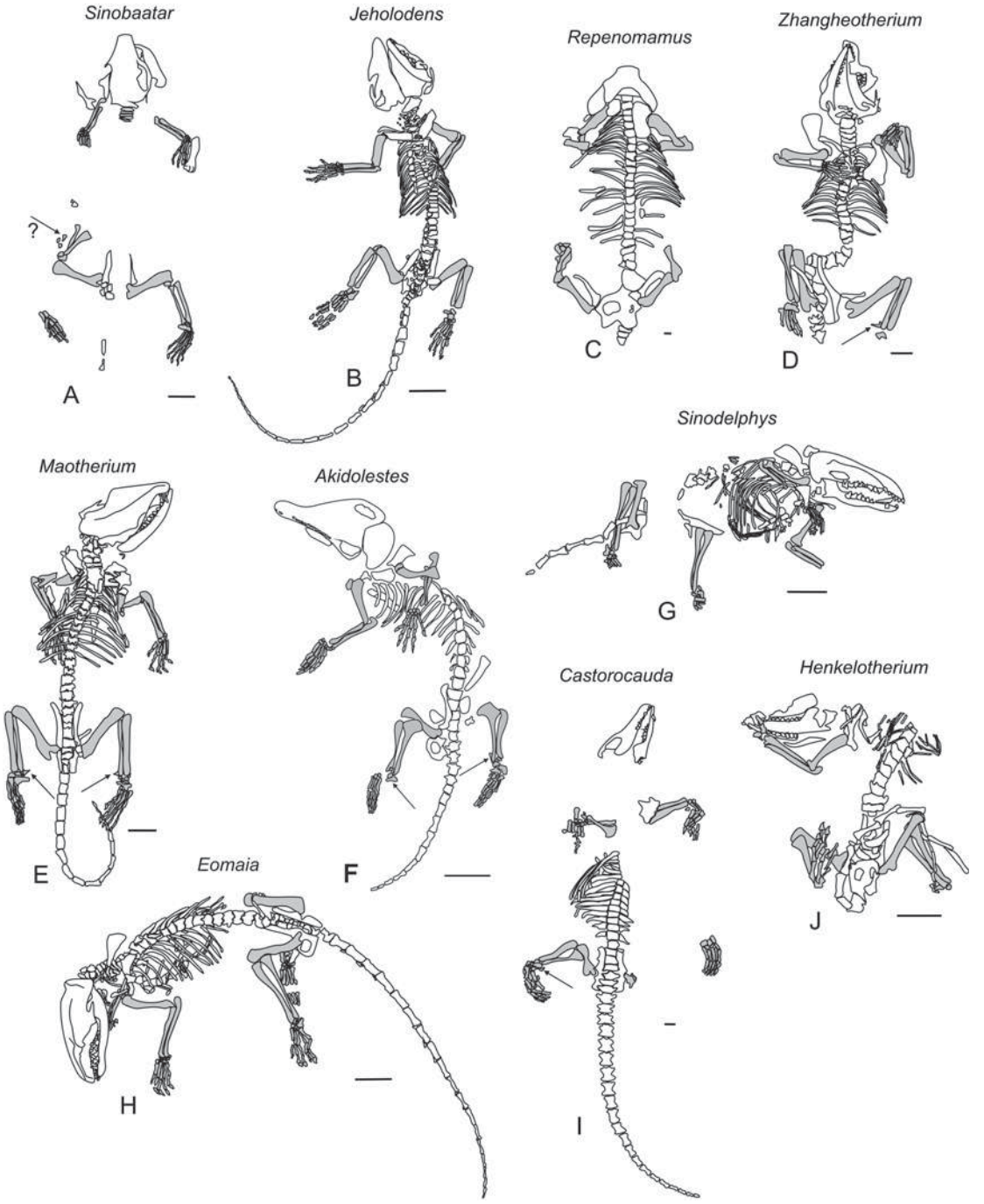
As the title of the Hu et al. (2005b) paper indicates, the new specimen provides direct evidence that large Mesozoic mammals fed on young dinosaurs. Speaking about the state of preservation of the *Psittacosaurus* skeleton, the authors write: "The head-body of the juvenile *Psittacosaurus* is estimated to be 140 mm, about one third of the head-body length of *R. robustus*" (Hu et al. 2005: 151). At the end of the paper the authors conclude: "These large Mesozoic mammals were probably carnivores that competed with dinosaurs for food and territory" (Hu et al. 2005: 152). In figure 15.1, I provide a reconstruction of *Repenomamus robustus,* having hunted a juvenile specimen of *Psittacosaurus.*

Taphonomic Evidence for Posture in Early Mammals

The issue of whether early mammals and related forms had a sprawling or parasagittal posture is a matter of argument – see, for example, Sereno (2006) and Kielan-Jaworowska and Hurum (2006) for contradictory views. In 2006, we (Kielan-Jaworowska and Hurum) published a paper especially devoted to the problem of posture of early mammals and their ancestors, in which we discuss taphonomic data that cast a new light on this problem.

The skeletons of mammals preserved in lacustrine environments may have different positions, depending on their limb posture. Weigelt (1989; see also the original German, 1927) introduced the term "passive position" for the position in which an animal dies. In his discussion of the preservation of an opossum carcass, he wrote that "we often find slightly damaged water carcasses in a completely passive position similar to the natural structure of the body." He continued, "We find this strictly lateral, passive position of the opossum carcass extraordinarily often in fossils" (Weigelt 1989: 86). Weigelt (1989) described the passive position in reptiles as dorsoventral. Kielan-Jaworowska and Hurum (2006) also noted that the skeletons of animals preserved in lacustrine environments (e.g., the Early Cretaceous Jehol Biota from China), in which numerous skin fragments with feathers and mammal skeletons with fur have been found, are differently preserved depending on their stance. Examination of the mammalian fossils from the Jehol Biota and from the Late Jurassic (Kimmeridgian) of Portugal demonstrated that mammals belonging to docodontans, eutriconodontans, multituberculates, "symmetrodontans," and "eupantotherians" have all been preserved dorsoventrally compressed, exposed in dorsal or ventral view, as is characteristic for animals with sprawling position of their limbs (figure 15.2). In the Jehol Biota, only the representatives of two tribosphenidan mammals (marsupials and placental) – *Sinodelphys* and *Eomaia*, which acquired parasagittal stance, are preserved lying on their sides (figures 15.2G–H).

In the well-known Eocene locality of Messel in Germany (Koenigswald and Storch 1998), where the bulk of mammalian taxa belong to placental mammals, and two to marsupials, all the skeletons (except for the bats and pangolins) have been preserved lying on their flanks in the typical mammalian passive position. The reason for this passive position



15.2. Diagrammatical drawings of the skeletons of mammaliaforms and Mesozoic mammals preserved in lacustrine sediments. A–H. The specimens from the Jehol Biota (Early Cretaceous, Yixian Formation). I. The skeleton of *Castorocauda lutrasimilis,* a docodontan from the Middle Jurassic of north-west China. J. *Henkelotherium guimarotae,* a "eupantotherian" from the Late Jurassic (Kimmeridgian) of Portugal. All redrawn and simplified from the original photographs or published drawings by Jørn H. Hurum and all rendered to approximately the same length. The limb bones are shaded in gray; arrows point to the os calcaris. Scale bars: 10 mm.

Drawing taken from Kielan-Jaworowska and Hurum (2006: figures 4 and 5), emended by Aleksandra Hołda-Michalska.

is obvious, as tribosphenidan mammals (both marsupials and placentals) presumably acquired parasagittal posture sometime during the Early Cretaceous, or even earlier, and their common resting (and dying) position, as nowadays, is on side. The reason for the different position of the skeletons of bats is also obvious, owing to the transformation of their forelimbs into wings, and in pangolins this is due to the scaly integument, which is sufficiently rigid to prevent preservation on the side. Reptiles and amphibians from the same locality are mostly preserved in the typical reptilian/amphibian passive position dorsoventrally compressed.

In four groups of early mammals from the Jehol Biota and from the Middle Jurassic lacustrine sediments from northeast China, in which preservation is indicative of the sprawling stance, the spur has been preserved. It has not been found in "eupantotherians" because, in the skeleton of the only representative, *Henkelotherium* from Guimarota coal mine in Portugal, the tarsus has not been preserved.

We (Kielan-Jaworowska and Hurum 2006, contra Sereno 2006) speculated that the skeletons of early mammals from Jehol Biota, belonging to multituberculates, eutriconodontans, and "symmetrodontans," have been dorsoventrally compressed owing to their sprawling stance, which resulted in the animals lying on their bellies or backs, rather than on their sides in a resting and dying position. Two other early mammal taxa, the docodontan *Castorocauda*, from the Middle Jurassic of northwest China, and the "eupantotherian" *Henkelotherium*, from the Kimmeridgian Guimarota coal mine of Portugal, have also been preserved lying on their backs, as is characteristic of mammals with sprawling legs. They are both preserved in lacustrine sediments and are compressed similarly to Jehol Biota specimens. The two species of *Repenomamus* were found in the lowermost Yixian Formation (Lujiatun bed) and are preserved in tuffs. These tuffs show less compaction than the younger, silty sediments of the Jianshangou and Dawangzhangzi beds, which contain the other mammals from the Jehol Biota discussed in Kielan-Jaworowska and Hurum (2006). The specimens figured by Hu et al. (2005b: figures 2 and 3) of *Repenomamus giganticus* and *Repenomamus robustus*, respectively, show the sprawling hind limbs in both species and the sprawling forelimbs in *Repenomamus robustus*.

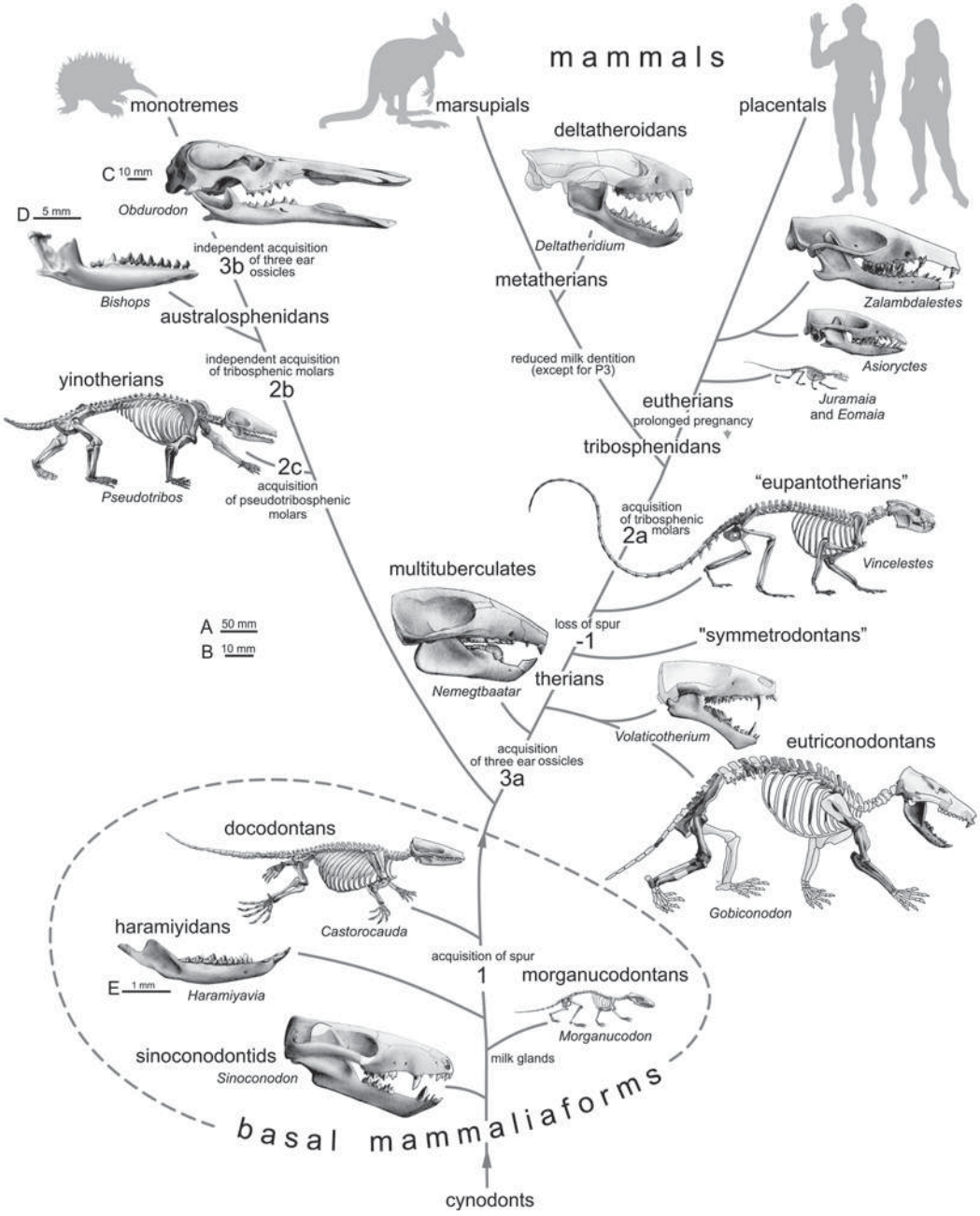
Maotherium sinense, a "symmetrodontan" from the Yixian Formation (figure 15.2E), demonstrates another interesting taphonomic feature. It is the only mammal from the Jehol Biota in which the humeri are broken into several pieces. I presume that this resulted from post-mortem damage caused by a more parasagittal posture of the forelimbs than the hind limbs. As the skeleton was preserved lying on its belly, as is characteristic for the preservation of individuals with sprawling hind limbs, the humeri arranged more parasagittal were broken when forced to acquire a sprawling position.

Out of eight taxa demonstrating the sprawling stance, the uncontested evidence of a spur, the os calcaris, and fused to this, an ossified cornu calcaris (figure 15.2, marked by arrows), have been preserved in

five specimens. It is also possible that the os calcaris was present in *Sinobaatar*. In my opinion it is likely that the spur might have been present in all the taxa of mammaliaforms and early mammals with a sprawling stance.

We also argued (Kielan-Jaworowska and Hurum 2006) that mammaliaforms (referred to by us as early mammals) and the mammals of the monotreme lineage had a sprawling limb posture and a venomous spur. Acquisition of the parasagittal stance was apparently characteristic only of tribosphenidans, in which the spur has not been found. It is not known whether the loss of a spur in mammalian evolution was related to the acquisition of the parasagittal stance, but such a possibility cannot be ruled out.

Nowadays the problems of acquisition of homeothermy by non-mammalian therapsids, mammaliaforms, and early mammals, as well as the various aspects of homeothermy in extant mammals, are studied by numerous scientists. The literature concerning this problem is enormous, and it would be beyond the scope of the present book to refer to it in detail. There are many difficulties for paleontologists wanting to establish whether a group of animals known exclusively from fossil remains was heterothermic or homeothermic. The problem is that indications of homeothermy – such as, for example, increase in concentration of mitochondria, high metabolic rates, and increased aerobic respiration – as a rule are not discernible in the skeleton. However, the first students of the heterothermy/homeothermy issue in the therapsids, mammaliaforms, and early mammals – for example, Watson (1931), Brink (1956, 1980), Crompton (1968), Hopson (1973), Jerison (1973), Crompton et al. (1978), and Jenkins (1990) – in spite of the limited anatomical knowledge on recent mammalian characters related to homeothermy, concluded and hypothesized that therapsid reptiles and early mammals had been at least half homeothermic.


mammals
monotremes
marsupials
placentals
deltatheroidans
C 10 mm
Obdurodon
D 5 mm
Deltatheridium
independent acquisition
3b of three ear ossicles
metatherians
Bishops
australosphenidans
Zalambdalestes
Asioryctes
independent acquisition
of tribosphenic molars
2b
reduced milk dentition
(except for P3)
yinotherians
Juramaia
and Eomaia
eutherians
prolonged pregnancy
tribosphenidans
2c
acquisition
of pseudotribosphenic
molars
Pseudotribos
"eupantotherians"
acquisition
of tribosphenic molars
2a
Vincelestes
multituberculates
A 50 mm
B 10 mm
loss of spur
-1
"symmetrodontans"
Nemegtbaatar
therians
Volaticotherium
acquisition
of three ear ossicles
3a
eutriconodontans
docodontans
Gobiconodon
Castorocauda
haramiyidans
acquisition of spur
1
morganucodontans
E 1 mm
Haramiyavia
Morganucodon
sinoconodontids
milk glands
Sinoconodon
basal mammaliaforms
cynodonts

Diversification of Mammaliaforms and Mesozoic Mammals: A Summary

16

IN THIS BOOK I PRESENT THE EVOLUTION OF MAMMALS DURING THE Mesozoic era, along with information on people working on them. I offer also several new life reconstructions of non-mammalian mammaliaforms and early mammals. In the nineteenth and first half of the twentieth centuries, when early mammals were known mostly from isolated teeth – rarely with jaw fragments – such teeth were identified as mammalian if they had multiple roots and complex crowns.

Extant mammals differ from other vertebrates in having three ossicles in the middle ear, the mandible built of two single bones (the dentaries), and the lower jaw suspensorium placed between the dentary condyle and the glenoid fossa in the squamosal bone. When it became evident that not all Mesozoic "mammals" have these characters, Rowe (1988) set up two new taxa, Mammaliamorpha and Mammaliaformes (which semantically are improper, as both mean exactly the same thing; see chapter 2). He left in Mammalia only those forms with three ear ossicles, a single bone in the lower jaw, and a dentary-squamosal jaw joint.

Luo (2007a, b), in his excellent reviews of Mesozoic mammal diversifications, recognized five "experiments" in the evolutionary path of early mammals and demonstrated their convergence with modern mammalian morphotypes. In the present book I recognize two more "experiments," represented by the multituberculates and zalambdalestids (see chapter 15).

Here I summarize the evolution of mammaliaforms and early mammals in figure 16.1, and I discuss three main anatomical innovations of Mesozoic times: (1) the acquisition and loss of the extratarsal spur, (2) the acquisition of tribosphenic molars, and (3) the acquisition of three ear ossicles.

16.1. Sequence of appearance of morphological adaptations in mammaliaform and early mammalian evolution: 1, appearance; and –1, disappearance of the spur; 2a, appearance of tribosphenic molars in tribosphenidans; 2b, 2c, parallel acquisition of tribosphenic type molars in australosphenidans and yinotherians, respectively; 3a, 3b, parallel acquisition of three ear ossicles in therian line and in monotremes. Stratigraphic scale omitted. Scale A is for skeletons, scale B for skulls, except for *Obdurodon* (scale C), *Bishops* (scale D), and *Haramiyavia* (scale E).

Original idea and artwork by Jerzy Dzik, emended by the author with comments by Zhe-Xi Luo and Richard L. Cifelli, and redrawn by Aleksandra Hołda-Michalska.

Acquisition and Loss of the Extratarsal Spur

The venomous spur occurs in the extant male platypus (*Ornithorhynchus*) and is very dangerous (Fenner et al. 1992). In echidnas the spur may occur also in females, but is not as dangerous as it is in the platypus during its breeding season (Calaby 1968; Griffiths 1968). In mammaliaforms and early fossil mammals the spur has been rarely found, at least in part because complete tarsi are seldom preserved (see figure 16.1, number 1). Among mammaliaforms, the spur has been found in a docodontan *Castorocauda* (see Ji et al. 2006: figure 1B; chapter 7 in this volume); in the Cretaceous eutriconodontan *Gobiconodon* (Chapter 8); in three Late Cretaceous multituberculates from Mongolia (*Kryptobaatar*,

Catopsbaatar, and *Chulsanbaatar*; see Hurum et al. 2006) and probably in *Sinobaatar* from the Jehol Biota (Kielan-Jaworowska and Hurum 2006: figure 4A); and in the "symmetrodontans" *Zhangeotherium*, *Maotherium*, and *Akidolestes* (Kielan-Jaworowska and Luo 2006: figure 4D, E, and F, respectively). As the spur has never been found in either "eupantotherians" or in tribosphenidans (previously boreosphenidans; see chapter 9 for explanation of synonymy), it seems that within the Theria *sensu lato* it disappeared in "eupantotherians" or early tribosphenidans (see figure 16.1, number 1).

We suggested (in Hurum et al. 2006) that the reason for the rare preservation of spurs in fossil material is that the tarsus of mammaliaforms/early mammals is rarely preserved – for example, only two bones (the calcaneus and astragalus) are known in morganucodontans (Jenkins and Parrington 1976). If the spur occurred in morganucodontans and haramiyidans, number 1 in figure 16.1 should be placed lower, below the branching for these groups. As we now know that the spur existed in four extinct groups of mammaliaforms or mammals, and in one extant group, it seems possible that it existed in all mammaliaforms and Mesozoic mammals, except for tribosphenidans. It cannot be excluded that the disappearance of the spur in "eupantotherians" or their relatives (leading to tribosphenidans) was related to the acquisition of a parasagittal stance. In such a posture, the hind legs tend to be placed close to one another, and the venomous spur, pointing medially, might easily hurt the opposite leg.

Acquisition of the tribosphenic molars

Crompton (1971) published his benchmark paper on the evolution of tribosphenic molars, but at that time the situation seemed clearer than it is today. It appeared almost certain from his study (figure 16.1, number 2a) that the tribosphenic molar pattern originated in the Northern Hemisphere sometime during the Early Cretaceous. Today we know that eutherians with tribosphenic molars (*Juramaia*) are known from the Late Jurassic (see chapter 14). According to Crompton (1971), the evolution of tribosphenic molars started with a primitive "symmetrodontan" (represented by *Kuehneotherium*), which had only three shearing surfaces, through more advanced "symmetrodontans" and "eupantotherians," and culminating in primitive to advanced therian mammals (tribosphenidans), having fully tribosphenic molars, with as many as six shearing surfaces.

Twenty-six years later, Tom Rich, Pat Vickers-Rich, and their colleagues (1997) described the first tribosphenic mammal from Gondwana (Australia), dubbed *Ausktribosphenos*, of Early Cretaceous age (figure 16.1, number 2b; see also chapter 9). The authors of *Ausktribosphenos* argued that it is a placental mammal and that placentals originated in Australia. We (Luo, Cifelli, and Kielan-Jaworowska 2001a) offered a phylogenetic analysis of early genera with tribosphenic molars and some extant forms and obtained a cladogram showing that there are two independent groups of mammals with tribosphenic molars. For one, from

Gondwanaland, we set up an infraclass Australosphenida (figure 16.1, number 2b); for the other one, from Laurasia, we erected the infraclass Boreosphenida (now Tribosphenida; figure 16.1, number 2a; see also chapter 9). Australosphenidans differ from tribosphenidans in having wrapping mesial and internal cingulids on the lower molars; on the tribosphenic molars from the Northern Hemisphere, the molars are either smooth or provided with a few cuspules. All Gondwanan mammals with tribosphenic molars have been known for many years exclusively from the lower jaws. Recently Tom Rich informed me (personal communication) of the discovery of the first upper teeth of tribosphenic mammals in Australia. These include a presumed P3 and two molars. These teeth have not been described as yet. Comments on the structure of the upper molars from the southern continents were drawn on the basis of the structure of the lower molars (Martin and Rauhut 2005). The latter authors studied shearing surfaces in *Asfaltomylos patagonicus* from the Middle Jurassic of Argentina and concluded that *Asfaltomylos* lacks the classical shearing surfaces 5 and 6 of Crompton (1971). These surfaces in northern tribosphenic molars occur in the talonid of the lower molars and also on the occluding protocone of the upper molars. The conclusion is that, in *Asfaltomylos*, upper molars apparently lacked the protocone, and if so, the australosphenidan tribosphenic molars had a different structure than those of tribosphenidans, and the two groups might have a different origin.

Chow and Rich (1982) described from the Late Jurassic of China the first dentary with pseudotribosphenic molars (named *Shuotherium dongi)*, in which the talonid is placed in front of the trigonid, rather than behind it, as characteristic of tribosphenic molars (Crompton 1971).

Subsequently, two species of *Shuotherium* (*S. kermacki* and *S. shilongi*; see Sigogneau-Russell [1998] and Wang et al. [1998], respectively) were erected, based on single upper teeth. I discuss the issue of tribosphenic versus pseudotribosphenic mammals in chapter 12 (see figures 12.4 and 12.5). Finally, Luo et al. (2007a) described from the Middle Jurassic of Inner Mongolia a skeleton with pseudotribosphenic molars, named *Pseudotribos robustus* (figure 16.1, number 2c). The upper and lower molars of *Pseudotribos* acted in a mortar-and-pestle manner, similar to tribosphenic molars, the only difference being the reversion of the talonid situated in front of, rather than behind, the trigonid.

The Origin of the Three Ear Ossicles

All living mammals are characterized by having three ear ossicles and are unique in this respect in the animal kingdom. Rowe (1988) divided the taxa previously classified as mammals, into the non-mammalian mammaliaforms and mammals. Mammalia *sensu* Rowe (1988) are characterized, among other things, by having three ossicles in the middle ear. Seventeen years after the publication of Rowe, Rich and colleagues (2005) studied the postdentary trough of the oldest fossil monotreme *Teinolophos* from the Early Cretaceous of Australia. However, Rowe et al. (2008, having

Tom Rich and Patricia Vickers-Rich, among others, as co-authors) partly rebutted the paper by Rich et al. (2005) and stated that the postdentary trough on the internal side of the dentary in *Teinolophos* is well preserved in this specimen, showing that the bones of the primitive reptilian jaw joint apparently had not yet been converted into ear ossicles (figure 12.4D, in this volume). As the molar tooth preserved in *Teinolophos* is similar to that of the geologically younger monotreme *Steropodon*, there are no doubts that both genera belong to monotremes. The extant monotremes have three ear ossicles. The authors concluded that three ear ossicles developed twice in mammals, independently in monotremes and in therian mammals (figure 16.1, number 3a and number 3b).

Three ear ossicles have not been found in eutriconodontans, but as the postdentary trough does not occur in them, one may presume that the bones forming the old reptilian jaw joint, in eutriconodontans migrated to the middle ear. Therefore, in figure 16.1, I place the line leading to eutriconodontans above number 3a – acquisition of three ear ossicles. The three ear ossicles occur also in multituberculates (see chapter 10). This is reflected in figure 16.1 by the divergence of multituberculates from the main line leading to the tribosphenidans. The details of this divergence are still not known. Numerous authors working on haramiyidans believe, on the basis of the structure of dentition, that multituberculates arose from haramiyidans (see chapter 6). But Jenkins, Gatesy, Shubin, and Amaral (1997) examined wear facets on the molars of *Haramiyavia* and concluded that it had orthal (vertical) jaw movement, in contrast to the horizontal anteroposterior movement in multituberculates (see chapter 9). I am of a similar opinion based on the structure of the masseteric fossa, which in *Haramiyavia* is very short, as it is in mammals with orthal movement of the lower jaw. In multituberculates, in contrast, longitudinal movement of the lower jaw took place with a backward power stroke. This is reflected in their masseteric fossa, which extends far anteriorly under p4 and is more anterior than it is in any other mammals. It seems to me that the origin of multituberculates from the line leading to Tribosphenida appears more probable. I place the multituberculates in figure 16.1 as an early branch of the line leading to tribosphenidan mammals. If, however, multituberculates did not originate from the therian line, as shown in figure 16.1, but from haramiyidans (as advocated by numerous haramiyidan specialists cited in chapter 6) – and as the dentary of *Haramiyavia* has an extensive postdentary trough, apparently with "reptilian" bones nested in it – one should conclude that the ear ossicles in multituberculates originated independently, for the third time in mammalian evolution, which I regard as highly improbable. I tentatively accept in the present book that the multituberculates arose from the therian line, as shown in figure 16.1.

Summary of Temporal Occurrences of Mammaliaforms and Mesozoic Mammals

The oldest-known mammaliaform is *Adelobasileus cromptoni*, erected by Lucas and Hunt (1990); see also Lucas and Luo (1993; figure 5.7, in this volume). *Adelobasileus* is represented by a partial braincase from the Carnian of Texas (225 Ma ago). Lucas and Luo (1993: 309) offered a cladistic analysis of *Adelobasileus*, concluding that "*Adelobasileus*, *Sinoconodon* and other mammals form a monophyletic group." In this book I assign *Adelobasileus* (in which the teeth are not preserved) to the Mammaliaformes.

A slightly younger mammaliaform is *Sinoconodon rigneyi*, placed by Kielan-Jaworowska et al. (2004: 162) in the subclass and order *incertae sedis*. *Sinoconodon* differs from other early mammaliaforms in the lack of wear facets on the molars. Most common of Early Jurassic mammaliaforms is *Morganucodon*, represented by numerous isolated bones of *M. watsoni* from fissure fillings in Wales. I offer a life reconstruction of *Morganucodon* sp. in figure 5.3 (in this volume). *Morganucodon* was described in detail by Kermack, Musset, and Rigney (1973, 1981). For *Morganucodon* and related genera the order Morganucodonta was established (see chapter 5).

The fissure fillings in Ponatlum Quarry in Glamorganshire yielded several fragments of edentulous dentaries and several isolated upper and lower molars and premolars, of *Kuehneotherium praecursoris*. As *Kuehneotherium* is very incompletely known, it is impossible to provide its life reconstruction.

Other taxa known from the latest Triassic and Early Jurassic belong to the Haramiyida. This group, traditionally regarded as related to Multituberculata, was for a long time known only from isolated teeth. Jenkins, Gatesy, Shubin, and Amaral (1997) made the most important discovery of haramiyidans. From the Late Triassic of Greenland they described dentaries and partial maxillae with teeth named *Haramiyavia clemmenseni*. The dentary of *Haramiyavia* possesses a trough for postdentary bones, as is characteristic for Late Triassic and Early Jurassic mammaliaforms. Jenkins et al. (1997) examined wear facets on the teeth of *Haramiyavia* and concluded that *Haramiyavia* had orthal jaw movement; on this basis, they excluded the Haramiyida from Allotheria, an idea that I accept in this book.

A very interesting discovery was the finding of a tiny skull of an Early Jurassic mammal from the Lower Lufeng Formation (195 million years old) of Yunnan, southeast China, dubbed *Hadrocodium wui* by Luo et al. (2001b; figure. 5.6, in this volume). The skull is only 12 mm long, and the estimated body mass of *Hadrocodium* is 2 g. It is the smallest Mesozoic mammaliaform/mammal. The authors assigned *Hadrocodium* to the Mammaliaformes, although, judging from figure 3 in their original paper (Luo et al. 2001b), *Hadrocodium* had several advanced characters, indicating that it lies closer to the Mammalia *sensu* Rowe (1988, 1993) than to the Mammaliaformes. Because of ambiguity I leave it for the time being tentatively within Mammalia *incertae sedis* (chapter 5).

A number of isolated teeth of Rhaetian (latest Triassic) mammaliaforms have also been described from Germany, Belgium, Luxembourg, France, and Switzerland. The earliest Mammaliaforms outside Europe are of Liassic (Early Jurassic) age. I do not figure these forms in this book.

The Middle Jurassic, until recently, was regarded as the most poorly sampled part of the meager record of Mesozoic mammals (see Kielan-Jaworowska et al. 2004: chapter 2). But in the last three decades new discoveries have changed this opinion. There is one reasonably well represented Middle Jurassic mammalian assemblage from Britain, represented by isolated teeth; see Freeman (1976a, b, 1979, 1982).

Nonetheless, it is clear from the few fossils available that important changes, reflecting a major turnover, had occurred during the Middle Jurassic. The Morganucodonta, so prevalent in earlier faunas, are represented by a single molar from England. Typical haramiyidans are missing from northern faunas, having been replaced by possible descendants: *Theroteinus* and *Eleutherodon*, both represented by isolated teeth. On southern landmasses, however, the haramiyidans apparently persisted until the beginning of the Cretaceous (Heinrich 1999, 2001).

Other groups of mammals and mammaliaforms arose and flourished during the Middle Jurassic. One such is the Docodonta, represented also by a single specimen from the Late Triassic. Docodontans (chapter 7) achieved their greatest diversity in the Middle and Late Jurassic, from where some 12 genera are known. By this time, they had acquired a dual-function (shearing and grinding) molar pattern; they were also diverse in body size, skeletal anatomy, and paleoecology. In the Jurassic, there occur at least two representatives of docodontans, known from complete skeletons. One is a highly specialized beaver-like docodontan mammaliaform, *Castorocauda* (set up by Ji et al. 2006), and the other is the Late Jurassic *Haldanodon*. I refer the reader to the reconstruction of *Haldanodon* in Martin and Novotny (2000). This taxon, found in the Kimmeridgian Guimarota coal mine in Portugal, shows adaptations similar to Recent desmans.

Eutriconodontans

The order Triconodonta was proposed by Osborn (1888) for mammals in which main cusps on the molars are placed in anteroposterior alignment. Until 1973, students of the triconodont-like mammals neglected important anatomical differences between the Late Triassic and Early Jurassic triconodontans and those from the Middle Jurassic to Early Cretaceous and classified all of them as belonging to the Triconodonta.

Kermack et al. (1973) separated the Late Triassic and Early Jurassic triconodontans into a new suborder – Morganucodonta – and assigned the Middle Jurassic–Early Cretaceous triconodontans to a suborder – Eutriconodonta, earlier established by Kermack and Mussett (1958). In figure 8.1, I present a reconstruction of *Gobiconodon ostromi* (see also chapter 8) as a representative of the Eutriconodonta, the largest of Mesozoic mammals, attaining the size of a fox.

The first gliding mammal, *Volaticotherium* from the Daohugou beds in Inner Mongolia, was unexpectedly discovered by Meng et al. (2006). The beds yielding *Volaticotherium antiquum* (see figure 8.3) are probably of the earliest Cretaceous age. The dentition of *Volaticotherium* is reminiscent of those of Eutriconodonta in having the main molar cusps arranged longitudinally. Meng et al. (2006) erected for it a new order, Volaticotheria, which in my opinion should wait until more material of *Volaticotherium* is found.

Monotremes versus Therians

More significant is the initial appearance of animals representing a fundamental split in Mammalia: the divergence of monotremes from tribosphenidans. Simpson (1936) erected the term "tribosphenic molars" for the molars that often occur in Mesozoic mammals but also occur in some present-day primitive mammals (chapter 12: figure 12.2A, in this volume). Crompton (1971) demonstrated in functional terms how tribosphenic molars might have developed from *Kuehneotherium* (which he assigned to the "symmetrodontans"), through "eupantotherians," and then reaching the tribosphenic condition. At that time the picture of the evolution of the main line of Mesozoic mammals leading to the Placentalia and Marsupialia appeared relatively simple. In the 40 years since publication of Crompton (1971), several new groups of Mesozoic mammals have been discovered. The main line leading to the tribosphenic molars presented by Crompton now seems valid only for mammals known from the Northern Hemisphere.

In 1997 mammals with tribosphenic molars were discovered by Tom Rich, Pat Vickers-Rich, and their colleagues in the Early Cretaceous (Albian) rocks of Australia (figures 9.4 and 9.5). The first specimen found – *Ausktribosphenos nyktos* – is a nearly complete dentary with three tribosphenic molars, an ultimate premolar, and a postdentary trough. Cretaceous mammals assembled by Rich and his team in Australia represent about 80 percent of the Mesozoic mammal specimens presently known from that continent. Rich and colleagues (1997) regarded *Ausktribosphenos* as a placental mammal and put forward a hypothesis that placental mammals originated in Australia. Subsequently, tribosphenic mammals have been found in Jurassic beds of Gondwana, in Madagascar (genus *Ambondro*) and in South America (*Asfaltomylos* and *Henospherus*.)

The idea of an Australian origin of placental mammals was met with skepticism by a great number of early mammal specialists. Luo, Cifelli, and Kielan-Jaworowska (2001a) offered a phylogenetic analysis of Mesozoic and some extant therians with tribosphenic molars. We obtained a cladogram clearly showing that forms with tribosphenic molars originated twice. One group – designated Australosphenida – arose on Gondwanan landmasses during the Jurassic. The other – named Boreosphenida (now Tribosphenida; see chapter 9) – originated in Laurasia, also during the Jurassic (at the time of our writing the oldest tribosphenidans were known from the Early Cretaceous; see figure 9.6). The

molars of australosphenidans differ from those of tribosphenidans by having the wrapping cingulid on mesial and inner sides of the crown, while in tribosphenidans the crowns are smooth or are provided with a few cuspules.

Martin and Rauhut (2005) studied wear facets in the lower dentition of *Asfaltomylos* (the upper dentition in Australosphenida was not known at that time). They found that Crompton's (1971) standard wear facets 5 and 6 of tribosphenidans are not developed; therefore it is uncertain whether a functional protocone, with its facets 5 and 6, would be present on the upper molars. It follows that the upper tribosphenic molars in australosphenidans differ from those in tribosphenidans by apparent lack of protocone, in addition to the presence of wrapping cingulid. The conclusion of Martin and Rauhut agrees with our earlier opinion (Luo, Cifelli, and Kielan-Jaworowska 2001a) that the two groups of tribosphenic molars, australosphenidans and tribosphenidans, made their appearance separately. Irrespective of whether the idea of Australian origin of placental mammals will turn out in the future to be right or wrong, the role of Tom Rich, Pat Vickers-Rich, and their team in identifying early mammal faunas from Australia is enormous.

Archer et al. (1985) described the first Cretaceous monotreme *Steropodon galmani* from the Early Cretaceous (middle Albian) of Australia (see figure 9.3). The only specimen of *Steropodon* is a fragment of a dentary with three molars and alveolus for the final premolar.

The split that marks the base of crown Mammalia occurred along geographic lines: Australosphenida on southern continents, and the Tribosphenida, the major group (some members of which later invaded southern landmasses), on northern continents.

The remaining Middle Jurassic mammals, those from Laurasia, represent several major groups, indicating that mammal diversification on northern continents was well under way. In all the cases, the typical mammalian middle ear is present or may be inferred to have been present in forms from this region.

Multituberculates

Multituberculates (chapter 10) are a side branch of early mammals, which diversified explosively later in the Mesozoic. From the Middle Jurassic they are known only from isolated teeth. Multituberculates were flourishing omnivorous and herbivorous mammals in the Late Jurassic, Cretaceous, and Paleocene, until the Eocene. In chapter 10, illustrations of their representatives show their diversification. In the enormous literature on multituberculates, of a special value are three meticulous volumes from the series Fossilium Catalogus, published by Hahn and Hahn (1983, 2006, and 2007), including complete data on structure and distribution and complete lists of the literature on haramiyidans and multituberculates. Unusually well preserved multituberculates were assembled by the Polish-Mongolian Paleontological Expeditions to the

Gobi Desert from the Late Cretaceous sediments, which increased the knowledge on their anatomy and habits (chapter 10).

Kielan-Jaworowska et al. (2004) followed Butler (2000) and assigned the two orders Haramiyida and Multituberculata to the subclass Allotheria. Although numerous authors are of the opinion that multituberculates might have originated from the Haramiyida (as, for example, suggested also by Hahn and Hahn 2006), I am now of the opinion that the placement of the two groups together in the subclass Allotheria is unjustified (see chapters 6 and 10). Rich et al. (2009) described a p4 with a fragment of a dentary from the Early Cretaceous of Australia, named *Corriebaatar marywaltersae*. This demonstrates that the Multituberculata had a cosmopolitan distribution during the Mesozoic and reached eastern Gondwana, probably in the Early Cretaceous.

Enigmatic multituberculate-like hypsodont and brachyodont teeth are known from the Late Cretaceous and Paleocene Gondwana landmasses. Krause and Bonaparte (1990) erected the suborder Gondwanatheria within the Multituberculata. Pascual et al. (1999) described a dentary of a Paleocene gondwanatherian – *Sudamerica*, with four molariform teeth, unknown in multituberculates – and placed Gondwanatheria in Mammalia *incertae sedis*. I regard Gondwanatheria as a side branch of Multituberculata.

"Symmetrodontans," "Eupantotherians," and the Origin of the Tribosphenic Molar

"Symmetrodontans" are a very important group of small Mesozoic mammals (see chapter 11), related, on the one hand, to eutriconodontans and, on the other, to "eupantotherians." For a long time "symmetrodontans" were known only from isolated teeth and small dentary fragments, but Hu, Wang, Luo, and Li (1997) described the first nearly complete skeleton of a symmetrodontan, *Zhangeotherium quinquecuspidens* (figure 11.2). It was found in the Early Cretaceous (possibly Barremian) Jehol Biota from China with the extratarsal spur preserved in it. Life reconstructions of *Zhangheotherium* were published Chang et al. (2003). I describe several symmetrodontan genera in Chapter 11.

Other small, mainly Jurassic, mammals are the "eupantotherians" (chapter 12). Marsh (1880) erected the order Pantotheria. Zittel later (1893) published a paleontology textbook in which he used the formal taxon "Trituberculata," mistakenly attributing it to Osborn. Zittel's textbook contributed to the popularization of the taxon Trituberculata until recently, but it is not accepted by most paleontologists now. I do not use the term "Trituberculata.

The terminology of "Symmetrodonta" and Pantotheria was confusing, as Simpson employed the term "Pantotheria" for an infraclass and the same term for an order. Kermack and Mussett (1958) erected the order "Eupantotheria" to replace the ordinal name Pantotheria, while retaining the term "Pantotheria" as the name of the infraclass. I follow Kermack and Mussett (1958) in using the ordinal name "Eupantotheria."

Kielan-Jaworowska et al. (2004: table 10.2) offered a Linnean classification of "Eupantotheria" and assigned to it 38 genera. The most completely known is the genus *Henkelotherium*, named by Krebs (1991), from the Guimarota coal mine in Portugal. Krebs (1991) offered a detailed description of *Henkelotherium* and its life reconstruction walking on a Gingko tree. The most completely preserved Early Cretaceous "eupantotherian" is *Vincelestes neuquenianus* from the Late Cretaceous La Amarga Formation of Argentina (figure 12.3).

Metatherians and Eutherians

In chapter 13, in addition to Tribotheria, known mostly from isolated teeth, I discuss the Metatheria, within which I recognize the Deltatheroida and Marsupialia. The most complete and the putative oldest representative of Marsupialia is *Sinodelphys szalayi* from the Early Cretaceous Yixian Formation, reconstructed in figure 13.4.

There are three Mesozoic Chinese eutherian genera – *Eomaia* and *Acristatherium* (the latter not described in this volume), from the Early Cretaceous and *Juramaia* from the Jurassic – that changed our view on the early evolution of eutherians. All three genera were found in northeast China. Most completely preserved is *Eomaia*, for several years cited as the oldest eutherian. Estimated ages of *Eomaia* and *Acristatherium* are about 124 Ma. The structure of the carpus and tarsus of *Eomaia* speaks for the arboreal mode of life. Luo et al. (2011) described *Juramaia sinensis* from the earliest Late Jurassic of northeastern China; its age is about 160 Ma (figure 14.1B). Only the anterior part of the skeleton, left mandible, maxilla and almost complete dentition have been preserved, with eutherian dental formulae. Luo et al. (2011) suggested a scansorial adaptation of *Juramaia*. All these early eutherians and the metatherian *Sinodelphys* were scansorial and differ from contemporary Mesozoic mammals, and from Late Cretaceous eutherians, most of which were terrestrial.

The majority of the Cretaceous eutherians were shrew or rat sized (chapter 14). I offer a reconstruction of the head of a small eutherian *Asioryctes gobiensis* (figure 14.3C) and also present a life reconstruction of *Zalambdalestes lechei* (figure 14.4). The lifestyle of zalambdalestids was similar to those of extant Macroscelididae from Africa, being terrestrial dwellers, often using saltation.

Luo and Wible (2005) described from the Late Jurassic of Colorado the mammal *Fruitafossor windscheffeli* (figure 5.10), characterized by highly specialized teeth, similar to extant xenarthran and tubulidentate mammals, with tubular, single-rooted molars of open-ended roots and the crowns lacking enamel. The dentary has a mammalian structure with a prominent dentary condyle, indicating a single mammalian dentary/squamosal jaw joint, and a prominent coronoid process. A wide Meckel's groove is present, but of the postdentary bones only the facet for the coronoid is preserved. Luo and Wible assigned *Fruitafossor* to Mammaliaformes, arguing that a wide Meckel's groove suggests that the postdentary bones (albeit not found, except for the facet for the coronoid) probably

were present. As we have no idea from which group of mammaliaforms *Fruitafossor* originated, I provisionally place it within the Mammalia *incertae sedis*, accepting that if more material of this taxon is found and indicates that the postdentary bones did not migrate to the middle ear, it should be classified as belonging to Mammaliaformes.

The Matter of Pseudotribosphenic Mammals

There is one more Late Jurassic enigmatic mammal from Sichuan in China, *Shuotherium dongi*, described by Chow and Rich (1982). The authors designated this type of molar as pseudotribosphenic and erected for it the new order Yinotheria. Subsequently, upper isolated molars fitting the lowers of *Shuotherium* were described from different regions of Eurasia. Finally Luo et al. (2007a) described from the Middle Jurassic of Inner Mongolia (China) the first pseudotribosphenic mammal, represented by the skeleton, designated *Pseudotribos robustus*. The holotype consists of two counterparts with fur traces, an incomplete skull with upper and lower dentition, and parts of the postcranial skeleton showing fossorial adaptations. Luo et al. (2007a) placed *Pseudotribos* in the Mammalia, although it is not known whether *Pseudotribos* had three ear ossicles, as it had a large postdentary trough.

Conclusions

In writing this book, I tried to understand the evolution of mammals for about 160 Ma of their existence during the age of dinosaurs. I present the evolution and diversification of early mammals, as far as I understand them now, in a schematic in figure 16.1, but these views are full of question marks.

Figure 16.1 shows that in the evolution of mammaliaforms and early mammals we see very often parallelism and the appearance of the same characters independently – for example, in australosphenidans and tribosphenidans. But one should be careful with accepting the picture of mammalian evolution presented in figure 16.1. I cannot exclude that some parallelism shown in this figure may be due to limited data available at present. No doubt that when more fossils of Mesozoic mammals are known, the characters that appear now to be due to parallelism might then appear to have a common origin, and the picture shown in figure 16.1 will be considerably changed.

Figure 16.1 shows the origin of three structures that made their appearance during the evolution of mammaliaforms and mammals in the Mesozoic era. I concentrated mostly on the discussion of the characters that concern the teeth and the skeleton, which are more often preserved in fossil material. The other changes that occurred in evolution of mammaliamorphs and mammals concerns the acquisition of homeothermy, which I discuss in chapter 15. The transition from heterothermy to homeothermy was a long process, which started at the level of therapsids and lasted many million of years. It affected various systems in the mammalian body. Homeothermic forms need more energy

for maintaining a constant body temperature than heterothermic taxa. Therefore homeothermic animals must make the most of food, and hence there are changes in dentition, the lower jaw structure and its suspensorium, and the acquisition of a secondary palate. For more efficient metabolism, food must be better oxidized, which causes the origin of a diaphragm. Homeothermic creatures need to move more efficiently, and the ancestors of mammals gradually changed from a sprawling stance to a parasagittal one.

During more than 60 years of my scientific life, our view on the evolution of life on Earth, including that of the early mammals, has changed several times. The last two decades have brought an unusual flowering of the discoveries of new Mesozoic mammals and other extinct animals, which is reflected in the enormous increase in paleontological literature. The conclusion drawn from these new discoveries is that mammaliaforms and early mammals were much more diversified than previously imagined. Astonishingly, there existed during the Jurassic and Cretaceous numerous forms that may be characterized as ecomorphological copies in almost all details of particular extant mammals that adapted themselves apparently to an almost identical mode of life. From among Mesozoic forms that have present-day equivalents one may list *Castorocauda lutrasimilis*, a middle Jurassic docodontan that imitates Recent beavers in many details; *Haldanodon exspectatus*, another docodontan that shows convergences with modern desmans; the Middle Jurassic *Volaticotherium sinense*, which imitates modern mammals adopted to a gliding flight; and the Upper Jurassic *Fruitafossor windscheffeli* from Colorado, which shows far-reaching convergences with modern edentates.

In addition to the genera and species cited in this book that show strong convergences in many anatomical details with certain present-day mammals, there are other Mesozoic mammaliaforms and early mammals that apparently had similar lifestyles to various present-day mammals. For example, numerous generalized insectivorous/carnivorous mammaliaforms, such as the Early Jurassic *Morganucodon*, are similar to present-day rats. In contrast, the eutriconodontans are generally similar in diet and apparently habits to some species of opossums.

The question arises as to why these early mammaliaforms and early mammals, so similar to some present-day forms, but not related to them, have been so much less successful than their Recent equivalents? The answer most probably is that in recent mammalian faunas 94 percent belong to placental mammals. Their enormous success depends in the first place on acquisition of the trophoblast, on the basis of which the placenta is formed. The trophoblast forms a barrier between the maternal tissues and the embryo and enables prolongation of the gestation period. Without the trophoblast, marsupials are unable to prolong their gestation period and are born at an extremely early level of anatomical development. The newborn marsupial must creep to the pouch (in most marsupials) to find a nipple on which it spends several weeks, and later, when free, it returns very often to the pouch of the mother, where it

finds shelter and food. As the newborn marsupial embryo must crawl to the nipple, its forelimbs must move in many directions, and that is why the marsupials never developed such specialized endings of the limbs as hoofs, wings, and flippers. A second, albeit probably less important, character complex is the acquisition of the tribosphenic molars by placental mammals (shared with marsupials), which are able to cut and grind food. In tribosphenic molars the lower tooth enters between two upper teeth, and the highest cusp of the lower tooth does not shear within the single upper tooth, as in many other mammaliaforms, but in between the two teeth. This type of tooth proved to be extremely efficient, and from it developed the unusually diversified teeth of placental and marsupial mammals during the Tertiary.

Morphological adaptations of mammaliaforms and early mammals, summarized in this chapter, are often represented by single specimens that were found far away from one another in time and space. One may argue that there existed more morphotypes in the Mesozoic, which will be discovered in the future. As at least half of them were found and recognized during the last two decades, one may expect that with a similar tempo of new discoveries, our current view on diversification of mammals during the 160 million years of their existence in the Mesozoic era, as well as their interrelationships, will be probably completely revised in the future.

The result of this work, as of all science, is not a petrified "*monumentum aere perennius*" (a monument more lasting than bronze), as dreamt by the Roman poet Quintus H. F. Horace, but an edifice endlessly reconstructed by us and those who will come after. Nature itself evolves endlessly, and we are a part of it. The difference between the natural and the human made is just an anachronic illusion. Looking at figure 16.1, one can imagine that in eons to come the extant biological depository of intellect – the human brain – now at the top level of evolution on the Earth, will take a new evolutionary step – the electronic intellect – symbiotic with humans, independent, or both.

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