LEGACY OF THE GOBI DESERT: PAPERS IN MEMORY OF ZOFIA KIELAN-JAWOROWSKA
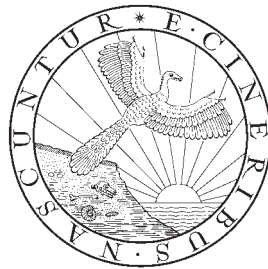
(DZIEDZICTWO PUSTYNI GOBI – PRACE KU PAMIĘCI
ZOFII KIELAN-JAWOROWSKIEJ)

EDITED BY

RICHARD L. CIFELLI AND ŁUCJA FOSTOWICZ-FRELIK

(WITH 120 TEXT-FIGURES)

Palaeontologia Polonica is a monograph series published by the Institute of Paleobiology of the Polish Academy of Sciences, associated with the quarterly journal *Acta Palaeontologica Polonica*. Its format, established in 1929 by Roman Kozłowski, remains virtually unchanged. Although conservative in form, *Palaeontologia Polonica* promotes new research techniques and methodologies of inference in palaeontology. It is especially devoted to publishing data, which emphasise both morphologic and time dimensions of the evolution, that is detailed descriptions of fossils and precise stratigraphic co-ordinates.

Manuscripts submitted to *Palaeontologia Polonica* should conform to the style of its latest issues. Generally, it is expected that costs of printing, which are kept as low as possible, are covered by the author.

Doctor Łucja Fostowicz-Frelik
Professor Richard L. Cifelli
Guest Editors of *Palaeontologia Polonica*

Dear Madam and Sir,

It is a great honour to be a part of this tribute to the memory of Professor Zofia Kielan-Jaworska and I wish to extend my warmest thanks to Doctor Łucja Fostowicz-Frelik and Professor Richard L. Cifelli for taking on the hard work of preparing the present publication.

I knew Professor Kielan-Jaworska personally and she impressed me not only as a scholar but also as a person: always frank, honest and uncompromising. As a scientist she worked with many leaders in the field while also initiating avenues of research that defined new directions for palaeontology in the 20th century.

These opinions found clear confirmation during the competition procedure in which Professor Kielan-Jaworska was awarded the Foundation for Polish Science (FNP) Prize in 2005. The prize was granted in the field of the life sciences and medicine for "a creative synthesis of research on the Mesozoic evolution of mammals presented in the fundamental work Mammals from the Age of Dinosaurs (2004)". The choice that the FNP Council makes every year is always preceded by an in-depth analysis of the candidates' achievements performed by a number of invited experts, who in this case unequivocally recognized Professor Kielan-Jaworska's work as outstanding.

Asked what palaeontology could teach us, the Professor replied that "it enables us to understand humans' place in the world. […] Humans are not separate from the rest of life, created by some magical manipulation, as people living in Mesopotamia 5,000 years ago imagined, but like the rest of the animate world they are a product of the powerful mechanisms of evolution. Thus, palaeontology teaches us modesty".

Modesty and humility should guide all scientists as they face the magnitude of the world around us, whose complexity they study every day. May these words become a motto for successive generations of researchers for whom Professor Zofia Kielan-Jaworska charted paths throughout her career — as a mentor, associate and friend.

Yours sincerely,

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PREFACE

Only a year has passed since Professor Kielan-Jaworowska's death and her image is still vivid in our memory. May it long remain so. She was an unquestionably towering figure in the field of vertebrate paleontology, a personality larger than life, totally devoted to science and practically consumed by it. Nonetheless, while recollecting the Professor it is essential to observe that professional activities never deprived her of being profoundly human. When times called, she did not flinch from doing right even when holding important professional posts; in the moments of test, Zofia showed the highest integrity and she should be remembered as such.

Kielan-Jaworowska's death left an unfillable void: something was irrevocably lost and cannot be recaptured because Zofia belonged to a world now almost gone, and was molded by different forces than prevail in today's science, which increasingly resembles a business-like enterprise. Kielan-Jaworowska's leadership role in the Polish-Mongolian Expeditions places her in the line of celebrated Gobi explorers which begins with Andrews, Granger and Morris.

The volume of *Palaeontologia Polonica* we now hand over to the readers was supposed to be a birthday gift on occasion of Zofia's 90th Anniversary; alas, it turned out to be her epitaph. The idea we had in mind was to gather Professor Kielan-Jaworowska's friends and close collaborators to honor her work and to keep her in that way a little longer with us. We are extremely grateful to all Authors who responded to our first call and offered their works to this volume at such a short notice. Also, we would like to thank those who initially answered us kindly but eventually were not able to contribute.

The present volume includes two kinds of papers: Three opening "eulogies" bring Zofia back to us as a person, and are followed by 14 original scientific contributions, collectively written by 42 colleagues, including the late Percy M. Butler, who also passed away in 2015. The papers span a variety of topics on Mesozoic vertebrates, from an overview of dinosaur findings in Mongolia, to recent discoveries in the Jurassic strata on Spitsbergen, summaries of triconodont diversity and the Late Triassic to Early Jurassic mammaliaform record of Britain, along with a reinterpretation of docodont and shuotheriid dental structure, and new information on metatherian and eutherian mammalian faunas of Asia and North America. A sizeable portion of this volume deals with multituberculates, a group especially dear to Zofia.

We are deeply grateful to all who helped to bring this volume out. In particular, thanks are due to the reviewers: Alyson Brink (Texas Tech University, Lubbock, TX, USA), Steve Brusatte (University of Edinburgh, UK), Richard L. Cifelli (University of Oklahoma, Norman, OK, USA), William A. Clemens (University of California at Berkeley, CA, USA), Gloria Cuenca-Bescós (Universidad de Zaragoza, Spain), Brian M. Davis (University of Louisville, Louisville, KY, USA), Jeffrey G. Eaton (Utah Museum of Natural History, Salt Lake City, UT, USA), Eric G. Ekdale (San Diego State University, CA, USA), Emmanuel Gheerbrant (Museum national d'Histoire naturelle, Paris, France), David Grossnickle (University of Chicago, IL, USA), Andrew B. Heckert (Appalachian State University, Boone, NC, USA), Simone Hoffmann (Stony Brook University, New York, NY, USA), Jerry Hooker (Natural History Museum, London, UK), Jørn H. Hurum (Naturhistorisk museum, Universitetet i Oslo, Norway), Richard F. Kay (Duke University, Durham, NC, USA), Zhe-Xi Luo (University of Chicago, IL, USA), David Martill (University of Portsmouth, UK), Thomas Martin (Universität Bonn, Germany), Jin Meng (American Museum of Natural History, New York, NY, USA), Wojciech Nemec (Universitetet i Bergen, Norway), Jingmai O'Connor (Institute of Vertebrate Paleontology and Paleoanthropology Chinese Academy of Sciences, Beijing, China), Tom Rich (Museum Victoria, Melbourne, Australia), Guillermo Rougier (University of Louisville, Louisville, KY, USA), Irina Ruf (Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany), Tom Stidham (Institute of Vertebrate Paleontology and Paleoanthropology Chinese Academy of Sciences, Beijing, China), Glen W. Storrs (Cincinnati Museum Center, Cincinnati, OH, USA), Corwin Sullivan (Institute of Vertebrate Paleontology and Paleoanthropology Chinese Academy of Sciences, Beijing, China), and John R. Wible (Carnegie Museum of Natural History, Pittsburgh, PA, USA). Finally, the junior editor is greatly obliged to her US-based counterpart, a wonderful colleague and critic, who from the beginning liberally gave his time to help with the production of this volume, and she hopes he likes the outcome.

<div align="right">The Editors</div>
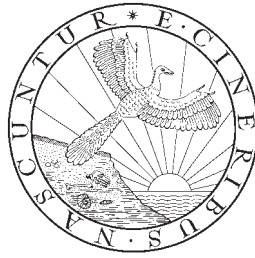
TRIBUTE TO ZOFIA

MAGDALENA BORSUK-BIAŁYNICKA

Fig. 1. Zofia Kielan in 1945, as a student at the University of Warsaw.

Zofia was born in 1925 within a short period between two world wars. She belonged to that generation of educated Polish people, which is passing away just now, in which there was instilled an enthusiastic atmosphere, reveling in the restoration of Polish Independence, lost for the whole nineteenth century. This atmosphere evoked in them a deep, intrinsic understanding of what the Homeland means and a readiness to defend it in case of danger. Unfolding events, beginning with the Nazi invasion of 1939, required them to back this readiness with action. During the Second World War Zofia helped carry her country's torch of freedom, going through underground education and secret military training. Eventually she took part as a military nurse of the Home Army (*Armia Krajowa* or AK) in the battles of the Warsaw Uprising (1944) against Hitler's troops. The experiences of the war left its survivors with the realization that everything may perish except education and what one may achieve by hard work. Working hard for the restoration of Poland's ruined scientific infrastructure, institutions and museum collections, all the while studying under difficult post-war conditions — that was what Zofia did in the 1940s (Fig. 1).

Zofia's worldview was also shaped by major upheaval in political, social and ideological changes that occurred in decades preceding her birth. Traditional religious belief prevalent through the nineteenth was being ousted by a scientific view of the world, sometimes in a climate of revolt. This was the source of Zofia's enthusiastic belief in the explanatory power of science and the importance of education, and a starting point of her future scientific career. Her general interests in natural sciences were steered toward palaeontology by Professor Roman Kozłowski, a renowned graptolite specialist (the only Polish laureate of the Wollaston Medal of the Geological Society of London), and her future supervisor, whom she met at the clandestine Warsaw University courses that she attended.

In the months that have passed since Zofias's death, her scientific career and personal character have been frequently discussed and written about. Herein I give some afterthoughts in celebration of her great life.

To all except a handful of scholars and close colleagues, the most surprising thing about Zofia's research program is that she began as an invertebrate paleontologist. She first worked on trilobites (the subject of her PhD, awarded in 1953 and published the following year), then on the jaw apparatuses of polychaete worms from the Paleozoic of Poland (published in 1966). Still, the most spectacular of her achievements and her most significant scientific contributions were made in vertebrate paleontology, and in particular, early mammalian history. Her interest in this subject dated back decades, but it was only in the 1960s that she got a chance to study vertebrate fossils, namely, the exquisite Late Cretaceous mammals collected by the Polish-Mongolian Paleontological Expeditions to the Gobi Desert — expeditions of which she was the organizer and often the leader. Mesozoic mammalian history henceforth became the main subject of Zofia's studies. Fifty years of her research yielded not only a huge supply of basic information on comparative anatomy and systematics, but also important contributions to several key problems of mammalian evolution, such as the position and evolutionary history of multituberculates; the relationships and timing of divergence be-

Fig. 2. Zofia Kielan-Jaworowska during one of the
Polish-Mongolian Expeditions.

tween monotremes and therians; the single versus multiple origin of the tribosphenic (multi-function) molar pattern and zoogeographical implications of this issue; as well as questions related to feeding, reproduction, and locomotion of early mammals. The early history of mammals, not well understood prior to Zofia's discoveries and studies, has become one of the best known parts of vertebrate phylogeny in recent times. Her contribution in this advance has been enormous: beyond the considerable volume of her own results, Kielan-Jaworowska stimulated further discoveries and ideas worldwide.

The Polish-Mongolian Expeditions were a massive undertaking, and Zofia oversaw all aspects of the program, from organization of field work (Fig. 2), to follow-up research on the fossils collected (by a team of colleagues Zofia appointed), to dissemination of results to the international scientific community through publication in a comprehensive monographic series of *Palaeontologia Polonica* — all this demonstrates Kielan-Jaworowska's extraordinary organizational abilities, her enormous energy, and her deep understanding of how science should work. She knew how to make the most of the fossils collected, through the process of meticulous, penetrating studies at various levels of interpretation; and she demonstrated the highest editorial standards in publishing the results of the expeditions. Moreover, she established an extensive international and interdisciplinary network of scientific contacts and collaboration, aimed at unifying the information from a global perspective. Yet she never forgot the particular "Polish Science" that she enhanced and gave high standards. This was her peacetime patriotism, of which we knew, though she never mentioned it. In spite of that, her contacts with foreign colleagues, from both West and East, were friendly, cooperative and very often supportive.

Apart from over one hundred publications concerning early mammalian history, about half of them resulting from collaboration, Zofia co-authored and co-edited two extensive compendia on Mesozoic mammals, the first one in 1979. Beginning twenty years later, she undertook the massive work of updating and summarizing the enormously expanded knowledge that accumulated in the two decades that passed since the appearance of the first treatise. This second compendium, *Mammals from the Age of Dinosaurs* (2004), was far more ambitious in scope than the first and was co-authored with two American colleagues, Rich Cifelli and Zhe-Xi Luo. This acclaimed book remains exceptional in its coverage of the subject and is a legacy left by Zofia's generation for evolutionary biologists to come.

It is widely known that Zofia Kielan-Jaworowska's professional activities extended far beyond pure research. Apart from more than twenty years of academic administration as Director of the Institute of Paleobiology and Head of the Vertebrate Paleontology Department at the same organization, she had appointments as Alexander Agassiz Visiting Professor, Harvard University (1973–1974); Visiting Professor at the Muséum national d'Histoire naturelle, Paris (1982–1984); and Professor in the Department of Paleontology, University of Oslo (1986–1995). Zofia also was engaged in several exploration projects, organized and took parts in conferences, and edited papers and journals. The importance of her editorial work, notably as the Chief Editor (1997–2007) of *Acta Palaeontologica Polonica*, was substantial, and we all, her students and younger colleagues, are indebted to her for her critical work and help on our research projects and our manuscripts.

We also remember how much Zofia appreciated the critical importance of popularizing natural science for the education of the young. She somehow always found time for this kind of activity and published some 70 popular articles and several books for different audiences, ranging from school children to university students. Kielan-Jaworowska also curated several important museum exhibitions in various places, including Warsaw (1968, 1985), Chorzów (1975), and Oslo (1993). Recently she published two editions (in English and Polish), of her scientific autobiography, including an academic-level popularization of current knowledge on

early mammalian evolution. This work also serves as a source book on all the eminent paleomammalogists of the time, her collaborators and friends.

Zofia's achievements have been recognized by numerous honors and awards. Two academies, the Polish Academy of Sciences and the Norwegian Academy of Science and Letters, and numerous learned societies made her their member. Among her awards is the Prize of the Foundation for Polish Science (awarded 2005), regarded as the most prestigious Polish scientific award. But to her, one of the most precious honors was the Righteous Among Nations title, awarded to the Kielan family (Zofia included) by Yad Vashem Authority of Israel, for sheltering a Jewish girl during the Second World War — an act that was punishable by death.

Since the beginning of this century Zofia's visits to the Institute of Paleobiology in Warsaw became infrequent and she did not travel abroad. She stayed in her house, where she kept an office and her extensive scientific library, situated in the green suburban village of Konstancin, some 20 km from Warsaw. Here she lived with her husband and (next door) her son's family. She continued her work at the house, where she received her friends and collaborators from various parts of the world, and so it naturally became a virtual center of Polish vertebrate paleontology. In this place she passed through the tragedy of her husband's death in 2011. He, Professor Zbigniew Jaworowski, was a widely known scientist and radiologist; a brilliant, optimistic and helpful man, her best friend and companion for more than sixty years. It was only her scientific work that helped sustain her after this loss. At that time, she especially welcomed contact with her colleagues and friends at the Institute, whom she treated with warmth and tenderness, like members of her family. She continued to grace us, her colleagues, with her knowledge, friendliness, and her smile. In return, we shared with her our deep estimation, gratitude, and admiration for her personality and her major contributions to paleontology.

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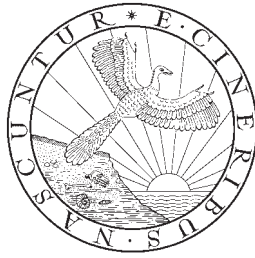
MEMORIES OF ZOFIE

PRISCILLA MCKENNA

My dear friend Zofie, who died at 89 in March 2015, was the internationally known Zofia Kielan-Jaworowska, specialist in the collection, study, and classification of fossil mammals, particularly those of the Mesozoic periods. She was expert with dinosaurs, too, but mammals were her true love.

My husband, Malcolm McKenna, also deeply interested in the study of Mesozoic mammals, had for many years been studying the geology and paleontology of central Asia with the hope of someday going there to collect and research the fossil mammals of the Gobi region of Mongolia.

When, in 1960, Malcolm became Frick Curator of Fossil Mammals at the American Museum of Natural History in New York City, he became the curator of the collections made in China and Mongolia during the Museum's Central Asiatic Expeditions conducted in the 1920s. Since 1923, the Mongolian Peoples' Republic had been under the control of the Soviet Union and had been held in isolation from all but the countries of the Soviet communist bloc. After joining the American Museum, in spite of the isolation, Malcolm managed to keep in sporadic touch by mail with his Mongolian counterpart, Demberlyn Dashzeveg.

Hope springs eternal, however, and Malcolm and I prepared for the remote possibility that field work in Mongolia might be resumed. We collected maps and studied Russian. We read books and talked to knowledgeable people, such as Owen Lattimore and Gombojav Hangin, the Mongolian patriot. And finally, in 1964, an opportunity opened to go to Mongolia as members of the second group of western tourists allowed into that country. It was a fortunate piece of timing, we thought, because the Polish Academy of Sciences/Mongolian Academy of Sciences were engaged in a major collecting expedition in the Gobi that summer; a very large expedition organized and led by Zofia Kielan-Jaworowska, whom Malcolm had met briefly in 1963.

Our group went to Mongolia and even into the Gobi, but no member of the Polish expedition was allowed to travel the 65 kilometers that separated us from them, and Dashzeveg was sent away somewhere out of our reach as long as we were in the country. A big disappointment on one front, but two good things happened. First, we both fell in love with Mongolia; and, subsequent to our trip, Malcolm and Zofie established a very close, lifelong working relationship, blessed by their shared and deep interest in the fossils of the Gobi, especially those of Mesozoic mammals.

Thus, I first heard of Zofie in 1964. At that time, it was a near impossibility for a major exploring expedition to be led by a woman—something that is commonplace now in the 21st Century. Naturally our interest in and desire to know her was aroused.

My first meeting with Zofie came when, during the subsequent winter, she traveled to New York to study the Museum's collections and to work with Malcolm on them, and she stayed with us in our home. I remember it vividly because, in her wish to bring us a gift, she had packed a bottle of Polish vodka into her suitcase, and, alas, it had leaked very generously throughout her case. So she and I spent our first hours together cleaning and deodorizing her wardrobe. After that, any formality between us that might have developed was totally gone, as it were, sent off on a flood of vodka.

Subsequently, during many sessions, we learned details of her organization of that successful Mongolian expedition and developed a deep admiration of her abilities, both as a leader and as a scientist. And, many years later, in the 1990s, when I was organizing the equipment and supplies for the American Museum/Mongolian Academy Expedition to the same areas of the Gobi, I copied some of her successful methods and thereby developed a deep understanding of and respect for what her organizational endeavor involved,

Fig. 1. "The outstanding Zofie:" Kielan-Jaworowska and colleagues, 1974. Photo taken by Malcolm C. McKenna at a congress in Moscow, 6–12 June, 1974. Participants, left to right: Altangerel Perle (Mongolian Peoples' Republic), Vyacheslav Chikhvadze (Russia), Nina Shevyreva (Russia), Zofia Kielan-Jaworowska (Poland), Konstantin Flerov (Russia), Ivan Pidoplichko (Russia), Boris Trofimov (Russia), ?, Valerii Reshetov (Russia), and Demberlyn Dashzeveg (Mongolian Peoples' Republic).

though I had no scientific leadership responsibilities as she did. The organizational skill and political adroitness that she demonstrated then were critical to the success of that whole effort.

In 1966, Malcolm and I, with our two oldest children, Douglas and Katharine, stayed with Zofie in her home in Warsaw. There we met her husband, Zbigniew Jaworowski (Zbyszek) who was not only her best friend and companion, but also the love of her life, and their son, Mariusz, close to the same age as our two. We were entertained very warmly there and also had the enormously impressive experience of watching the construction of a sea-going yacht that Zbyszek was building in his back garden. From there, Zofie took us on a tour of northern Poland where we visited a forest preserve, formerly the hunting preserve of the King, where some European bison (wisent) breeding was taking place, and an Ice-age, human-occupied cave was being excavated by Professor Solecki of Columbia University. Some years later (1976), Zofie and Zbyszek sent Mariusz to spend the summer with us, in order for him to learn American-style English. We had a lot of fun taking him fossil hunting in the Rocky Mountains and river running on the Green River of Utah. Later that summer, he spent the better part of a week memorizing the contents of a book of "Polish Jokes" in American English that he found on our bookshelf.

Over the years Zofie's paths and ours crossed frequently, except for a relatively short period of political turmoil in Poland, when she requested that we not contact her. She and Malcolm worked together in the USA, in Poland, and in Norway; and they exchanged ideas elsewhere (Fig. 1). We learned much about her life experiences, during and after World War II as well as in the Gobi, and we came to be very fond of her and to have great appreciation of her talents. When she came to New York, she always stayed with us, and sometimes she would take time off from scientific research and she and I would do some female things like buying new clothes. Zofie was a beautiful woman who always dressed stylishly. One time I helped her buy a rabbit fur coat and matching hat at Bloomingdale's. That winter, she had an accident driving a Volkswagen Beetle, and she always claimed that the thick fur coat saved her life. Now, as I sit at my desk typing these memories of her, I am being watched by the small brass Buddha that she brought me from Mongolia.

When I think of the experiences of Zofie's life — of her impressive lifetime accomplishments and of the obstacles that she had to overcome in order to achieve those accomplishments, not only during the Nazi occupation[1] but in the following years of totalitarian government in Poland — I find myself without words to adequately express my admiration and respect.

In her teens, she pursued her education in Warsaw, risking the death penalty to study at the clandestine high school and university (an uncle of Zbyszek's was an organizer of the network of clandestine schools); she participated fully in the Resistance; (she ran around on the streets of Warsaw working as a medic with a paleontology textbook in her backpack; just in case there was a little extra time in which to pursue her scientific study!). She spoke to me movingly of the elation felt by the Resistance fighters when the Russian Army approached Warsaw, thinking that Poland was about to be rid of the oppressive Nazi occupiers, and of the Resistance fighters' profound and tragic disillusionment when the Red Army camped on the other side of the River and stayed there, hoping that the Nazis and the Resistance would kill each other off and make things easier for the new conquerors.

In the wake of World War II, using her amazing linguistic talents (Polish, Russian, English, French, Norwegian, etc.), Zofie, along with others, including Malcolm McKenna, pursued cooperative research programs with colleagues from Mongolia to California and at many points in between, thus leading the way to the post-war establishment of vertebrate paleontology and related Earth sciences as world-wide, collaborative scientific endeavors. And during the Cold War, she defiantly refused to collaborate with the attempts of the authoritarian eastern bloc governments to keep their people isolated from the West.

Inspired by her deep love of her scientific work, Zofie demanded the best from herself and usually from her co-workers. I have always felt that, given the way her expectations were honed in the most challenging possible environment (i.e., education under threat of death!), she felt that she had to make the best use of her talents and her time, and sometimes that was hard for her co-workers to adjust to. However that may be, it was surely the basis of her very high level of productivity.

With her strong and enduring courage, unquenchable spirit, brilliant and talented mind, boundless energy and perseverance, personal and scientific integrity, warm personality, and her passion for her scientific work, she set an example for all of us. My friendship with Zofie has been one of the great privileges of my life.
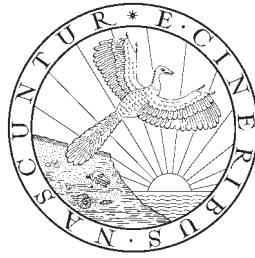
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[1] For a brief description, in Zofie's own words, of her experiences under the "Teutonic barbarism" (her words) of the Nazi occupation, refer to Chapter 4, p. 35, of her book "In Pursuit of Early Mammals (Kielan-Jaworowska 2013).

ZOFIA KIELAN-JAWOROWSKA
AND THE GOBI PALAEONTOLOGICAL EXPEDITIONS

JOHN R. LAVAS

During an illustrious scientific career that lasted more than 60 years, the late Zofia Kielan-Jaworowska greatly advanced the direction of research in several branches of invertebrate and vertebrate palaeontology. The general public largely knew Zofia as the leader of the famous joint Polish-Mongolian Gobi Expeditions of the 1960s–1970s and the spectacular (mainly dinosaurian) fossils that resulted from those ventures. Indeed, an enduring image that I associate with her name shows Zofia standing beneath one of her discoveries, the enigmatic theropod *Deinocheirus*. Momentous as such finds were, Zofia's principal research area was the phylogenetic relationships of the Mesozoic mammals retrieved during those expeditions, specifically evidence from their brain structure and musculature. It is within this realm that she left her greatest scientific legacy in what had previously been a relatively poorly-developed branch of palaeontology due to the paucity and fragility of fossil material. As well as attaining the forefront of her chosen field, Zofia was a humanist with a unique ability to forge successful collaborations between researchers from the former Council for Mutual Economic Assistance (COMECON) countries and their Western counterparts at a time in history when it was difficult to do so. The inclination to rank Zofia alongside her compatriot Marie Curie (1867–1934) is not only appropriate in terms of the impact each made to science, but the fact that Zofia's late husband was a radiobiologist and that they had spent two years working in Paris is surely more than coincidental. I very much appreciate the opportunity to provide my perspective on the achievements of someone who was both a peerless scientist as well as a scientific leader of her era.

My association with Zofia began as a result of my authorship/co-authorship of popular titles in palaeontology and related fiction literature. The topic of my first monograph was one that was close to her own accomplishments, and I suspect it was this affinity that led her to take a particular interest in the project. The book, *Dragons from the Dunes: the Search for Dinosaurs in the Gobi Desert* (Lavas 1993), was the first popular work to review one century of palaeontological field-work conducted in Mongolia (1892 to 1992). That publication could never have been compiled, nor found its target audience, were it not for Zofia's assistance. I never met Zofia, nor did I in fact even speak to her directly, as all our correspondence was at first by letter or fax, and later via email. However, her responses to my enquiries over the years were always so prompt and helpful that at times it almost seemed as if she was answering from an adjoining office. Some recollections of my correspondence with Zofia are presented in the last section.

BEGINNINGS

Zofia's difficult war-time experiences as a student in German-occupied Poland are detailed in depth elsewhere in this volume (see also Cifelli *et al.* 2015). With all Polish secondary and higher education schools closed during the occupation, I suspect that her unbounded enthusiasm for learning partly stemmed from having to take school lessons at private apartments and later attending clandestine classes given by Warsaw

University. The war also altered her views on the Catholic faith, and she became an agnostic which was very atypical of Polish society at that time. Whilst still at high school she had expressed an early interest in vertebrate evolution and the biological aspects of palaeontology. Following the end of the war, she met the celebrated Polish palaeontologist Roman Kozłowski (1889–1977) who supervised her Masters (1949) and doctoral theses (1953, published as Kielan 1954), both of which concerned Devonian trilobites. Later, under Roman Kozłowski's supervision, she conducted research on Palaeozoic polychaete jaw structure. During a mountaineering field-club trip in 1950, Zofia met Zbyszek Jaworowski, whom she married eight years later.

In her autobiography (Kielan-Jaworowska 2005; see also Kielan-Jaworowska 2013) Zofia mentioned that she had often dreamt of participating in palaeontological field-work in Mongolia ever since reading of the pioneering Central Asiatic Expeditions (CAEs) to Mongolia and China by the American Museum of Natural History, New York (AMNH) from 1922 to 1930. Led by Roy Chapman Andrews (1884–1960) and head palaeontologist Walter Granger (1872–1941), these expeditions retrieved several types of dinosaurs and nests of dinosaurian eggs, the remains of Tertiary mammals and the earliest then-known mammalian skulls (from Cretaceous strata). In 1949 Zofia learned that the Palaeontological Institute of the Russian (at that time, Soviet) Academy of Sciences (PIN) had conducted three major expeditions to Mongolia in 1946 (reconnaissance), 1948 and 1949. Led by the palaeontologist Ivan A. Efremov (1908–1972) and the taxonomist Anatole K. Rozhdestvensky (1920–1983), these expeditions explored even larger sectors of the country and located many new fossil sites containing numerous dinosaurian and mammalian fossils. The most important area was the celebrated Nemegt Valley in southern Mongolia, recognised as one of the world's key Mesozoic fossil repositories.

The subsequent Polish-Mongolian Expedition series took place over three periods; 1963–1965, 1967–1969, and 1970–1971. Together with the CAEs and the Russian Academy of Sciences Expeditions, they comprised the three definitive series of large-scale Gobi field-work of the 20th Century. In his book *Men and Dinosaurs* (Colbert 1968), distinguished American palaeontologist Edwin Colbert (1905–2001) dubbed this period of endeavours as the "Asiatic Dinosaur Rush". Each series of expeditions had, in their turn, captivated the imagination of scientist and public alike, and this was especially true of Poland where the remains of dinosaurs were previously unknown (that part of Europe having been submerged during much of the Mesozoic, although recent years have witnessed spectacular discoveries of Triassic vertebrates). In fact in 1963, no museum in Poland possessed any dinosaurian remains. Although the Polish-Mongolian Expeditions were followed by subsequent Gobi field-work, notably by the AMNH (beginning in 1990), and the ongoing joint Soviet-Mongolian field-work that began in 1969, none of these would be on such a committed or extensive scale as those of the Asiatic Dinosaur Rush. In order to place the Polish-Mongolian Expeditions in context, the following section includes an overview of the preceding American and Russian field-work in the Gobi.

PIONEERING AMERICAN AND RUSSIAN FIELD-WORK IN THE GOBI

In the 1920s Central Asia held a powerful allure for vertebrate palaeontologists, due to reasons that date from the latter years of the 19th Century. At that time, vertebrate palaeontology had developed to an advanced level in the United States and some European countries, with one of the main topics of debate being the origin of placental mammals (considered as the most successful mammalian group, ahead of the monotremes and marsupials). North American and European Palaeocene strata had yielded a rich placental fossil fauna and yet the older Cretaceous strata were seemingly devoid of them. However, the evolutionary development already evident in Palaeocene mammals suggested that they had been the product of a significant prior history. The consensus was that placentals had originated in some unknown region during the Cretaceous before migrating to North America and Europe. In the early 20th Century the eminent palaeontologist at the AMNH was Henry Fairfield Osborn (1857–1935), and he suggested that the place to search for the earliest placentals was Central Asia. A decade later the AMNH curator William Diller Matthew (1871–1930) advanced a similar view in his influential book *Climate and Evolution* (Matthew 1915). One of the natural historians based at the AMNH at the time was Roy Chapman Andrews. He had organised a zoological collecting expedition to southwest China and the Tibetan border in 1916–1917 and had spent time

collecting in Mongolia on a second expedition in 1919. Andrews was inspired by the arguments of Osborn and Matthew and began promoting a series of elaborate expeditions to eastern Central Asia with the main intention of searching for evidence of early hominids.

The concept of conducting field-work in this part of the world presented a truly daunting prospect. Much of the region is accounted for by the Gobi Desert which forms a vast arc-shaped plateau straddling the high east Central Asian tableland between the elevations of 1600 and 2000 m. A large portion of the Gobi, in turn, falls within the borders of Mongolia, one of the world's largest land-locked countries and also one of the least inhabited. Because of its remoteness, this area remained largely unknown to Westerners as late as the 1920s. Even the origin of the word "Gobi" was lost in antiquity; "Wall of spears", "Desert of Sand" and "Great" are said to be just some of its many meanings in different languages. Due to its acutely continental climate, the Gobi is subjected to greater temperature variations than any other desert (45ºC in July to -40ºC in January) which effectively excludes the possibility of field-work during winter months. Notable 19th Century explorations in the area included those of Pavlinoff and Matusovski in 1870, Ney Elias in 1872–1873, von Richthofen in 1873 and Nikolay Przhevalsky (1839–1888), the Russian geographer and explorer who led four major expeditions between 1870 and 1885. However, there had only ever been one report of a fossil in the entire area. In 1892 the Russian geologist, explorer and author Vladimir Obruchev (1863–1956) found some rhinoceros teeth on the caravan trail between the Mongolian capital Urga (now Ulaanbaatar) and the Chinese border. In 1902, Colonel Manakin of the Russian Army collected remains of the hadrosaur *Mandschurosaurus* from the Amur River between Russia and Manchuria, with further material being recovered in 1915–1917. Then in 1920, the Russian palaeontologist Aleksei A. Borissiak located a rich fossil deposit near the Aral Sea in Kazakhstan, the geology of which indicated that the Gobi might yield interesting Cenozoic and possibly even Cretaceous fossils. The Kazakh fossils included those of the largest known land mammal, the giant hornless rhinoceros *Indricotherium* (= "Beast of Indrik", a mythical giant animal of Russian folklore) which was only exceeded in size by the largest sauropod dinosaurs.

The CAEs were the most expensive land-based ventures to be organised by the US at that time, costing an estimated $700,000. Being multi-disciplinary in nature, they included not only palaeontologists, but also geologists, botanists, topographers, and zoologists. As head palaeontologist and scientific coordinator, Walter Granger had valuable experience of fossil collecting in the American West (including the Como Bluff and Bone Cabin quarries) and in the Tertiary strata of Egypt's El Fayum. Other notable AMNH participants were George Olsen, Peter Kaisen, and Albert Johnson. The CAEs were supplied by camel caravans and used special Dodge cars for scouting duties. With their headquarters based at Peking (Beijing), the expeditions made summer forays into the Gobi in 1922, 1923, 1925 (the largest of the series), 1926, 1928, and 1930 (the last three seasons' field work being restricted to areas outside of Mongolia due to political reasons). Granger also organised four winter expeditions to southern and western China during this period. The highlight of the CAEs came in July 1923 at the Flaming Cliffs of Bayn Dzak (Bayan Zag in later publications; Fig. 1) in southern Mongolia. These are eroded buttresses bordering a topographical basin of 18 km diameter. Here, Olsen found the first dinosaurian eggs to be identified (by Granger).

It is often stated that these were the first dinosaurian eggs to be found. In fact dinosaurian eggshells were already known from the French Pyrenees as early as 1859 and almost complete eggs were found in Provence 10 years later (in each case their identity was not confirmed until after the CAE discoveries). Numerous eggs and even large communal nests of eggs were uncovered at Bayn Dzak in close proximity to over 100 skulls and skeletons of the small dinosaur *Protoceratops*, which was originally thought to have laid the eggs (Fig. 2). Also found there was the small theropod *Oviraptor* (= egg thief, because of its association with a nest). Subsequent discoveries in the 1990s indicated that the eggs had in fact been laid by *Oviraptor* and that it was possibly guarding them at the time of burial. Other dinosaurs found by the CAEs include the early ceratopsian *Psittacosaurus*, the ankylosaur *Pinacosaurus*, and the small theropods *Saurornithoides* and *Velociraptor*. While preparing for the 1925 expedition Andrews visited an archaeological excavation of Tang Dynasty tombs north of Urga. These were being supervised by the Russian General Pyotr K. Kozlov, an indefatigable 65 year-old explorer who had actually been an expedition companion of Nikolay Przhevalsky.

In 1925 the CAEs unearthed 10 tiny Mesozoic mammalian skulls or jaws at Bayn Dzak, including the first Cretaceous therian skulls (all were thought to be insectivores and were later placed in four new genera). Political changes within Mongolia restricted the CAE work in the country after 1925, and rising xenophobia in China also impacted on their field-work after 1926. Ironically, the 1930 season produced the largest bulk of fossils, principally those of the Miocene shovel-tusked proboscidean *Platybelodon*. Other Tertiary mam-

Fig. 1. A caravan of Bactrian camels bearing supplies for the Central Asiatic Expeditions of the American Museum of Natural History, arrives at the "Flaming Cliffs" of Bayn Dzak (known as Bayan Zag in recent literature). J.B. Shackelford; courtesy of American Museum of Natural History Library, neg. 410767.

mal finds included fragmentary remains of titanotheres and indricotheres (the latter from Central Mongolia) and a huge skull of the mysterious Eocene mammal *Andrewsarchus*. Upon reviewing the impressive results of the AMNH field-work, Osborn surmised that the CAEs had only scratched the surface of the Gobi, and that further Mesozoic treasures awaited discovery. Andrews was less optimistic, having written in 1926 that he had likely already exploited the most fossiliferous areas of the country. When he had written this, interest in palaeontology and palaeoanthropology had shifted to other continents, notably Africa due to early hominid finds such as *Australopithecus* (1924).

Although the original palaeoanthropological aims of the CAEs had not been fulfilled, they had been eclipsed by the finds of dinosaurian eggs and Mesozoic mammalian skulls. Results of the CAE field-work were published in the *Natural History of Central Asia* series, *American Museum Novitates*, and *Bulletin of the American Museum of Natural History*. Following Granger's death in 1941, the AMNH renamed its Asiatic Hall of Fossils as the Walter Granger Memorial Hall. In 1998 Walter Granger's great-nephew, Vincent Morgan, established the Walter Granger Award, which I designed. Zofia Kielan-Jaworowska was named as the first recipient of this memorial award, which was conferred on 7 November 1998 (the 126th anniversary of Walter Granger's birth).

Although some authors mention the CAEs and subsequent expeditions being made to "Outer Mongolia", that name was only valid between 1915 and 1924, after which it became "Mongolia" (or officially the Mongolian People's Republic). On 11 July 1921, just prior to the first CAE season, a socialist government had come to power in Outer Mongolia as a result of a revolution against Buddhist landowners and Chinese rule. Then in 1931, Japanese forces invaded the neighbouring territory of Inner Mongolia and installed a puppet leader of what was to be known as "Manchuria". From the early 1920s Mongolia came increasingly under Soviet political and cultural influence, and in 1941 the Mongolian Scientific Commission approached the Soviet Academy of Sciences with a proposition of conducting palaeontological expeditions within the country. The German invasion of the Soviet Union in June 1941 intervened, however, and all negotiations were placed on hold. By 8 May 1945, the war with Germany was over, although the conflict in Asia continued. The Soviet declaration of war with Japan (8 August 1945) was followed by a major Soviet army and naval campaign in Manchuria until the Japanese surrender on 14 August. Negotiations between Mongolia and Russia resumed in 1946 and later that year, the PIN dispatched a reconnaissance expedition to the Gobi. Chief advisor for the expeditions (and participant on the reconnaissance one) was the Director of the Institute (and Academician)

Fig. 2. At Bayn Dzak the Central Asiatic Expeditions found numerous skeletons of the dinosaur *Protoceratops andrewsi* representing a range of sizes. In the same strata were found numerous eggshells and whole eggs that were the first to be identified as being dinosaurian in origin. Bayn Dzak has also yielded important remains of Mesozoic mammals, 50 skulls of which were subsequently removed by the Polish-Mongolian Expeditions during six seasons of field work. (Orlov Palaeontological Museum; courtesy of S.M. Kurzanov and the Russian Palaeontological Institute).

Yuri Orlov (1893–1966), who was a leading authority on mammals and reptiles. The vertebrate palaeontologist Ivan Efremov was chosen to lead each expedition, along with head taxonomist Anatole Rozhdestvensky (aged just 26 at the time). Efremov was already well-known in Russia as a popular science fiction author and had also founded the discipline of taphonomy (the study of fossilization patterns and processes). Other participants included the palaeontologist E.A. Maleev, chief fossil preparator J. Eaglon, the geologist N. Novojilov, and the gifted palaeontologist/zoologist/artist Konstantin K. Flerov, whose lucid reconstructions of prehistoric fauna can be seen at the PIN Museum and the State Darwin Museum in Moscow.

The Russian team entered Mongolia from the north and found that the capital (earlier re-named Ulan Bator) had been transformed into a modern city totally unrecognizable from the village-sized outpost that had greeted the CAEs in the 1920s. Many new buildings lined the city's broad avenues and parks, and the country's first university (Mongolian State University) had recently been founded (1941). Expedition members spent two months on reconnaissance, during which they discovered the vast Nemegt Valley, a huge oblong-shaped basin 180 km east to west and 40–70 km north to south.

The 1948 expedition (Figs 3, 4) included 15 scientific participants plus labourers. Heavy duty ZIL trucks were used to haul supplies and fossil monoliths (specimens encased in blocks of plaster of Paris), while 4WD GAZ field cars were used for observation and scouting work. This mechanization enabled the team to cover greater distances than earlier expeditions, exploring over an arc of more than 1300 km across the country. The first excavations were conducted at Bayn Shireh (eastern Mongolia), where the Cretaceous ankylosaur *Talarurus* was found. Then the team re-visited Bayn Dzak and removed more dinosaurian eggs and associated *Protoceratops* skeletons, as well as the ankylosaur *Pinacosaurus*.

Many dinosaurian cemeteries were located across a broad area of 100 km of the Nemegt Valley, the most important sites being "Nemegt" and "Altan Ula" in the north, and "Tsagan Khushu" in the south. Nemegt Cretaceous deposits produced another ankylosaur (*Tarchia*) and numerous finds of the giant hadrosaur

Saurolophus angustirostris (the mounted skeleton in the Orlov Museum gallery stands 7.6 m tall), and the equally numerous tyrannosaur *Tarbosaurus*, of which seven skeletons were excavated (Fig. 5). At the Dragon's Tomb site were found seven complete *Saurolophus* skeletons and even associated skin impressions. Other Nemegt sites produced incomplete remains of sauropods, ornithomimosaurs, and various other small theropods. The most enigmatic finds of 1948 were large forelimb bones and associated gigantic claws (70 cm long). At the time these were misidentified as the remains of turtle-like reptiles (and named *Therizinosaurus* = scythe lizard) but Rozhdestvensky later inferred that they likely belonged to a new "giant sloth"-like theropod. At Lake Orok Noor in 1948, the expedition collected indricothere remains to add to those found by Borissiak. The 1949 PIN expedition included 33 participants and re-traced the 1948 routes as well as venturing to the western borders of Mongolia. Here, at Altan Teli, they located a fossiliferous deposit of Pliocene mammals containing the remains of thousands of animals including the rhinoceros *Chilotherium*, woolly mastodons, ancestors of the giraffe, spiral-antlered antelopes, ancestral horses (*Hipparion*), and numerous rodents. Finally the team returned to earlier excavation sites in the Nemegt Valley and the southeastern Gobi.

The PIN expeditions generally employed a different method of fossil removal and transport to that used by American palaeontologists. A wooden "crate" was built around the fossil and plaster poured into it. Once set, a trench was then dug around the fossil, the "monolith" overturned and the crate completed from the other side. This technique enabled fossils to be transported over very rough ground with reduced risk of breakage. In total some 120 tonnes of monoliths (460 crates) were transported to Moscow, while one of the complete (adult) tarbosaur skeletons was given to the Mongolians to be mounted in the capital's Municipal Museum.

The results of the Russian Expeditions were published in various Russian and Chinese journals including *Trudy Paleontologitscheskogo Instituta*, *Paleontologitscheskiy Zhurnal*, and *Vertebrata PalAsiatica*. Efremov provided overviews in *Trudy Mongolskoj Komisii AN SSR* and *Trudy Mongolskoj Komisii Akademii Nauk SSSR* and there were also two popular books; namely Rozhdestvensky's *Hunting for Dinosaurs in the Gobi Desert* (1960; sometimes cited as *In the Footsteps of Dinosaurs in the Gobi Desert*), which was translated into French and German at the time (and subsequently into Japanese), and Efremov's *Road of the Wind* (1956, in Russian). Results of the subsequent long-term Russian field work in Mongolia that began in 1969 can be found in *Transactions of the Joint Soviet-Mongolian Palaeontological Expeditions*.

THE POLISH-MONGOLIAN EXPEDITIONS

Details of the Polish-Mongolian Expeditions are covered elsewhere (see Kielan-Jaworowska 2013), so the following is a brief overview. In 1955 Zofia had travelled to Russia (for the first time) and also to Sweden and Czechoslovakia. In Moscow, she visited the PIN Museum and met Anatole Rozhdestvensky, whom she recalled as a friendly and modest person. He gave her a guided tour of the fossil collections and recounted some of the adventures he and his comrades had experienced in the wilds of Mongolia. The museum housed one of the world's largest palaeontological collections but had an unusual history. During WWII, at the height of the German Army's advance on Moscow, the collections had been dismantled and moved to Alma-Ata for safety, but the museum re-opened again to the public in 1944. It had been the recipient of almost all the Mesozoic and Cenozoic fossils retrieved on the 1940s Gobi expeditions, and photos from this era show halls with scarcely enough room for passage between the exhibits. Further space limitations forced its closure for a time in 1955. In 1966 it was renamed after the institute's former director Yuri Orlov, and in 1972 construction began on another much larger purpose-built museum in southwestern Moscow. This building was declared open in 1987 and remains one of the world's largest (if not the largest) dedicated palaeontological museums.

In 1961 a convention of representatives of the various academies of sciences from the COMECON countries was held in Warsaw. During the proceedings, Roman Kozłowski raised the possibility of further exploitation of the Gobi's vertebrate fossils. The following year, an agreement was signed for an initial three seasons of field work that would involve both Polish and Mongolian palaeontologists. Zofia Kielan-Jaworowska was nominated to lead the Polish side, with Naydin Dovchin leading the Mongolian side. Other participating Polish palaeontologists included Magdalena Borsuk-Białynicka, Teresa Maryańska, Aleksander Nowinski, and Halszka Osmólska, while palaeontologists from the Mongolian side included Demberlyin Dashzeveg, Naydin Dovchin, and Rinchen Barsbold. By this time, the Mongolian capital was served by rail links (the Irkutsk–Ulaanbaatar–Beijing lines) and airlines to neighbouring countries, which meant that all heavy equip-

Fig. 3. **A**. Some participants of the 1948 Russian Gobi expedition (left to right): I. Sidorov, P. Petrunin, N. Brilijv (on truck) I. Alexandrov, Namnandordg, J. Eaglon, I. Efremov, Y. Orlov, I. Likhatchev (on truck), N. Shkilev, N. Vilezhanin, V. Pronin, Damdin. Not present are T. Bezborodov, M. Lookijnova, E.A. Maleev, N. Novojilov, V. Presniakov, and A.K. Rozhdestvensky. **B**. One of the first photographs taken of the famous Nemegt Valley during the 1946 reconnaissance expedition. (From the archives of A.K. Rozhdestvensky; courtesy of S.M. Kurzanov and the Russian Palaeontological Institute).

ment and supplies for field-work could be rail-freighted to Ulaanbaatar, with Zofia and her team flying from Warsaw via Moscow. Nonetheless, as Zofia pointed out to me, her expeditions had to contend with many of the same difficulties as had plagued the logistics and field-work of all earlier expeditions.

The 1963 reconnaissance expedition was supervised by Julian Kulczyki and visited previously-worked sites such as Bayn Shireh, Bayn Dzak, the Nemegt Valley, and nine localities south of Sayn Shand. This was followed by the main seasons' field-work of 1964 (beginning in the south of Mongolia) and 1965. Part of the 1964 season was supervised by Kazimierz Kowalski due to Zofia's commitments to complete her

Fig. 4. **A**. Head taxonomist A.K. Rozhdestvensky in the foreground as an expedition truck tyre is exchanged. **B**. Three 1948 expedition members at the Altan Ula locality (left to right): J. Eaglon, A.K. Rozhdestvensky and M. Lookijnova. **C**. Head preparator J. Eaglon at the "Dragon's Tomb" site with a skeleton of the giant hadrosaur *Saurolophus angustirostris*. **D**. Plaster-encased bones of *Saurolophus angustirostris* being loaded onto a lorry during the 1949 expedition. (From the archives of A.K. Rozhdestvensky; courtesy of S.M. Kurzanov and the Russian Palaeontological Institute).

polychaete research. The 1964 season had 16 participants, while there were 23 in 1965 (counting drivers and extra assistants). In both years, Cenozoic outcrops in central and western Mongolia were explored, including the rich fossil beds of Altan Teli. As in the 1940s, these expeditions used heavy trucks (Polish "Star 66" models) for hauling supplies and crated fossils (other hired vehicles included Tatra, ZIL and GAZ models). Due to the rough desert terrain, the expeditions adopted the monolith technique for removing and transporting fossils. One month of each season was assigned to work at Bayn Dzak, where more dinosaurian remains (*Protoceratops*, *Pinacosaurus*) and eggs were extracted. Work here also yielded over 20 skulls of Cretaceous therian and multituberculate mammals. As Zofia noted in her final book *In Pursuit of Early Mammals* (2013), whilst excavating larger dinosaurs in Mongolia presented logistical difficulties, finding Mesozoic mammalian fossils posed problems at the other end of the size scale; they were very difficult to even see. She found the best way to locate them was with a hand lens while crawling on bandaged hands and knees.

After Bayn Dzak, most of the 1964 and 1965 seasons were spent at Nemegt, but the three smaller expeditions of 1967–1969 were again spent at Bayn Dzak, searching for Mesozoic mammals. In total some 50 Mesozoic mammalian skulls were found during six seasons of field-work at Bayn Dzak. Excavations at Nemegt retrieved six incomplete tarbosaur skeletons, and there were many discoveries of new dinosaurian types including sauropods (*Opisthocoelicaudia* and a skull of *Nemegtosaurus*), large ornithomimosaurs (*Gallimimus*), and the giant forelimbs of the unusual theropod *Deinocheirus*, which Zofia personally discovered. Nemegt also produced further *Saurolophus* remains as well as a lambeosaurine hadrosaur (*Barsboldia*), and skulls and fragmentary skeletons of the first pachcephalosaurs known from this part of the world (*Tylocephale, Prenocephale*, *Homalocephale*, and *Goyocephale*). More ankylosaurids (*Tarchia* and *Saichania*) and new protoceratopsians (*Microceratops* and *Bagaceratops*) were added to the collections during the 1970–1971 seasons. The most significant discovery of 1971 was the famous "fighting dinosaurs"

Fig. 5. Dinosaurs recovered from the Nemegt Valley by the Russian Gobi expeditions of the 1940s included *Tarbosaurus* (**A**) and the hadrosaur *Saurolophus angustirostris* (**B**). (Orlov Palaeontological Museum; courtesy of S.M. Kurzanov and the Russian Palaeontological Institute).

fossil from Toogreeg (30 km west of Bayn Dzak), where a *Velociraptor* and a *Protoceratops* were found together in a death embrace. This was the first preserved example of mortal combat between dinosaurs.

At the completion of each expedition, the fossils were divided between the Polish and Mongolian partners, the Polish portion being transported to Warsaw by train. Once the scientific descriptions had been completed in Poland, the fossils were returned to Mongolia unless there was more than one specimen of each type, in which case the extra fossils remained in the Polish collections. There were also a number of casts made of unique fossils, such as *Deinocheirus*. The descriptions were published in 10 volumes of *Palaeontologia Polonica* (of which Zofia was editor) between 1969 and 1984, and many of the prepared duplicate or cast specimens were placed on a permanent display called "Evolution on Land" in the Warsaw Palace of Culture. Another more public manifestation of the results of the expeditions was an impressive outdoor park at Chorzow (Silesia) which featured life-sized restorations of Gobi dinosaurs (Fig. 6). These cleverly-fashioned concrete constructions were designed by the expeditions' technician Wojciech Skarżyński who was descended from the family of famous Polish painters Juliusz Kossak and Wojciech Kossak.

The Polish-Mongolian Expeditions are considered by the scientific community to be one of the most important palaeontological ventures ever undertaken (Kielan-Jaworowska 2013), and they coincided with renewed academic interest in aspects of dinosaurian physiology, ethology, and theropod-avian relationships. They influenced such research by augmenting and re-evaluating the discoveries of earlier expeditions, adding new taxonomic groups to the known Mesozoic fauna, and providing evidence of dinosaurian phylogeny, ontogeny, ecology, and life-habits (Lavas 1993). The expeditions had an even greater impact on the study of Mesozoic mammals; in 1963 the world total of Mesozoic mammalian skulls or jaws was only one dozen specimens. The Polish-Mongolian Expeditions added no fewer than 150 new specimens, some with associated (and extremely rare) postcranial remains. Such fossils not only re-defined subsequent research on early mammals but also clarified the classification of existing specimens (Cifelli *et al.* 2015). During her career, Zofia authored or co-authored around 220 publications, including seven books, most of which concerned Mesozoic mammals.

PERSONAL REFLECTIONS

In the 1980s I assembled a large collection of technical papers on archosaurs dating from the dinosaur renaissance era of the 1960s–1980s, with the intention of compiling a popular review on the topic. My original interest in the Gobi had been inspired many years earlier by Edwin Colbert's (1968) book *Men and Dinosaurs*. In chapter eight, Colbert presented a narration of the CAE field-work as well as a shorter but tantalising review of the Russian expeditions. At that stage, the Polish-Mongolian Expeditions were still underway and Colbert's summary of them was thus very brief. Then I read the English language version of Zofia's popular book *Hunting for Dinosaurs* (Kielan-Jaworowska 1969). This edition outwardly appeared rather inconspicuous with its soft-cover and non-descript jacket, but I was totally captivated as soon as I read the opening paragraphs. Zofia's first-hand account not only contextualized the previous American and Russian expeditions, but her evocative writing style successfully conveyed the remoteness, difficulty and romance of working in such an exotic region so far from civilisation. I also read Roy Chapman Andrews' books *On the Trail of Ancient Man* (1926) and *The New Conquest of Central Asia* (1932), and eventually managed (via circuitous means) to source the two popular non-English titles on the Russian expeditions (Rozhdestvensky's 1960 *Chasse aux Dinosaures dans le Desert de Gobi; les Aventures d'une Expedition Sovietique* and Efremov's 1956 *Road of the Wind* [in Russian]).

In September 1982 I wrote to Zofia seeking advice on whether a popular review of archosaur research might have publication potential. In October I received a reply from the Institute of Paleobiology, Warsaw, informing me that Zofia was in Paris until the end of September 1983, and that my letter had been forwarded to her. Zofia soon replied to me; she was impressed with the compilation and thought it had valuable content, but suggested that there might be more publication potential should I decide to write a popular book using existing material for the technical content. I followed her advice and contacted a number of palaeontologists who had worked in the Gobi, one of whom was Sergei M. Kurzanov of PIN (based at the Orlov Museum). I told him of my project and lack of access to material from the Russian expeditions of the 1940s, which were very poorly-known in the West. Fortuitously, he was able to assist in this regard by selecting numerous photos and negatives from Rozhdestvensky's archives, as well as material from more recent Russian field-work. He also organised for various exhibits at the Museum to be photographed on my behalf.

Throughout the compilation of the book, which took a decade, I corresponded intermittently with Zofia. Amongst other things, she sent me reprints of her technical papers, the volumes of *Palaeontologia Polonica* containing narratives of the Polish-Mongolian Expeditions, peripheral popular material, and a copy of her curriculum vitae. She told me of the life-sized dinosaur reconstructions at Chorzow and sent photos of the models. In May 1990 the bulk of the manuscript was completed and was sent to her for evaluation. By this stage, Zofia and her husband had moved to Norway where she had accepted the position of Professor of Palaeontology at the University of Oslo (in 1987). In July 1990, Zofia wrote back to say that she had read large sections of the manuscript with a keen interest (including the sections of non-expedition content). She also included several pages of helpful detailed corrections relating to historical and taxonomic details.

Once the book was printed (mid 1993) I sent Zofia complimentary copies and in September she wrote back with thanks, describing the final work as very detailed and objective in its historical treatment of the various expeditions. Included with her letter were five pages of listed names and contact details of palaeontologists from many different countries. Specific dinosaur specialists were noted, as was anyone who had conducted field-work in the Gobi. This information proved invaluable, as I soon realised that Zofia's endorsement carried a great deal of weight in academic circles. As a result of this the book sold very well, the main audience being palaeontologists and museum libraries, along with public and university libraries.

After 1993 my correspondence with Zofia lapsed for a time after I became involved with a multi-authored volume, *The Complete Dinosaur*, for which I wrote one chapter on the history of dinosaur collecting in Asia (Lavas 1997). There were also research projects concerning Walter Granger to which I contributed text and reconstructions. Our correspondence resumed when I produced two anniversary editions of Sir Arthur Conan Doyle's novel *The Lost World* (Lavas 2002; Lavas *et al.* 2012) and Zofia provided information on one of Doyle's contemporaries, the author Erazm Majewski (1858–1922), who was not widely known beyond Eastern Europe.

When her husband passed away, Zofia described in an email how the garden of her house adjoined the home of her son Mariusz and his young family. She remarked how fortunate she was to have them living so close by at that time. I was aware that she remained academically active because she included me in her
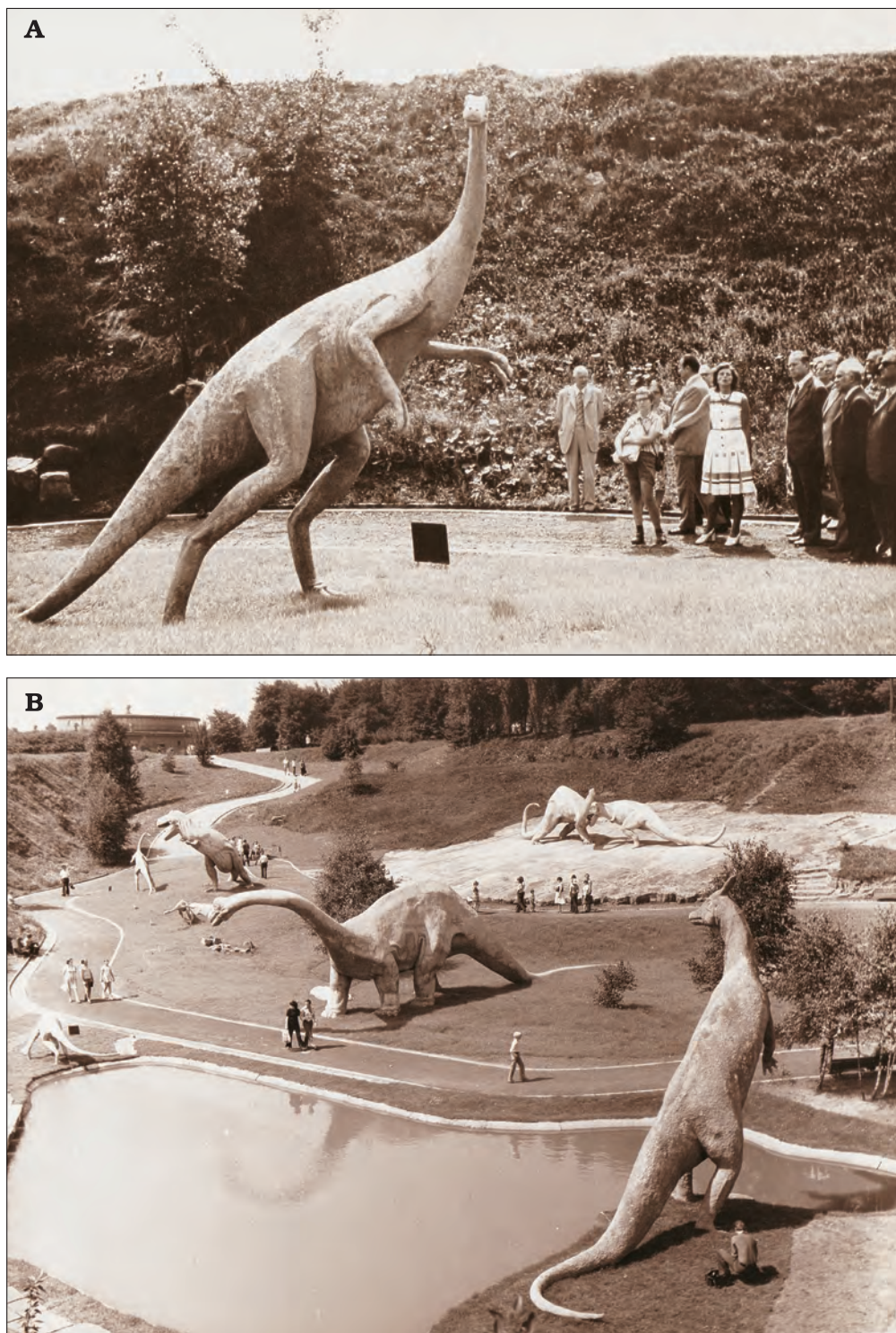
Fig. 6. **A**. Zofia Kielan-Jaworowska at the opening of the dinosaur park at Chorzow, Silesia, with a model of the ornithomimosaur *Gallimimus bullatus* in the foreground. **B**. General overview of the park. (Wojciech Skarżyński; courtesy of Z. Kielan-Jaworowska).

group email updates. Our final correspondence took place in February 2013 after I sent her a copy of *The Lost World* Centenary Edition (Lavas *et al.* 2012) and she arranged for a copy of her book *In Pursuit of Early Mammals* (Kielan-Jaworowska 2013) to be sent to me. In that work she recalled her 2002 return to Mongolia for the first time in 31 years, along with her husband and 10 year-old grand-daughter. They had joined one of the so-called "Nomadic Expeditions" tours which flew tourists from Ulaanbaatar to a small airfield near Bayn Dzak, then drove them directly to the famous Flaming Cliffs. Zofia noted that, far from the remote

and peaceful locality that she had known from her field-work in the 1960s, Bayn Dzak had since become a crowded tourist destination visited by hordes of sightseers. Her group went on to visit some of the famous Nemegt Valley excavation sites where Zofia, ever watchful, even managed to locate a new accumulation of sauropod bones in the easternmost sector (later lamenting that they were unable to expose the skeleton due to limited time and equipment). What had once been a wild and desolate destination only attained by a major expedition in the 1940s was now part of a tourist itinerary. However, some aspects of the trip had not changed over time; the grandeur and beauty of the desert landscape with its solemn lines of deeply-eroded cliff faces, and the friendliness and hospitality of the local Mongol shepherds.

It was with sadness, not to mention initial disbelief, that I happened to see Zofia's obituary in *Nature* (Cifelli 2015) several months after she had passed away. Although I had not heard from her since 2013, she had always seemed so alert and active in previous correspondence that I took it for granted (as I'm sure many others may likewise have done) that she would still be with us for some time yet. By any measure, Zofia lived a truly remarkable life, from her time as a student trying to survive in war-ravaged Poland to eventually becoming the foremost scientist in her field. A very humanistic philosophy enabled her to successfully bring together numerous researchers from both East and West who would otherwise not have had the opportunity of such collaboration. The contributions to this memorial volume bear testament to Zofia's extensive and enduring legacy, not only within professional palaeontology but also to the wider international community.

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NEW EVIDENCE ON THE STEM PLACENTAL MAMMAL *PARANYCTOIDES* FROM THE UPPER CRETACEOUS OF UZBEKISTAN

ALEXANDER O. AVERIANOV and DAVID ARCHIBALD

A newly discovered maxillary fragment (ZIN 102716) of *Paranyctoides quadrans* from the Bissekty Formation (Upper Cretaceous, Turonian) at Dzharakuduk, Uzbekistan shows this species has a P5 about half the labiolingual width of M1 and an infraorbital foramen placed above P4 near the anterior margin of the orbit and below the maxillolacrimal contact. The maxillary foramen, likely posterior to M1, is positioned more posteriorly compared to other stem placental mammals. The infraorbital canal is roofed by a thin plate of maxilla with facets for the lacrimal and jugal above. The posterior part of this roof may be formed entirely by the lacrimal. In *Paranyctoides* the upper posterior premolars (P4–5) and molars were confined to the posterior third of the maxilla below the orbit, as in the stem therian *Eomaia*. In a majority of stem placentals, including Early Cretaceous *Prokennalestes* and *Acristatherium*, the upper posterior premolars and molars occupy the posterior half of the maxilla, with P4–5 placed in front of the orbit. A new phylogenetic analysis places *Paranyctoides* in a polytomy with *Sheikhdzheilia*, *Lainodon*, and Zhelestinae.

Key words: Mammalia, Placentalia, *Paranyctoides*, Upper Cretaceous, Uzbekistan.

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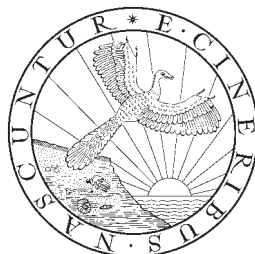
INTRODUCTION

The stem placental mammal *Paranyctoides* is among the rarest mammalian taxa in the Upper Cretaceous of Asia and North America (Fox 1979, 1984; Cifelli 1990; Nessov 1993; Archibald and Averianov 2001; Averianov and Archibald 2003, 2013a). It is one of the few generic-level mammalian taxa known from these two continents. Montellano-Ballesteros *et al.* (2013) argued that these were in fact generically distinct taxa. Subsequently, Averianov and Archibald (2013b) demonstrated much of the argued differences are the result of misinterpretation of morphological characters of the Asiatic taxon and thus at least for now there is no basis to recognize two genera.

Two species are currently recognized, *P. quadrans* in the Turonian–?Coniacian of Asia and *P. sternbergi* in the Campanian–Maastrichtian of North America (Averianov and Archibald 2013a, b). Until recently, our knowledge of *Paranyctoides* was limited to isolated teeth and dentary fragments. Recent phylogenetic analyses placed *Paranyctoides* in a more terminal position to Zhelestidae (Wible *et al.* 2007, 2009) or as sister taxon to Zhelestidae (Archibald and Averianov 2012; Averianov and Archibald 2013b; Manz *et al.* 2015). *Paranyctoides* is clearly distinct from most other Cretaceous stem placental mammals by its transversely unexpanded upper molars (Butler 1990), similar in this respect only to *Bobolestes* (see below). Here, we report on the discovery of the first maxillary fragment of *Paranyctoides*. This specimen (ZIN 102716) was found recently among the thousands of unsorted bones from the CBI-14 locality, Bissekty Formation, Dzharakuduk in Uzbekistan, from where the Asiatic species, *Paranyctoides quadrans*, was previously described (Nessov 1982, 1993; Archibald and Averianov 2001; Averianov and Archibald 2013a). Although incomplete, ZIN 102716 reveals an unusual structure of the infraorbital canal and the posterior part of the maxilla, differentiating *Paranyctoides* from the majority of other Cretaceous stem placental mammals.

Institutional abbreviations. — CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg; ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg.

Measurements. —AW, anterior width; L, length; PW, posterior width. All measurements are in mm.

SYSTEMATIC PALEONTOLOGY

Mammalia Linnaeus, 1758

Theria Parker *et* Haswell, 1897

Eutheria Gill, 1872

Eutheria *incertae sedis*

Genus ***Paranyctoides*** Fox, 1979

Paranyctoides quadrans (Nessov, 1982)

(Fig. 1)

For synonymy see Averianov and Archibald (2013a, p. 18).

Holotype: CCMGE 7/11758, right M1.

Type locality and horizon: Dzharakuduk, Kyzylkum Desert, Uzbekistan; Bissekty Formation, Upper Cretaceous (middle–upper Turonian)

Referred specimens. — Specimens listed by Averianov and Archibald (2013a, p. 18) and ZIN 102716, left maxillary fragment with M1 and alveoli for P5 and distal root of P4 from the type locality (locality CBI-14, Dzharakuduk).
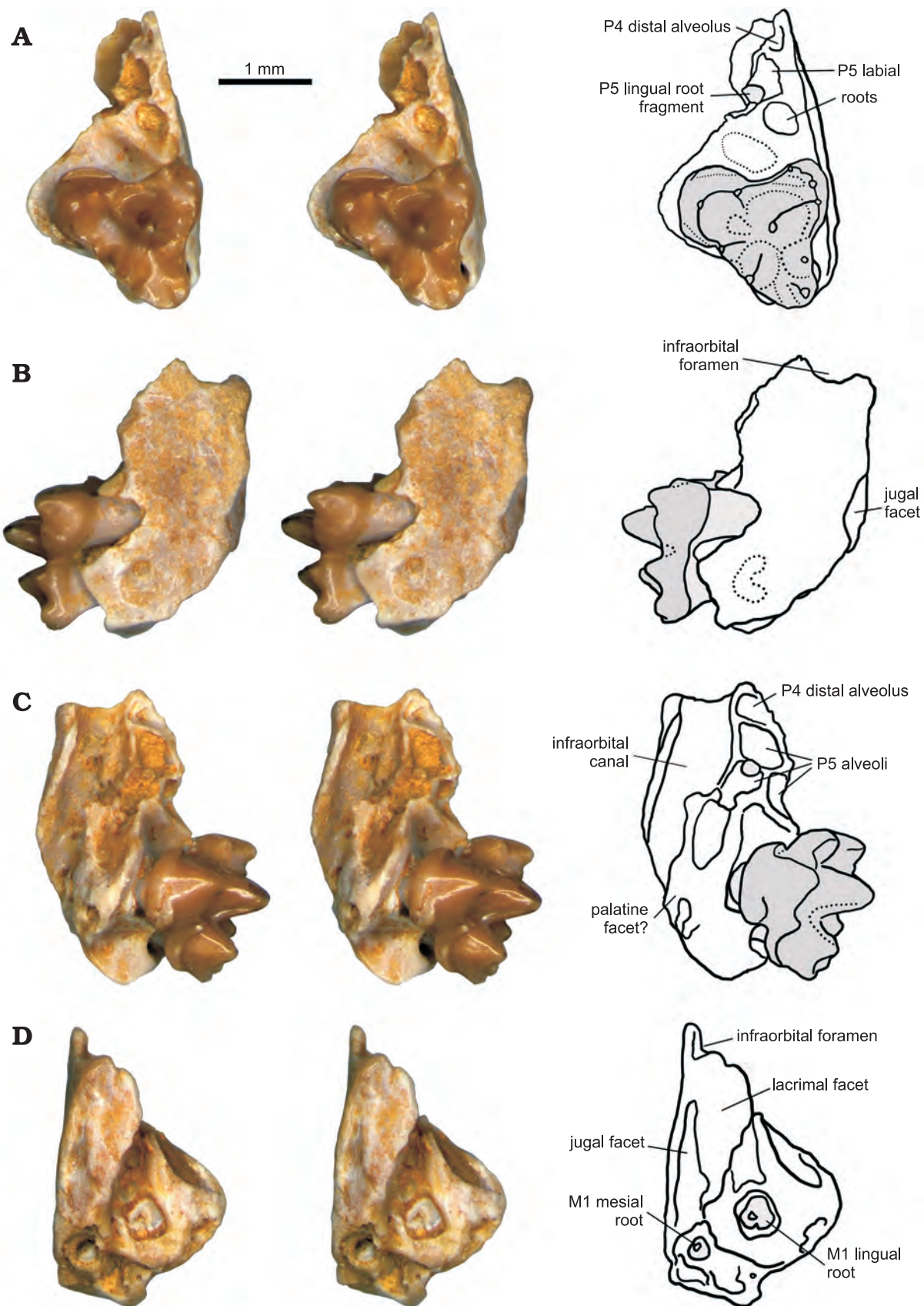
Fig. 1. *Paranyctoides quadrans*, ZIN 102716, left maxillary fragment with M1 and alveoli for P5 and P4, Dzharakuduk, Uzbekistan, Bissekty Formation, Upper Cretaceous (Turonian), in occlusal (**A**), labial (**B**), lingual (**C**), and dorsal (**D**) views. Photographic stereo-pairs and explanatory drawings.
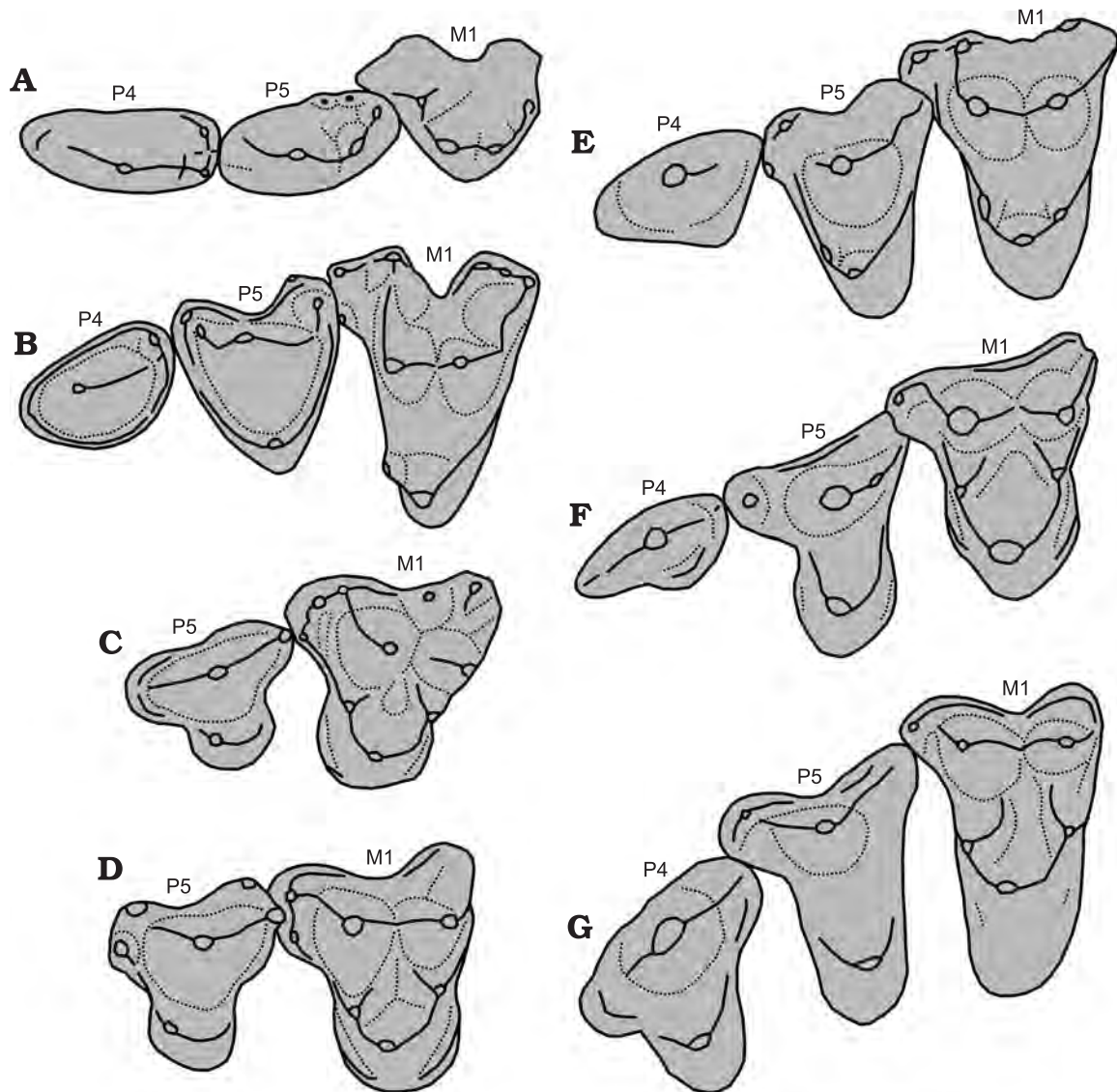
Fig. 2. Posterior premolars and M1 in selected stem therian and stem placental mammals in occlusal view. **A**. *Peramus tenuirostris*, after Clemens and Mills (1971, pl. 1). **B**. *Juramaia sinensis*, after Luo *et al.* (2011, fig. 2). **C**. *Paranyctoides quadrans*, based on ZIN 102716 with P5 hypothetically reconstructed. **D**. *Paranyctoides sternbergi*, after Montellano (1992, fig. 28a) and Montellano-Ballesteros *et al.* (2013, fig. 1J). **E**. *Prokennalestes trofimovi*, after Kielan-Jaworowska and Dashzeveg (1989, fig. 1A). **F**. *Aspanlestes aptap*, after Archibald and Averianov (2005, fig. 1E). **G**. *Kulbeckia kulbecke*, after Archibald and Averianov (2005, fig. 1G). Not to scale.

DESCRIPTION

ZIN 102716 is a left maxillary fragment with M1 and alveoli for P5 and the distal root of P4 (Fig. 1). The anterior margin of the palatal process is broken anterior to the level of M1 protocone. Posterior to this level a flattened area might represent the palatine facet (Fig. 1C). There are three alveoli for P5, two labial and one lingual. There is only a remnant of the lingual root (Fig. 1A, C). It is not complete lingually but because about two-thirds of its circumference is preserved it is likely not to have been much larger than what is present. The reconstructed labiolingual width of P5 is about half that of M1 (Fig. 2C). There are no diastemata between P4–5 and P5–M1. The height of the maxilla between the alveolar surface and the infraorbital canal is very small at P5, suggesting that this tooth had very short roots. The posterolateral edge of the infraorbital foramen is preserved above the distal alveolus of P4 (Fig. 1B, D). Two of three roots of M1 are exposed in the floor of infraorbital canal (Fig. 1D), in contrast with the other stem placental mammals, which have the

roots of M1 exposed in orbit floor, posterior to the maxillary foramen (posterior opening of the infraorbital canal). This suggests a more posterior position of the maxillary foramen in *Paranyctoides*, possibly between M1 and M2, or above M2. The infraorbital canal is roofed dorsolaterally by a thin maxillary plate with a flattened dorsal surface (Fig. 1D). On this surface there is a depressed triangular area posterolaterally that likely is the jugal facet (Fig. 1B, D). The second distinct facet on the dorsal surface of infraorbital canal roof, a flat surface anteromedial to the jugal facet, is likely a facet for the lacrimal (Fig. 1D). The medial margin of the maxillary plate above the infraorbital canal is intact with the lacrimal likely forming the dorsomedial roof of the infraorbital canal. The lacrimal component of the infraorbital canal roof apparently increased in width posteriorly. It is unclear if lacrimal participated in the roof of the infraorbital foramen. Most likely the foramen was entirely within the maxilla as in all known stem therian and placental mammals.

The M1 is little worn and agrees in morphology and size (Figs 1, 2C; L = 1.6; AW = 1.6; PW = 1.7) with an isolated M1, the holotype of *P. quadrans* (CCMGE 7/11758; L = 1.5; AW = 1.6; PW = 1.7). The outline of the crown approximates the shape of an isosceles triangle, with the mesial and distal sides of similar length. The labial margin is concave with a shallow ectoflexus. The parastylar lobe is protruding mostly mesially. The metastylar lobe is directed distolabially. There is a distinct ectocingulum labial to the paracone and connected to the parastyle. A small stylocone is on this ectocingulum. Distal to the stylocone there are two stylar cusps, C and D, the first of which is somewhat larger. Both of these cusps are present on the holotype of *P. quadrans*, although they are less developed there. There is a short ridge directed from cusp D towards the metacone but not reaching the base of the latter. The stylar shelf, a flattened area between the bases of the labial cusps and ectocingulum or stylar cusps, is absent labial to the paracone and narrow labial to the metacone. The metacone is distinctly smaller and lower than the paracone. The centrocrista is straight. The preparacrista is directed mesiolabially and connects to the stylocone. The postmetacrista is distally convex and connected to stylar cusp D. There is no metastyle. The postmetacrista is moderately worn, while the preprotocrista is unworn. The same is characteristic of the holotype of *P. quadrans*. On the parastylar lobe there are a large parastyle and much smaller preparastyle. The parastylar lobe is separated from the base of the paracone by a distinctly worn parastylar groove (= protoconid notch). The crown is distinctly constricted between the trigon and labial part. The trigon is narrower labiolingually compared with the labial part, in contrast with the majority of other Late Cretaceous stem placentals that have the trigon labiolingually wider than the labial part (Fig. 2). The protocone is large and is somewhat taller than the metacone. Its apex is situated opposite the paracone. The conules are well developed and winged, located about midway between the protocone and labial cusps (the paraconule is a slightly closer to the protocone than is the metaconule). The conules project well above the pre- and postprotocrista. The internal conular cristae extend labially towards the bases of their respective labial cusps. The trigon basin is deepest between conular internal cristae and the centrocrista. The preparacrista (= preparaconule crista) extends labially towards the preparastyle. The postparacrista (= postmetaconule crista) extends labial to the metacone apex but does not reach the labial margin. The precingulum and postcingulum are much better developed compared with the holotype of *P. quadrans*. The postcingulum is somewhat shorter. The protoconal cingula extend labially towards the area dorsal to the conules and are well separated lingually.

PHYLOGENETIC ANALYSIS

For the phylogenetic analysis we used the data matrix created by Wible *et al.* (2009) and consisting of 408 characters as modified by Archibald and Averianov (2012) and Averianov and Archibald (2013b). Additional postcranial characters 409–415, scorings of several additional taxa, and scoring corrections of the previously included taxa has been adopted from Goswami *et al.* (2011) and Manz *et al.* (2015). A new cranial character 416 is introduced and discussed herein. The newly-recovered maxillary fragment ZIN 102716 allows coding of the following five morphological characters whose state was previously unknown for *Paranyctoides*.

46(0): Ultimate upper premolar size (occlusal surface) relative to first upper molar: smaller or subequal. This character in its current formulation has little phylogenetic value for the analyzed taxa, as the derived state, ultimate upper premolar larger than M1 in occlusal surface, occurs sporadically in few terminal taxa within different clades. However, *Paranyctoides* is clearly different from other Cretaceous stem placental
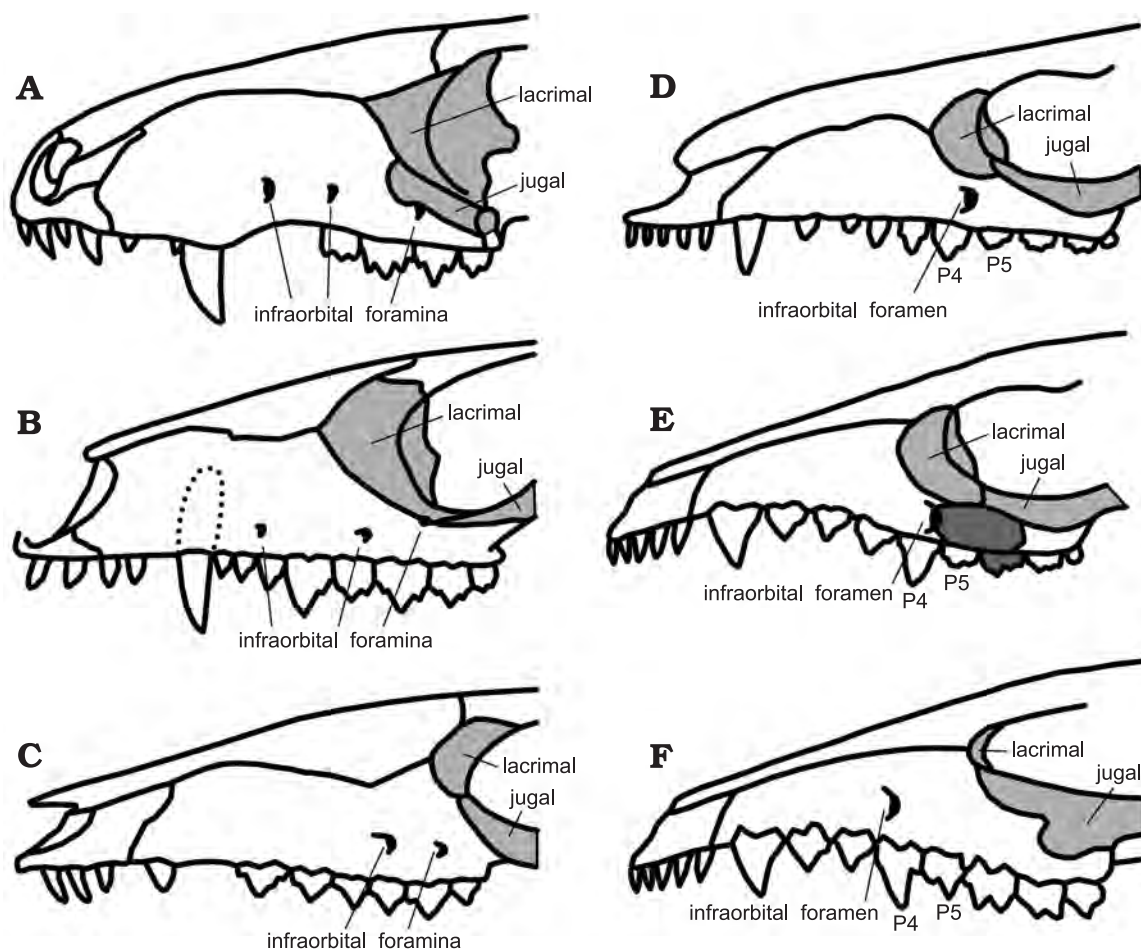
Fig. 3. Anterior part of the skull in lateral view of selected stem mammals (A, B), stem therians (C, D), and stem placentals (E, F). **A**. *Sinoconodon* sp., after Crompton and Luo (1993, fig. 4.9). **B**. *Morganucodon watsoni*, after Kermack *et al.* (1981, fig. 99A). **C**. *Maotherium sinense*, after Rougier *et al.* (2003, fig. 2A). **D**. *Eomaia scansoria*, after Ji *et al.* (2002, fig. 1c). **E**. *Paranyctoides quadrans*, hypothetical reconstruction based on maxillary fragment ZIN 102716, shown in dark grey. **F**. *Asioryctes nemegtensis*, based on Wible *et al.* (2009, fig. 35). Lacrimal and jugal are shown in light grey. Not to scale.

mammals, including *Prokennalestes*, in having P5 distinctly narrower labiolingually compared with M1 (Fig. 2). In this *Paranyctoides* approaches the condition of the stem therian *Juramaia* (Fig. 2B). It is not clear, however, if this is a retention of the plesiomorphic state or a neomorphic character correlated with distinct labiolingual narrowing of upper molars in *Paranyctoides*.

164(1): Exit(s) of infraorbital canal: single. Although the maxilla is incompletely known for *Paranyctoides*, a large infraorbital foramen placed above P4 is a typical condition for the Cretaceous stem placental mammals, suggesting that the infraorbital canal had a single anterior exit as in those taxa. In more basal mammals with multiple exits of the infraorbital canal (state 0) the posterior infraorbital foramen is distinctly smaller (Fig. 3). The single infraorbital foramen is characteristic for *Peramus* and more derived stem therian mammals.

165(1): Infraorbital foramen position: dorsal to penultimate premolar or more anterior. This state is characteristic for *Peramus* and more derived stem and crown therian mammals. A more derived state, infraorbital foramen placed dorsal to the first molar or more posterior [165(2)], is acquired independently in some clades of crown group placentals.

166(0): Infraorbital canal length: long (more than one molar length). A plesiomorphic state that is found in all stem therian and stem placental mammals. The infraorbital canal is shortened [166(1)] in Glires and some Primates and some insectivorous mammals.

New character 416: Infraorbital canal position: near the anterior margin of orbit, below lacrimal or jugal (0), or well anterior to the anterior margin of orbit (1). For the taxa with multiple exits of the infraorbital canal the larger anterior foramen is considered. As was discussed by Krause *et al.* (2014), the posterior infraorbital

foramen that is at the maxillojugal or maxillolacrimal suture (Fig. 3A, B) is for the lacrimal branch of the infraorbital nerve. In the stem therian *Maotherium* the posterior infraorbital foramen is placed entirely within the maxilla but still near the anterior end of the orbit (Fig. 3C). In *Maotherium* most of the cheek teeth are placed anterior to this infraorbital foramen. In the stem therian *Eomaia* the single infraorbital foramen is placed above P4 and below the anterior margin of the orbit and the maxillolacrimal suture (Fig. 3D).

The single known specimen of *Eomaia scansoria* was originally interpreted as being a basal eutherian with five premolars and P5 placed below the infraorbital foramen (Ji *et al.* 2002). Averianov *et al.* (2010) suggested instead that on this specimen there are six premolars including one delayed deciduous premolar, and P4 is placed below the infraorital foramen. O'Leary *et al.* (2013) found that *Eomaia* is a stem therian. Luo *et al.* (2011) described *Juramaia sinensi*s as a basal eutherian identifying it as having six premolars including delayed dP3, and P4 below the infraorbital foramen, which supports the interpretation of dental formula in *Eomaia* proposed by Averianov *et al.* (2010). In the data matrix by Wible *et al.* (2009) *Eomaia* is coded as having P4, not P5 below the infraorbital foramen, which follows our interpretation of this taxon. What seems most likely is that *Eomaia* and *Juramaia* are both stem therians and both retain a delayed dP3.

In *Eomaia* the posterior premolars (P4–5) and all molars are confined to the posterior half of the maxilla below the lacrimal and jugal. A similar condition is found in the stem therian *Peramus* (Clemens and Mills 1971, pl. 1). Among the stem placental mammals this primitive condition has been retained only in *Paranyctoides*, while in other stem placentals, including the Early Cretaceous *Prokennalestes* and *Acristatherium* (Hu *et al.* 2010), the infraorbital foramen is placed well anterior to the orbit and P4–5 and M1–3 occupythe larger portion of the maxilla (Fig. 3F).

The character-taxon matrix (Supplementary Online Material available at http://www.palaeontologia.pan.pl/SOM/pp67-Averianov_and_Archibald_SOM.txt), consisting of 416 characters and 91 taxa, was analyzed using PRAP, parsimony ratchet analysis using PAUP (Müller 2007), and PAUP* 4.0b10 (Swofford 2002). The equal-weight analysis with 10,000 ratchet replications produced 6799 most parsimonious trees with the tree statistics shown in Table 1. The strict consensus tree shows little resolution among Zhelestidae. To increase resolution and recover a clearer phylogenetic signal, a successive weighting analysis (Farris 1969) was conducted. Using PAUP, the characters were reweighted by the maximum value of rescaled consistency indices (RC), and a heuristic search with 10,000 random sequence addition replicates and TBR (tree bisection and reconnection) branch swapping was performed. During reweighting 367 characters (88.2%) received a weight of less than 1. Tree statistics stabilized after three successive runs of the reweight analysis (Table 1). The fragment of the strict consensus tree of 15 most parsimonious trees recovered in the last analysis, relevant to the phylogenetic position of *Paranyctoides*, is shown on Fig. 4.

The current phylogenetic hypothesis is different in a number of details from the previously published cladogram (Averianov and Archibald 2013b, fig. 2). *Deccanolestes*, which was previously the sister taxon for the clade *Paranyctoides* + Zhelestidae, is clustered with *Afrodon* (Adapisoriculidae) and moved to the insectivorous lineage within the crown-group placentals. *Bobolestes* is the sister taxon for the clade comprised of two clades, *Paranyctoides* + Zhelestidae and a clade containing the remaining stem and crown-group placentals. The taxa mentioned above are not included within the segment of the phylogeny that is figured on Fig. 4. In the previous analysis *Paranyctoides* was the sister taxon for the Zhelestidae. Now *Eozhelestes* is the sister taxon for the remaining taxa of this clade and *Paranyctoides* is nested in a polytomy with *Sheikhdzheilia*, *Lainodon*, and Zhelestinae (Fig. 4). Uncertain and basal positions for *Eozhelestes*, *Sheikhdzheilia*, and *Lainodon* can be affected, however, by the fragmentary nature of these taxa. The upper molars are not known for *Eozhelestes* and only one fragmentary upper molar is known

Table 1. Statistics for equal weight (PRAP and PAUP) and reweight (PAUP) analyses.

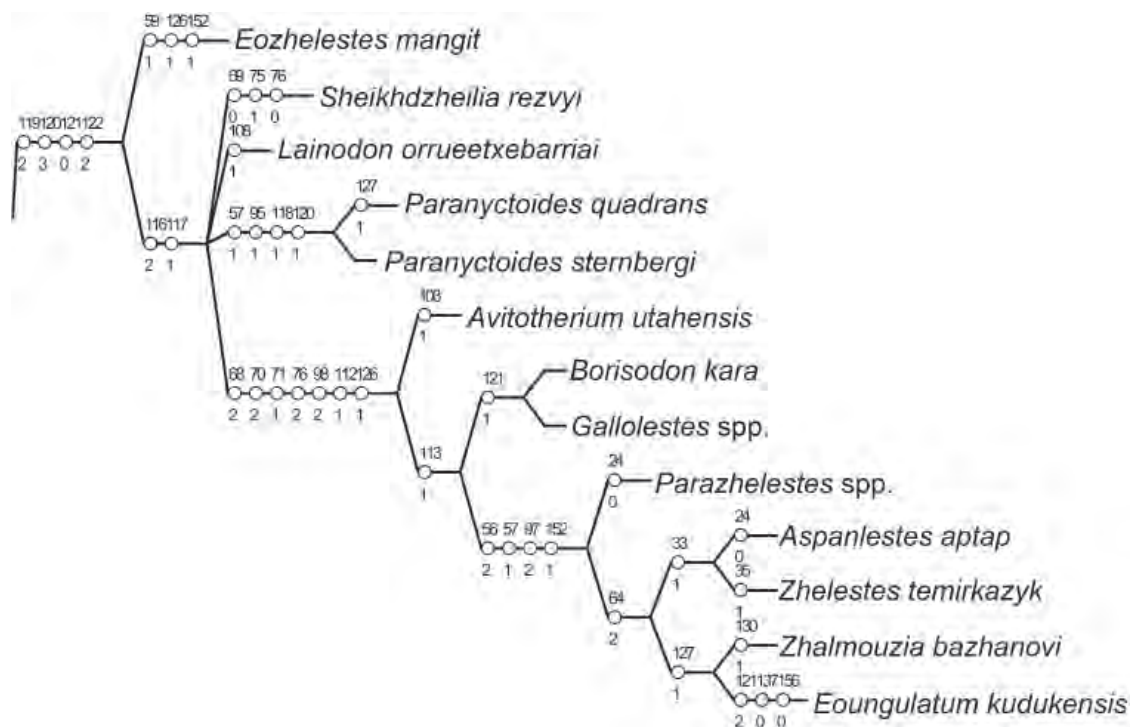| Parameters	Equal weight analysis	Reweight analysis 1	Reweight analysis 2	Reweight analysis 3
Number of trees (N)	6799	15	15	15
Tree length (L)	2766	337.1	334.7	334.7
Consistency index (CI)	0.220	0.378	0.381	0.381
Retention index (RI)	0.570	0.676	0.678	0.678
Rescaled consistency index (RC)	0.125	0.256	0.258	0.258
Homoplasy index (HI)	0.780	0.622	0.619	0.619

Fig. 4. Fragment of strict consensus tree of 15 most parsimonious trees produced by PAUP reweight analysis showing interrelationships within Zhelestidae and *Paranyctoides*. Only unambiguous characters are shown (white circles are homoplasies). The numbers at the circles are characters (above) and states (below).

for *Lainodon* (Averianov and Archibald 2005; Archibald and Averianov 2012; Gheerbrant and Astibia 2012). In *Sheikhdzheilia* the upper molars are as wide labiolingually as in other zhelestids (Averianov and Archibald 2005). The only stem placental mammal, which has the upper molars as narrow labiolingually as in *Paranyctoides*, is the Cenomanian *Bobolestes* (Averianov and Archibald 2005). However, both taxa cannot be closely related because *Bobolestes* has a molariform p5 whereas the available evidence in *Paranyctoides* suggests this tooth was likely a simpler, premolariform tooth (Averianov and Archibald 2005, 2013b).

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DIVERSITY OF TRICONODONTS IN THE MIDDLE JURASSIC OF GREAT BRITAIN

PERCY M. BUTLER and DENISE SIGOGNEAU-RUSSELL

We describe a range of triconodont mammalian teeth from the Forest Marble (Middle Jurassic) of Kirtlington Quarry (Oxfordshire), Watton Cliff, and Swyre (both Dorset), and demonstrate the presence of a variety of morganucodontans, including *Morganucodon tardus* sp. n., *Cherwellia leei* gen. et sp. n., and *Stylidens hookeri* gen. et sp. n. "Amphilestidae" are represented by three species, *Phascolotherium simpsoni* sp. n., *P.* cf. *bucklandi*, and *Amphilestes* cf. *A. broderipii*, as well as by upper molars referable to *Phascolotherium*. Gobiconodontidae and Triconodontidae are represented by, respectively, *Gobiconodon bathoniensis* sp. n., and *Eotriconodon sophron* gen. et sp. n.

Key words: "Amphilestids", Bathonian, gobiconodontids, morganucodontids, triconodontids.

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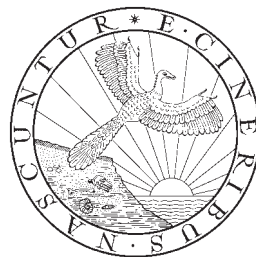
INTRODUCTION

Early mammals with triconodont teeth, characterized by three main, longitudinally aligned cusps, were formerly grouped in the order Triconodonta Osborn, 1888 (*e.g.*, Lillegraven *et al.* 1979). As conceived by Simpson (1928), the order Triconodonta contained only Triconodontidae Marsh, 1887, with subfamilies Triconodontinae Marsh, 1887 and Amphilestinae Osborn, 1888. Subsequent revisions led to a notable expansion of the concept of Triconodonta. Thus, Jenkins and Crompton (1979) reestablished the family level for Triconodontidae and Amphilestidae, and included Morganucodontidae Kühne, 1958. The family Megazostrodontidae Gow, 1986 was added to separate *Megazostrodon* Crompton *et* Jenkins, 1968, from Morganucodontidae, where the genus had been initially included. Chow and Rich (1984) recognized Gobiconodontinae as a subfamily of "Amphilestinae"; Jenkins and Schaff (1988) subsequently raised the former to family status.

Subsequent work recognised the triconodont molar pattern as plesiomorphic for Mammalia, and rejected Triconodonta as a paraphyletic grouping comprising markedly different mandibular, cranial and postcranial morphologies. As a result, Morganucodontidae and Megazostrodontidae, which do not fall into crown Mammalia, were excluded from the class as a whole (Rowe 1988; Rougier *et al.* 1996); but they were later reincorporated as the stem mammalian order Morganucodonta Kermack *et al.*, 1973 by Kielan-Jaworowska *et al.* (2004). "Amphilestidae" and Gobiconodontidae, together with Triconodontidae, are treated by these authors as Eutriconodonta Kermack *et al.*, 1973. Additional finds in South America (Rougier *et al.* 2007), Morocco (Sigogneau-Russell 1995, 2003a), Tanzania (Heinrich 1998), North America (Cifelli and Madsen 1998; Rose *et al.* 2001), China (Ji *et al.* 1999; Li *et al.* 2000, 2003; Rougier *et al.* 2001; Kusuhashi *et al.* 2009; Gao *et al.* 2010), Central Asia (Martin and Averianov 2007, 2010), Mexico (Montellano *et al.* 2008), and the UK (Clemens 2011) have extended our knowledge of the diversity of "triconodont" mammals. In several cases, however, only isolated molars have been found and their relationships remain unclear.

This paper presents new triconodont teeth from the late Bathonian (Middle Jurassic) of Britain. The Jurassic Period, which lasted 56 Ma (Gradstein *et al.* 2012), remains very sparing of mammalian fossils, with the "middle Jurassic [being] the most poorly represented epoch in mammalian history", and "most of the known record comes from Britain" (Kielan-Jaworowska *et al.* 2004, p. 33). For many years, however, the only Middle Jurassic mammals with triconodont teeth from Britain were the two species of "amphilestids" from the middle Bathonian "Stonesfield Slate", Taynton Limestone Formation: *Amphilestes broderipii* (Owen, 1845) and *Phascolotherium bucklandi* (Broderip, 1828), collected in the late 18th and early 19th centuries and restudied by Simpson (1928). More recently Freeman (1976, 1979) described a collection of mammals from the Kirtlington Mammal Bed, Forest Marble Formation (late Bathonian) of the Old Cement Works Quarry, Kirtlington, Oxfordshire, including a morganucodontan, *Wareolestes rex* Freeman, 1979. In the 1980s, intensive work in this quarry and at two other Forest Marble sites, Watton Cliff and Swyre, Dorset, by the late Prof. K.A. Kermack and colleagues from University College, London, resulted in the discovery, among other material, of some 700 isolated mammalian teeth (Kermack 1988). These have formed the basis for a number of papers describing constituents of the fauna: docodonts (Kermack *et al.* 1987; Sigogneau-Russell 2001, 2003b), allotherians (Kermack *et al.* 1998; Butler and Hooker 2005), shuotheriids (Sigogneau-Russell 1998), and trechnotherians (Sigogneau-Russell 2003c).

The triconodont teeth from the Forest Marble Formation of Kirtlington, Watton Cliff, and Swyre (Freeman's and University College collections) described in this paper are now housed in the Earth Sciences Department, Natural History Museum, London, UK.

Institutional abbreviations. — M (Mammalia) and OR (Old Register), specimens deposited at the Natural History Museum, London, UK (full current acronym includes the prefix .PV; former acronyms include BMNH and NHM); MNHN SA, specimens from synclinal d'Anoual, Morocco, and deposited at Museum national d'Histoire naturelle, Paris, France; OUM, Oxford University Museum, Oxford, UK; PM TGU, Paleontological Museum, Tomsk State University, Russia.

tion of the drawings), from the Paleontology Department, Museum national d'Histoire naturelle, Paris, have given some life to the dry descriptions of the authors. Finally, Françoise Pilard, from the same Institution, kindly agreed to make endless modifications and additions to the figures, long after her retirement.

TRICONODONT MOLAR PATTERN

The basic triconodont molar cusp pattern, with cusps in line, inherited from that of cynodonts, is relatively simple: two-rooted lower molars, relatively narrow transversely with a dominant middle cusp (a, according to the nomenclature used for *Morganucodon* Kühne, 1949 by Crompton and Jenkins 1968), flanked by lower mesial (b) and distal (c) cusps, the latter being followed by a small "talonid" cusp (d). More mesial cuspules (e and f) may delimit a sulcus, into which fits the d cusp of the preceding tooth. A lingual cingulum is usually present, with, at least in the early forms, a dominant cuspule under the distal part of a: the Kuehnecone of Parrington 1967 (= g of Crompton and Jenkins 1968, already present in the cynodont *Thrinaxodon*). Two-rooted upper molars are structurally similar to the lowers, but are relatively wider transversely and lower crowned, with less elevated cusps. Cusp A, in the centre again, dominates the mesial (B) and distal (C) cusps; more distal cusp D is more or less well defined. A complete cingulum encircles the crown lingually and labially. Accessory mesial cingular cuspules (E lingually and F labially) may be present.

Within this rather uniform morphological scheme, however, wear facets show that two types of occlusal relationships occurred (Mills 1971; Crompton 1974). In the morganucodontan Morganucodontidae, lower cusp a occludes immediately anterior to upper cusp A, between A and B; in the eutriconodontan Triconodontidae, though considered as not being directly related to the former, similar occlusion occurs (Crompton 1974; Cifelli *et al.* 1998). In the other eutriconodontan families, the "Amphilestidae" and Gobiconodontidae, by contrast, lower and upper teeth alternate, with the result that lower cusp a occludes farther forward, anterior to B and near the junction between two upper molars. To complicate matters, in the morganucodontan Megazostrodontidae genus *Megazostrodon* Crompton *et* Jenkins, 1968, occlusion has been shown (Crompton 1974) to be of the "amphilestid" type; but *Dinnetherium* Jenkins *et al.*, 1983, also a megazostrodontid according to the characters of its lower jaw (Gow 1986), has a morganucodontid type of occlusion.

Generally in mammals, upper and lower molars evolve together so that cusps can be homologised by their occlusal relations. Applying this criterion, Mills (1971) concluded that the cusps of *Morganucodon* and *Megazostrodon* were not homologous. We consider the resemblance too detailed to support this hypothesis. Either the two types of occlusion evolved independently in pre-occlusal triconodont teeth (*e.g.*, *Sinoconodon* Patterson *et* Olson, 1961); or, more probably, one type (the *Morganucodon* type?) evolved first and was converted into the other by changing the relative position of opposing teeth. In support of the latter alternative, Parrington (1978) noted some variation in the occlusal pattern in *Morganucodon*, and a distinct arrangement occurs in *Bridetherium* (Clemens, 2011).

In morganucodontids the functional pattern is produced as the result of wear. In *Morganucodon* this results in the removal of much of the B and C (b and c) cusps (see Crompton and Jenkins 1968). The *Megazostrodon* type of occlusion, in which A and a occlude into the pre-formed valleys between two opposing teeth, might be advantageous in requiring less loss of tooth material. Perhaps for this reason the alternating type of occlusion characterises the amphilestids and later mammals in general. Only the Triconodontidae retain the *Morganucodon* arrangement; they appear to have reduced tooth loss by developing more accurately fitting cusps. However, intermediates between the two modes of occlusion have not been identified.

SYSTEMATIC PALEONTOLOGY

Class **Mammalia** Linnaeus, 1758

Order **Morganucodonta** Kermack *et al.*, 1973

The morganucodontan molar structure remains the basic triconodont one, though cusp b may not be separated from the cingulum on the lower molars. It has been most studied in *Morganucodon*, of which there is

plentiful material from the Rhaetic and Early Jurassic of Britain and China (*e.g.*, Mills 1971; Parrington 1971, 1978; Kermack *et al.* 1973; Crompton 1974; Crompton and Luo 1993). Associated teeth and jaws are known for three other Early Jurassic genera: *Erythrotherium* Crompton, 1964, *Megazostrodon* Crompton, 1974, and *Dinnetherium* Jenkins *et al.*, 1983 (see also Crompton and Luo 1993). The last two genera were placed by Gow (1986) in a separate family Megazostrodontidae on the basis of mandibular characters, despite their different modes of occlusion, as noted above. The order Morganucodonta as compiled by Kielan-Jaworowska *et al.* (2004) includes, besides the above-mentioned genera, *Wareolestes* Freeman, 1979, *Helvetiodon* Clemens, 1980, *Brachyzostrodon* Sigogneau-Russell, 1983, *Indotherium* Yadagiri, 1984, *Gondwanadon* Datta *et* Das, 1996 (in fact possibly a sinoconodontid), and *Indozostrodon* Datta *et* Das, 2001. Of these, *Wareolestes*, *Brachyzostrodon*, and *Indozostrodon* were placed in the family Megazostrodontidae by Kielan-Jaworowska *et al.* (2004), the others remaining in the Morganucodontidae. It is well worth keeping in mind that the familial position of several of these taxa, independent (as noted above) of the type of occlusion, remains highly speculative. This remark applies to the placing of taxa known only by isolated teeth and, in particular, to four of the five types of morganucodontan described in this paper, which are all classified as Morganucodonta incertae sedis.

Morganucodontans (with the exception of *Dinnetherium*) also differ from eutriconodontans in the mode of interlocking of adjacent teeth: d makes contact between b and e, instead of e and f (Sigogneau-Russell 2003a). Owing to a lingual ridge connecting it to e, b has an anterior face, more or less transverse to the longitudinal axis of the crown. On upper molars, B is similarly linked to the labial cusp E. In "amphilestids", b and B are more distally placed, on the longitudinal main crest of the tooth, and the interlocking groove is between E (e) and F (f). B is also transversely developed on upper molars of gobiconodontids, but this is due to a curvature of the crown. It should be noted that the articulation of the d cusp in the e–f embrasure of "amphilestid" lower molars is shared not only "with obtuse-angled symmetrodonts" (Kielan-Jaworowska *et al.* 2004, p. 237), but also with triconodontids (Cifelli et al. 1998) and gobiconodontids (Kielan-Jaworowska and Dashzeveg 1998, p. 422; e–f groove of Sigogneau-Russell 2003a, p. 47, fig. 12).

Family **Morganucodontidae** Kühne, 1958
Genus *Morganucodon* Kühne, 1949

Type species: *Morganucodon watsoni* Kühne, 1949.

Morganucodon tardus sp. n.
(Fig. 1A)
LSID urn:lsid:zoobank.org:act:EC47A860-3226-4FF5-A1B1-80CE730A3770

Holotype: M34984, a right upper molar, lightly worn.
Etymology: From Latin *tardus*, late; this is the geologically youngest species of the genus.
Horizon and locality: Watton Cliff, Dorset, UK; late Bathonian.

Diagnosis. — Differs from *Morganucodon watsoni* Kühne, 1949 by the relative proportions of the three main cusps as seen in side view (A being larger and less pointed), and by the wider and non-crenulated labial cingulum. Differs from *M. peyeri* Clemens, 1980 and *M. oehleri* Rigney, 1963 by the non-crenulated labial cingulum. Differs from *M. heikuopengensis* (Young, 1978) in its larger size and relative proportions of the three main cusps.

Description. — M34984 (L = 1.42 mm, W = 0.88 mm) is a small right upper molar (size range of *Morganucodon watsoni*). It shows the transverse disposition of the anterior cusp (B) and a horizontal labial cingulum ledge. The lingual cingulum is faintly crenulated and narrow. A and C are aligned, B is more labial and linked to both cingula, as is the very small D cusp. A is much higher than B and C; its mesial profile is moderately convex, so that its tip is not as sharp as in specimens of *M. watsoni*. E is weakly developed and F absent, hence there is no anterior sulcus, just a flattening. Wear has affected the lingual face of B and the anterior part of the cingulum. Cusps are flatter labially than in *Morganucodon watsoni*, the labial cingulum is wider and the cingular denticulations negligible. No complete upper molar of *Morganucodon peyeri* is known, but from the synthesis given by Clemens (1980, p. 78), the main discrepancy lies again in the weak labial cingulum. From the brief description given by Luo and Wu (1994), *M. oehleri* may resemble *M. tardus* in the great height of the A cusp, but it differs in the strongly crenulated labial cingulum. As for *M. heikuopengensis,* it is more like *M. watsoni* in these characters. Among the molariforms from the Early Jurassic of Wales described by Clemens (2011), those labelled as Group 2 have the greatest resemblance to *M. tardus*, but they are much smaller.
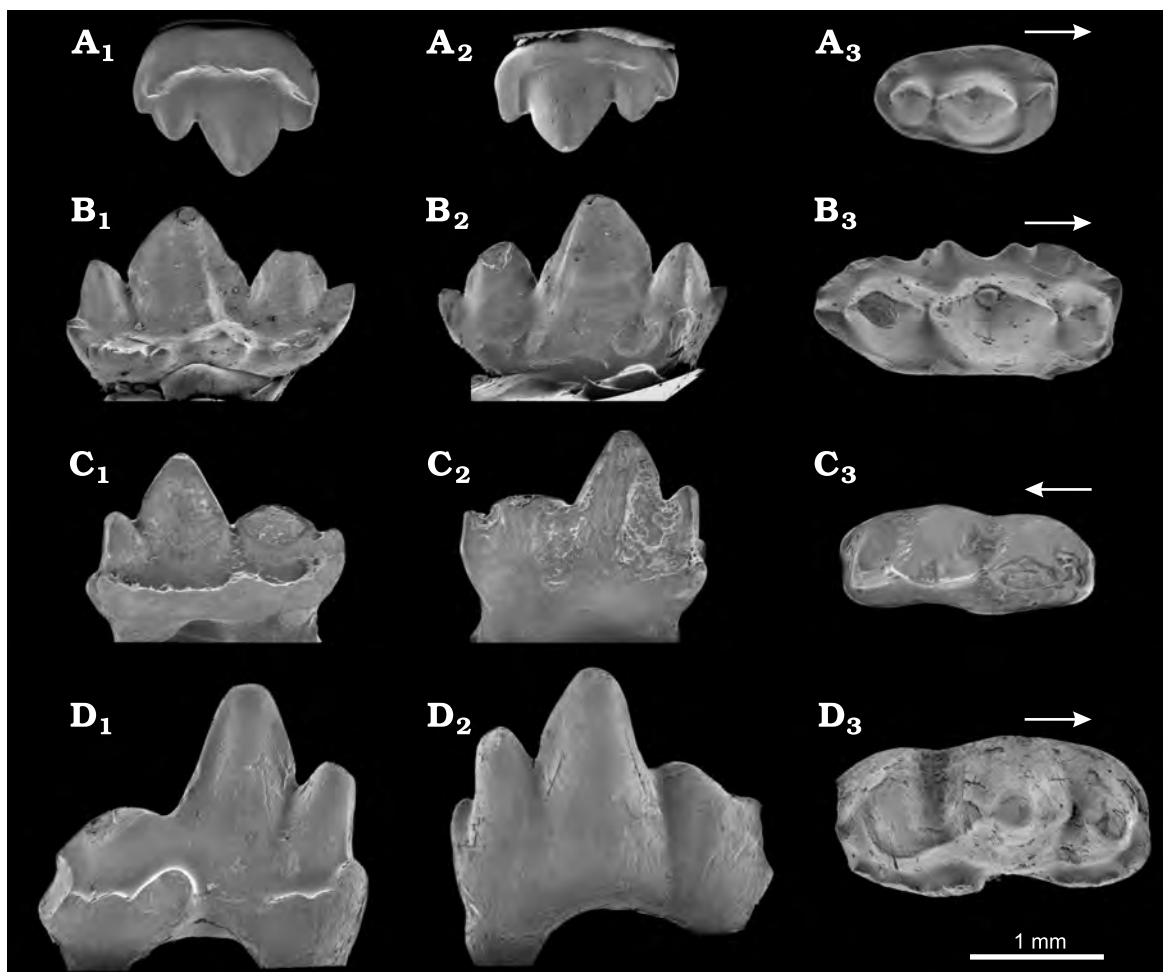
Fig. 1. Morganucodonta from the Middle Jurassic of Great Britain. **A**. *Morganucodon tardus* sp. n., holotype M34984, Watton Cliff, Dorset, UK; late Bathonian, right upper molar in labial (A_1), lingual (A_2), and occlusal (A_3) views. **B**. *Cherwellia leei* gen. et sp. n., holotype M46811, Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian, right lower molar in lingual (B_1), labial (B_2), and occlusal (B_3) views. **C**. *Stylidens hookeri* gen. et sp. n., holotype M84127, Watton Cliff, Dorset, UK; late Bathonian, right lower molar in lingual (C_1), labial (C_2), and occlusal (C_3) views. **D**. *Stylidens* gen. n., sp. indet, M46554, Swyre, Dorset, UK; late Bathonian, left lower molar in lingual (D_1), labial (D_2), and occlusal (D_3) views. SEM photos; roots cropped as needed. Arrows point anteriorly.

Family indet.
Genus *Wareolestes* Freeman, 1979

Type species: *Wareolestes rex* Freeman, 1979.

Emended diagnosis. — Morganucodontan with upper molar having a relatively high and robust cusp A, pyramidal with lingual and labial ridges on it slopes. B and C subequal, B slightly smaller, but not incorporated into the cingulum, which is continuous from E around the mesial border. D is a relatively small cusp on the cingulum. Lingual cingulum non-crenulated and narrow, rising to a point below A, where it is almost interrupted. Labial cingulum broader and cuspidate, with the highest cusp opposite to A, to which it is linked by a ridge. Cusp F hardly individualized. Owing to damage of the type specimen, it is not clear whether the labial cingulum was divided into two parts, as cited in the diagnosis of family Megazostrodontidae by Kielan-Jaworowska *et al.* 2004.

Differs from the M2 of *Megazostrodon* by larger size, more dominant cusp A, presence of enamel ridges, and of a cingulum cusp labial to A. Differs from the upper molars referred to *Brachyzostrodon* (Hahn *et al.* 1991) by slightly larger general size, cusp A less globular and relatively higher, better individualisation of cusp D, coarser enamel ridges, lingual cingulum rising sharply in the middle of A, presence of a median labial cingulum cusp. Differs from *Indozostrodon* mostly by the relative proportions of cusps A, B, and C.

Wareolestes rex Freeman, 1979

(Fig. 2A)

Holotype: M36525**,** a right upper molar (originally described as a right lower molar); L = 2.31 mm, W = 1.24 mm.

Type horizon and locality: From the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian.

Discussion. — Morganucodonta, and more precisely Megazostrodontidae, were judged to be represented at Kirtlington by the genus *Wareolestes* Freeman, 1979, based on one molar identified by its author as a lower, and diagnosed as possessing "a kuehneocone directly lingual to the main cusp ... and a poorly defined buccal cingulum" (Freeman 1979, p. 158). According to Freeman's determination, cusp "b" (broken) was nearly as high as "c" but shorter mesio-distally. Enamel ridges striate the disto-lingual side of the middle cusp "a". The "lingual cingulum" forms a high wall anteriorly, but "e" and "f" are hardly distinct; the small cingular cusp "g" is connected to the main cusp by a ridge, and is followed posteriorly by two cuspules. The "labial cingulum" is faint ("subdued"; Freeman 1979, p. 159), non-cuspidate, and interrupted under the high central cusp, but it widens posteriorly. Wear is detectable on the side opposite to "g", below the tip of the main cusp and less clearly down it and on the distal cusp.

Freeman's identification of the holotype of *Wareolestes rex* as a lower molar thus rested largely on the presence of what was considered as a Kuehnecone, g. However, on lower molars of other morganucodontans (*Morganucodon, Megazostrodon, Brachyzostrodon*), cusp g stands below the a–c notch, while the supposed "g" in *Wareolestes* is more mesial, directly opposite the main cusp, to which it is connected by a ridge. Moreover, the presence of two cingula (labial and lingual) suggests an upper molar, as Hahn *et al.* (1991) noted. Also, the presence of "well-developed labial cingular cusps" is cited as a diagnostic character for megazostrodontid upper molars by Kielan-Jaworowska *et al.* (2004, p. 179). Finally the "b" cusp is independent from the anterior cingulum, like the B cusp on upper molars of morganucodontans. The main difficulty with the interpretation of M36225 as an upper molar lies in the fact that the main cusp is higher relative to tooth length than on the uppers of *Brachyzostrodon*; however it is nearly as high on M1 of *Megazostrodon* (Crompton 1974, pl. 2B; it is lower on other molars of the genus) and equally high on the holotype of *Helvetiodon* that Clemens (1980) provisionally interpreted as an upper molar.

We therefore reinterpret the holotype of *Wareolestes rex* as an upper molar; in that case, the strong cingulum with the "g" cusp has to be labial (as in *Brachyzostrodon*; Hahn *et al.* 1991): a large lingual cusp would interfere with occlusion against the lower molar, which bites lingual to the upper. Wear is very slight, but it supports the new interpretation: a polished facet on the tip of A extends onto the side with the weak cingulum, which must therefore be lingual.

Helvetiodon was classified as a morganucodontid by Kielan-Jaworowska *et al.* (2004); however, the strong cingular cuspules and the division of the labial cingulum in two parts suggests that it might be closer to the megazostrodontids, and possibly related to *Wareolestes*. Indeed, the upper molar, while being much smaller, resembles M36525 in the high, robust cusp A; but B is a small cusp on the cingulum. The lateral cingula of the two genera correspond best if the holotype of *Helvetiodon schutzi* Clemens, 1980 is a left tooth, not a right tooth as interpreted by Clemens (1980). Then the enlarged cingulum cusp of *Helvetiodon* is labial, and the interrupted cingulum, absent under A, is lingual. With this orientation, *Helvetiodon* differs from *Wareolestes* in the more distal position of the labial cingulum cusp, in the small cingular cusp B, and in the presence of denticulations on the lingual cingulum.

Known only by a single molar, the familial affinity of *Wareolestes rex* is uncertain. The labial cingulum, though its mesial part is broken, was evidently more complex than in *Morganucodon*, and the presence of a G cusp contrasts with the ectoflexus of *Megazostrodon*. Evidence of function is inconclusive. The relationships of A to b and c of the lower molar are unclear. Hahn *et al.* (1991) noted that, in the megazostrodontid *Brachyzostrodon*, wear is largely confined to the tips of the cusps. Similarly, in *Wareolestes,* the form and size of cusp A seems better adapted for a puncturing than for a shearing function.

Wareolestes sp. indet.

(Fig. 2B)

Referred specimen. — M46775 (Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian).

Description. — M46775, the distal half of a molar with the middle cusp broken in the middle, is about 25% smaller (L = 1.00 mm, W = 0.70 mm) than, but apparently close to, the holotype of *Wareolestes rex*. We
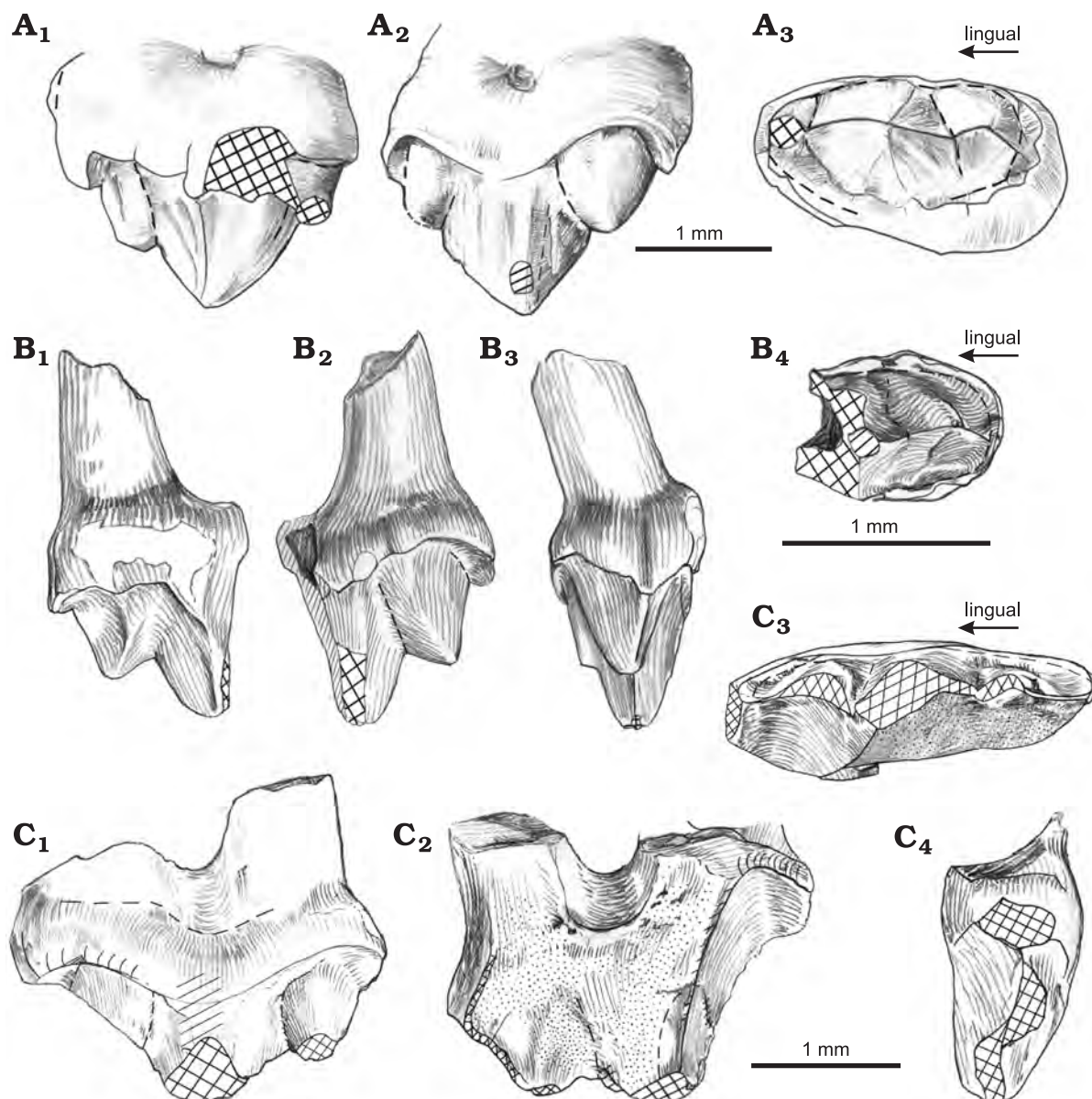
Fig. 2. Morganucodonta from the Middle Jurassic of Great Britain. All specimens from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian. **A**. *Wareolestes rex*, holotype M36525, right upper molar in labial (A$_1$), lingual (A$_2$), and occlusal (A$_3$) views. **B**. *Wareolestes* sp. indet., M46775, right upper molar in labial (B$_1$), lingual (B$_2$), distal (B$_3$), and occlusal (B$_4$) views. **C**. Gen. et sp. indet., M46194, right upper molar in labial (C$_1$), lingual (C$_2$), occlusal (C$_3$), and mesial (C$_4$) views. Arrows point anteriorly. Cross hatching refers to a broken surface and parallel hatching indicates wear.

interpret it as a right upper molar. Cusps C and D, which are well preserved, stand in line on the posterior crest of A. Vertical wrinkling of the posterior surface of A is not discernible, but C has a vertical ridge on its labial side, which is much fainter on the holotype of *W. rex*. On both sides, the cingulum is well indicated and grossly denticulate. Labially, it rises in the middle where it links to the middle ridge of A, but, owing to breakage, the presence of a "G-like" cusp cannot be confirmed. Lingually, it bears low undulations, one close to D and two further forward. Finally, a slight indentation is present on the distal face of D; this feature is absent on the holotype, and could well question the mesio-distal orientation adopted here. The proximal half of the distal root is preserved. It is inclined lingually at about 20° to the vertical axis of the crown. If the root was vertical, the lingual surface of the crown, which occludes with the lower teeth, would be inclined lingually. This resembles *Morganucodon* where, according to Mills (1971, p. 37), "the long axis of the upper molars leans notably lingually", so that the functioning surface is vertical (Mills 1971, p. 41, fig. 2B). The enamel is partly missing; hence, no wear facet is discernible.

M46775 differs from the holotype of *Wareolestes rex* not only by its smaller size, but also by the slightly taller cusps, the more accentuated lingual cingulum, the presence of a labial ridge on C, and absence of wrinkling of the enamel of cusp A. It is possible that the tooth represents an "amphilestid"; however, the state of preservation does not allow definitive identification.

Gen. et sp. indet.

(Fig. 2C)

M46194 (L as preserved = 2.80 mm, W = 1.10 mm), from Kirtlington, is the largest morganucodontan tooth in the collection. It is poorly preserved, having suffered much post mortem damage as well as wear, making interpretation somewhat uncertain. It is described as a left upper molar. As seen in crown view, the blunt, wider end is taken as mesial, the narrower end as distal. The crown is proportionately narrower than that of the holotype of *Wareolestes rex*, but the enamel is missing on a large part of the lingual face. Cusps were aligned; the mesial one, B, has been completely removed by wear, but it was larger than in *Wareolestes*. Cusp A was large, robust, and centrally placed. C and D are similar in proportions to those of *Wareolestes*. The labial cingulum forms a regular bulge, without any denticulations unlike in megazostrodontids. There may have been a lingual cingulum, the two cingula meeting anteriorly into cuspules E and F, but the area is damaged. The mesial root was slightly larger than the distal one. A possible rectangular "wear" surface is observed in the middle of the main cusp, labially. Two interpretations can be offered: if the rectangular surface on the main cusp represents wear, then it could indicate the labial face of a lower molar, as also suggested by the relative narrowness of the tooth. If this surface is an artefact, then it represents an upper molar (the interpretation adopted here) with a cusp B completely worn lingually by cusp a of the lower molar. It would then differ from the holotype of *Wareolestes rex* not only by its size and proportions, but also by its pointed distal end, by B larger than C, by its stronger labial cingulum and the relative size of the roots (mesial one larger). In any case, the tooth is evidence of another type of morganucodontan in the fauna, but its state of preservation does not allow confident identification.

?Order **Morganucodonta** Kermack *et al.*, 1973

As mentioned above, in morganucodontans, cusps b–B may have an anterior face, more or less oblique relative to the longitudinal axis of the crown; this is because lingual and labial crests of these cusps link them independently to the anterior cuspules e and f (E and F). It is mostly on this criterion that the following molars are considered as possibly belonging to this order, though uncertainties remain.

Family indet.
Genus *Cherwellia* gen. n.

LSID urn:lsid:zoobank.org:act:E1F7A297-9D98-4DB2-A334-D1280CFD6D4B

Type species: *Cherwellia leei* sp. n.
Etymology: From the River Cherwell, which flows near Kirtlington.

Distribution. — As for the type and only species.

Diagnosis. — As for the type and only species.

Cherwellia leei sp. n.

(Fig. 1B)

LSID urn:lsid:zoobank.org:act:57BA710D-0094-46D5-90F0-307E012C4787

Holotype: M46811, a right lower molar.
Etymology: For the British artist Mr. A.J. Lee, whose drawings were of so much help in the preparation of this paper.
Horizon and locality: Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian.

Diagnosis. — Relatively large lower molar showing the morganucodontan disposition of b and the presence of a g cusp. Differs from *Morganucodon* by cusp a relatively lower and less acute with a more convex mesial crest, the deeper incisures between the three main cusps, b as high as c but shorter mesio-distally, and presence of cusp f. In the morganucodontid *Gondwanadon*, which also has e and f cusps, b is larger than c, and the three cusps are less deeply separated. Differs from megazostrodontids in the proportions of the main cusps, the presence of f (except *Dinnetherium*), and the occlusal relations, which appear to be of *Morganucodon* type.

Description. — M46811 (L = 2.60 mm, W = 1.09 mm) is a right lower molar, as indicated by the absence of a labial cingulum and the presence of a lingual g cusp. Cusp a is relatively low, broadly triangular in lateral view, and separated from b and c by deep notches. Cusp b is comparatively large, equal in height to c, but shorter mesiodistally; it is obliquely disposed, linked by a lingual ridge to a distinct e. Cusp f is weaker, labial to the base of b, and there is a very shallow anterior indentation (rather a flattening) between e and f. Cusp d is small relatively to c and reached by the complete lingual cingulum, which forms a ledge and shows a moderate g cusp opposite to the groove between a and c.

Wear has created three flat oval surfaces at the labial base of the tooth: between a and b, between a and c, and below c; the median crest of a and c is also narrowly flattened by a vertical wear facet, as is also the labial face of b. Such wear is the first to show up in morganucodontan lower molars ("In *Megazostrodon...*as in *Eozostrodon*, wear commences on the cingular area"; Crompton 1974, p. 419; or at the base of the cusps, see Mills 1971, p. 40, fig. 1). If the occlusal pattern of M 46811 is of the *Morganucodon* type, and if it is a lower molar, the upper cusp A would occlude between a and c, wear on b would be due to B, and the more distal wear on c would be due to C.

Comparison. — As mentioned above, the absence of a labial cingulum and the presence of a g cusp identify the tooth as a lower molar. However, the weakness of the anterior indentation, the lowness of a, the relative size of d, the large size of b, the small size of cuspule f, and the deep incisures between cusps a–b and a–c all differ from morganucodontid lower molars of the Early Jurassic. On the contrary, b is also large in the megazostrodontid *Megazostrodon*, but M46811 differs in the lower and broader a, smaller d, the presence of cuspule f, and the more crenulated lingual cingulum with a smaller g. Also, wear on the anterior surface of b, due to A, is absent. M46811 differs from *Brachyzostrodon* by its less sturdy main and cingular cusps, presence of f, and smooth enamel. Moreover, wear on the anterior surface of b is absent. *Dinnetherium* shares with M46811 the *Morganucodon* type of occlusal cusp relationships (Crompton and Luo 1993) and the presence of f, but in *Dinnetherium* the cusps are high and acute, b is equal to c, and g is rudimentary. Finally, the size of M46811 is close to that of *Wareolestes rex*: could this tooth be a lower molar of this taxon? The relative height of the more blade-like cusp a, compared to the stout, crushing, cusp A of the holotype of *Wareolestes rex* precludes their mutual occlusion. The same relationship applies to the problematic M46194 (listed as gen. et sp. indet. above): its massive A cusp could not have functioned with the smaller a cusp of M46811. Thus this tooth indicates the presence of another morganucodontan taxon in the fauna.

Genus *Stylidens* gen. n.

LSID urn:lsid:zoobank.org:act:C9874C21-6E13-49E9-8946-4B74F9BE01A0

Type species: *Stylidens hookeri* sp. n.
Etymology: From Latin *stylus*, pointed instrument and *dens*, tooth, in reference to the shape of the cusps.

Distribution. — As for the type and only species.

Diagnosis. — As for the type and only species.

Stylidens hookeri sp. n.

(Fig. 1C)

LSID urn:lsid:zoobank.org:act:6F2A6053-AF28-4FED-8186-603D59AA9F06

Holotype: M84127, a right lower molar with tip of cusp c broken off (Fig. 1C).
Etymology: For Dr. J. Hooker, in recognition of his contributions to knowledge of British fossil mammals.
Type horizon and locality: Watton Cliff, Dorset, UK; late Bathonian.

Diagnosis. — Lower molar with cusps a and b acutely conical. Sulcus between a and c wider than between a and b, and continuous with a vertical groove on the labial side. Differs from other morganucodontans, including *Cherwellia*, by the height and disposition of the cusps, recalling the situation in *Amphilestes* Owen, 1859, but differing from the latter in the asymmetrical crown, the transverse disposition of b, the indication of a g cusp, and the type of occlusal relations.

Description. — M84127 (L = 1.85 mm, W = 0.80 mm) is a relatively large and unworn but damaged right lower molar. Cusp b has a transverse anterior face due to crests linking it to e and f. The main cusp a is anterior to the middle, as in *Morganucodon*; it is a high, narrow cone, with an apical angle of 50° laterally. Cusp b is also a narrow cone, about half the height of a; the base of c (tip broken off) shows that it was notably larger than b. The sulcus between a and c is wider and lower than that between a and b; it is continued labially by a

groove that extends to the base of the crown. The distal crest of a is diverted slightly more lingually than the mesial crest. The lingual face of cusp b is clearly distally orientated**.** The lingual cingulum is faintly crenulated, and g is represented by a long bump rather than a cusp. There is no labial cingulum, but the posterior part of the labial margin is swollen. The distal root, the only one partially preserved, is slightly flattened transversely and inclined distally. Wear is detectable at the base of the groove between a and c; it indicates that the occlusion of A against a and c was more accurately related to the a–c notch than in *Morganucodon*, and hence more like that of the Triconodontidae.

Comparisons. — M84127 shows some resemblance to *Cherwellia*, especially in the relationship between b, e, and f at the mesial end of the crown. However, in *Stylidens*, the a cusp is taller, narrower, more acute, and meets b and c at a higher level; such differences exceed those observed along the jaw in *Morganucodon* for instance (Kermack *et al.* 1973), Cusp f also occurs in *Dinnetherium,* but b and c are of equal size, hence the tooth is more symmetrical. The general outline and shape of the cusps evoke the eutriconodontan *Amphilestes* (see below), in which b is upright, taller than c, and slightly diverted lingually. However, the mesial and distal cusps are here not symmetrically disposed, and the tooth is straight longitudinally, whereas there is a slight curvature on *A.* cf. *broderipii* (M46744; see below); the crown is less compressed, and e and f are bumps rather than columns. Finally, each of these cuspules is linked by a crest to b, which thus has an anterior face, as in morganucodontans.

Stylidens sp. indet.

(Fig. 1D)

M46554 (L = 2.64 mm, W = 1.20 mm) is a left lower molar with cusp c broken off. It is from the late Bathonian of Swyre, Dorset, UK. This tooth is morphologically close to M84127, with the same mesiodistal compression, the same conical shape of a (apical angle of 40° laterally) and b, and with similar labial grooves between a and c. However, not only is the size notably larger, but b is barely transverse, having only one weak crest going to e, so that its lingual face is barely oblique; and the f cuspule is replaced by a low cingulum. The lingual cingulum is more grossly denticulate with a more salient g cusp, and it is interrupted in the middle of a. There were two subequal, circular roots, in vertical line with the cusps, the distal one being slightly inclined distally. The enamel is not well preserved, but d is apparently worn and so is the sulcus between a and c basally, where A may have occluded, as in M84127 and morganucodontids. Though a wide range of size has been reported to exist in *Morganucodon* (Parrington 1971, p. 257), the differences concerning b and f cast doubt on the attribution of M 46554 to the species *Stylidens hookeri*, but a close relationship is undeniable.

Finally, the two teeth representing the genus *Stylidens* agree in several points with *Cherwellia* (M 46811; Fig. 1B); especially the anterior end of M84127 (but not M46554) and M46811 (b, e, and f) are quite similar. However, the main cusps are relatively taller and unite at a higher level in *Stylidens.* Finally*, Cherwellia* and *Stylidens* differ from *Bridetherium* Clemens, 2011, by being more asymmetrical, e and g better developed, the a cusp lower in proportion to crown length, the more distal g cusp, and the proportionally larger b and c.

Altogether, these isolated specimens do not help to trace the evolutionary history of Morganucodonta during the Middle Jurassic, nor do they help to clarify the confused problem of the evolution of dental occlusion in this order. Nonetheless, the specimens document previously unappreciated diversity of morganucodontans (including the family Morganucodontidae) during the Middle Jurassic.

Order **Eutriconodonta** Kermack *et al.*, 1973

Family **"Amphilestidae"** Osborn, 1888

Lower molars belonging to members of this family share with those of eutriconodontan Gobiconodontidae "their basic structure" (Kielan-Jaworowska and Dashzeveg 1998, p. 417), while they differ from those of the Triconodontidae by the dominance of cusp a over b and c (Simpson 1925a, 1928). They are characterized by a high, centrally placed cusp a, subequal b and c, and an e–f interlocking mechanism with cusp d of the preceding lower molar. Occlusion differs from that of the Morganucodontidae and Triconodontidae and is of the megazostrodontid, gobiconodontid and "therian" type, with alternating upper and lower molars (Mills 1971).

Chow and Rich (1984) recognized two subfamilies of "Amphilestidae", "Amphilestinae", and Gobiconodontinae; the latter was elevated to familial rank by Jenkins and Schaff (1988), a position adopted by Kielan-Jaworowska *et al.* (2004). These two families differ from each other by the proportions of the dentary, the dental formula, and the modalities of dental replacement. Moreover, the Gobiconodontidae are

derived in the enlargment of the anterior dentition and the arched disposition of cusps of upper molars (except in *Gobiconodon zofiae* Li *et al.*, 2003).

Simpson (1928) included four genera in the "Amphilestinae", all known by lower dentitions only: *Amphilestes* Owen, 1871, *Phascolotherium* Owen, 1838, both from the middle Bathonian of the "Stonesfield Slate", UK; and *Comodon* Kretzoi *et* Kretzoi, 2000 (replacement name for *Phascolodon* Simpson, 1925b) and *Aploconodon* Simpson, 1925b, from the Morrison Formation of North America. Kielan-Jaworowska *et al.* (2004) added the questionably referred genera *Klamelia* Chow *et* Rich, 1984 (characterized by unequal b and c cusps on lower molars), *Liaotherium* Zhou *et al.*, 1991 (known only by a dentary bearing an incomplete last molar), *Tendagurodon* Heinrich, 1998 (distinctive in lacking a lingual cingulum), *Triconolestes* Engelmann and Callison, 1998 (distinctive cusp pattern), and *Paikasigudodon* Prasad *et* Manhas, 2002 (the first ?"amphilestid" genus diagnosed on an upper molar; see below). The inclusion of these diverse and poorly known genera understandably compelled Kielan-Jaworowska *et al.* (2004) to recognize Amphilestidae as a probably paraphyletic "Amphilestidae", definable only on primitive characters.

More recently, a genus has been described from the Early Cretaceous of western Siberia, *Kemchugia* Averianov *et al.*, 2005, based on an upper molar and a partial lower molariform (see below). Subsequently, Rougier *et al.* (2007) described *Hakusanodon*, based on a lower jaw from the Lower Cretaceous of Japan, which they considered "as closely related to Eurasian and North American Jurassic amphilestids" (Rougier *et al.* 2007, p. 73). Hooker and Lawson (2011) described an unnamed partial lower molar as representing the youngest member of the family (Cenomanian, UK). Finally, the discovery of *Juchilestes* Gao *et al.*, 2010, based on a partial skull with complete upper and lower dentitions, sheds new light on "amphilestid" relationships.

Genus *Amphilestes* Owen, 1859

Type species: *Amphilestes broderipii* (Owen, 1845).

Amphilestes cf. *A. broderipii*
(Fig. 3A, B)

The genus *Amphilestes* was rediagnosed (Simpson 1928, p. 71) on its dental formula and on "molar cusps high and slender, molar cingulum rising below the main cusp, molar enamel not pitted". Two teeth from the late Bathonian correspond to the above generic diagnosis: M35000, from Watton Cliff; and M46744, from Kirtlington.

M35000 (lower right molar; L = 1.45 mm, W = 0.70 mm; Fig. 3A), was previously figured by Freeman (1979, p. 149, pl. 16, figs 1, 2) but not described. It is in the size range of *A. broderipii*. As in this species, the three main cusps are closely apposed, though the tip of cusp c diverges slightly. Cusp a is broken off; its base shows that it was narrower mesiodistally than in the Oxford specimen of *A. broderipii* (OUM J 20079)**.** Cusp b is slightly higher than c, and more closely joined to a. Mesially, e and f form two high vertical columns separated by a narrow sulcus; distally, cusp d is in line with c. These cusps, as well as cusps e and f, are relatively higher than in the three original specimens of *A. broderipii*. In occlusal view, a slight convexity of the crown can be seen, with c slightly more lingual than a and b. The lingual cingulum forms a ledge mesially and distally but is much narrower in the middle where it rises under a, as in *A. broderipii*. One of the illustrations published in Freeman (1979, p. 149, pl. 16, fig. 2) gives the impression of the tooth having two cingula; based on this view, Averianov *et al.* (2005) identified it as an "amphilestid" upper molar. However, reexamination of the specimen itself shows that the "labial cingulum" is the swollen margin of the crown under b and c (similar to *Megazostrodon* m1 and m2, Crompton 1974, p. 408, fig. 6); it is rounded in profile and not sharp like the lingual cingulum. We thus maintain that M 35000 is a lower molar.

M46744 (lower right molar; L = 1.27 mm, W = 0.52 mm; Fig. 3B), from Kirtlington, appears very similar; its cusps are more closely aligned but the labial face is again convex. Cusp a is narrower mesio-distally than in the Oxford specimens (OUM J.20078, 20079); b and c have been truncated. Lingual to d is a minute cuspule, absent in M 35000. Cusp e is slightly lingual to b, as on M 35000; cuspule f has been hollowed vertically by wear. A deep groove has been worn labially between a and b (due to occlusion with cusp C of the corresponding upper molar), as well as near the base between a and c (due to occlusion with cusp B of the following upper tooth) and also on d. The removal of cusp f and wear of d would be attributable to the tip of A at the end of the masticatory stroke, as it bit between two lower teeth. Thus alternation would apply, not only to the teeth, but also to the individual cusps (see below). The two Oxford specimens of *A. broderipii*
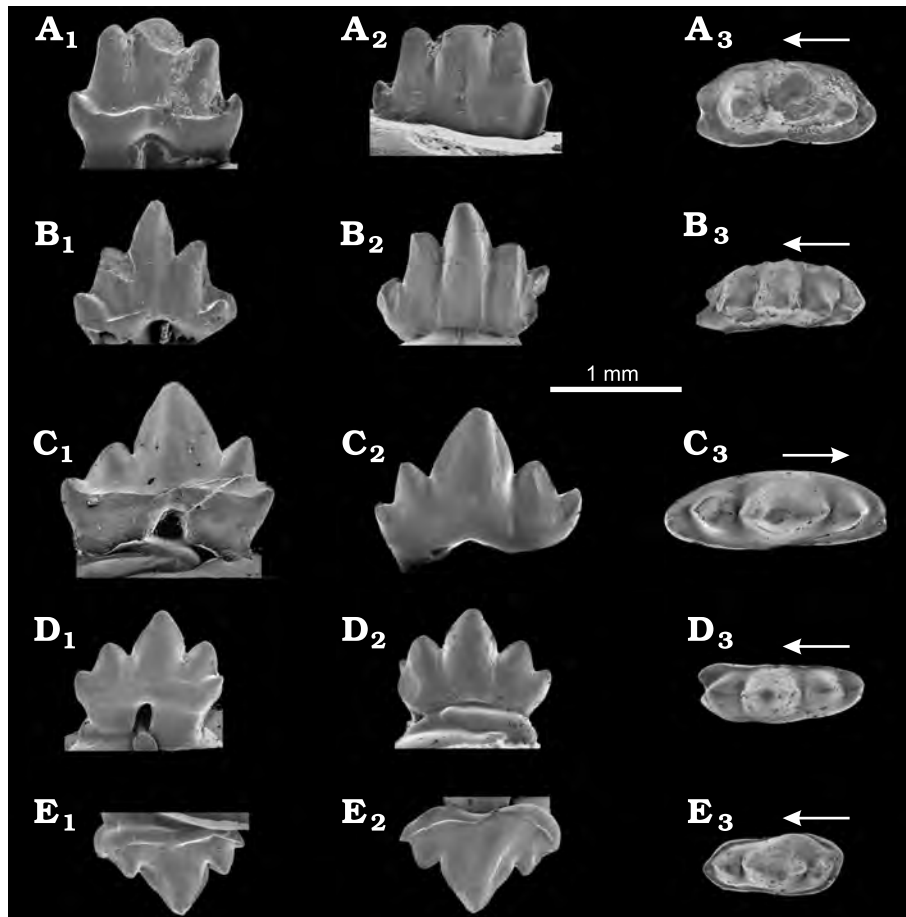
Fig. 3. "Amphilestidae" from the Middle Jurassic of Great Britain. **A**, **B**. *Amphilestes* cf. *A. broderipii*. **A**. M35000, Watton Cliff, Dorset, UK; late Bathonian, right lower molar in lingual (A_1), labial (A_2), and occlusal (A_3) views. **B**. M46744, Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian, right lower molar in lingual (B_1), labial (B_2), and occlusal (B_3) views. **C**. *Phascolotherium* cf. *P. bucklandi*, M46694, Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian, left lower molar in lingual (C_1), labial (C_2), and occlusal (C_3) views. **D**, **E**. *Phascolotherium simpsoni* sp. n. **D**. Holotype M46115, Watton Cliff, Dorset, UK; late Bathonian, left lower molar in lingual (D_1), labial (D_2), and occlusal (D_3) views. **E**. M46440, Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian, right upper molar in labial (E_1), lingual (E_2), and occlusal (E_3) views. SEM photos; roots cropped as needed. Arrows points anteriorly.

(OUM J.20078 and J.20079) are mostly unworn; only the base of the sulcus between a and c is worn on m3 of J.20078, while on J.20079 it is b of m3 which is vertically worn.

The attribution of M35000 and M46744 to the type species remains uncertain, mostly because of the height of the mesial and distal cusps, hence the tentative referral.

Genus *Phascolotherium* Owen, 1838

Type species: *Phascolotherium bucklandi* (Broderip, 1828).

Referred species. — The type, and *Phascolotherium simpsoni* sp. n.

Comments. — The emended generic diagnosis of Simpson (1928, p. 73) states: "molar cusps larger, less slender, more compressed [than *Amphilestes*]; internal cingulum rising slightly at two places, just anterior and posterior to the main cusp; molar enamel pitted or finely rugose". The following additional information is derived from M7595, *Phascolotherium bucklandi*, which has been freed from matrix and can now be viewed from both sides. In *Phascolotherium*, cusps are relatively lower than in *Amphilestes* and they are triangular rather than columnar in side view (although the distinction is not as sharp in the first molar of *Amphilestes*). Cusp a is longer mesiodistally and its mesial and distal crests are curved in lateral view, but the whole cusp is less convex labially than in *Amphilestes*. Cusps b and c are smaller relative to a, and slightly divergent instead of vertical. On m1 to m3, a small circular facet on the labial side represents f, which would

have been worn off by the tip of A. Contact between the teeth obscures the relationship between e and f, but it would seem that these cuspules are less deeply separated from each other than in *Amphilestes.* Finally, the cingulum is variable in configuration on the molars of the jaw of M7595, and even appears to be crenulated on some. Not much difference in size is observed from m1 to m4.

Three specimens are known from Stonesfield, all belonging to the single species *P. bucklandi.* The rugosity of enamel referred to in the diagnosis is present in all three specimens (Simpson 1928, p. 75) and is therefore unlikely to be due to immaturity or postmortem damage; enamel structure is probably involved. Yet all the late Bathonian specimens which in other respects resemble *Phascolotherium bucklandi* have smooth enamel. This might justify generic separation, but in view of the lack of other significant differences, we refrain from this step pending a closer examination of the enamel of *P. bucklandi.*

Phascolotherium cf. *P. bucklandi*
(Fig. 3C)

M46694, (left lower molar; L = 1.55 mm, W = 0.55 mm; Fig. 3C), from Kirtlington, shows the same size, shape and general proportions of the cusps as those of M7595.The cusps are aligned; b and c are relatively low and divergent as on the holotype (OR112) of *P. bucklandi*, but cusp a is not as broad in lateral view; cusps e and f are hardly separated and not higher than d. The lingual cingulum, which is nearly level, rises slightly toward the middle (a character seen in *Amphilestes*), where it diminishes for a short distance under a; the two elevations characteristic of *P. bucklandi* are absent. A vertical furrow hollows the base of the tooth between a and c (owing to occlusal wear by corresponding cusp B); moreover the distal side of c and the mesial side of d are worn (due to A) and there is a small facet on f (due to A on the preceding upper molar). Except for the smooth enamel and the course of the cingulum, this tooth could be classified as *P. bucklandi.*

Phascolotherium simpsoni sp. n.
(Figs 3D–E, 4, 5A–C)
LSID urn:lsid:zoobank.org:act:53A32C2E-85C5-467B-8750-22CCCAF634B6

Holotype: M46115, a left lower molar.
Etymology*: To honour the contribution of G.G. Simpson to the knowledge of the "British Mesozoic Mammalia".
Type locality and horizon: Watton Cliff, Dorset, UK; late Bathonian.

Referred material. — M46513, right lower molar; M46036, anterior half of a right lower molar; M46503, right lower molar; M46440, right upper molar; M46762, right upper molar; M46538, left upper molar; M46536, ?left upper molar. All referred specimens are from Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian.

Diagnosis. — Lower molars differ from those of *Amphilestes* in having cusps b and c more separate and slightly divergent. Differs from *Phascolotherium bucklandi* in smaller size, cusp a less enlarged in comparison with b and c; e and f better developed and separated by a deep indentation; lingual cingulum without elevations; smooth enamel.

DESCRIPTION

Lower molars. — The holotype, M46115 (L = 1.20 mm, W = 0.50; Fig. 3D) is 30% smaller than the teeth of *Phascolotherium bucklandi* and is more similar in size to those of *Amphilestes broderipii*. It shows a deep mesial indentation between cusps e and f (which is lower), somewhat as in *Amphilestes*. In crown view the labial border is slightly convex, the lingual border straight, a contour recalling that of *Comodon* (Sigogneau-Russell 2003a). In lateral view, the cusps are broadly triangular, with b and c divergent from a, as in *Phascolotherium bucklandi*; but these cusps are larger relative to a, somewhat as in *Amphilestes.* However, b and c are less upright and their crests slightly convex in lateral view, especially when compared with M35000 and M46744 (although the difference is less with respect to the anterior molars of *Amphilestes* as seen in OUM J.20078). Finally, the faintly crenulated cingulum is horizontal and does not rise in the middle as in *Amphilestes*, nor does it show the elevations characteristic of *Phascolotherium bucklandi*. The enamel is smooth. Cusp f and the base of cusp b have been worn labially into a round wear facet (probably due to A of the preceding upper molar) as on the first three molars of *P. bucklandi* M7595; there is also possible wear on the mesial and distal faces of a.

Three other lower molars are referred to *Phascolotherium simpsoni* but differ from the holotype in some details.
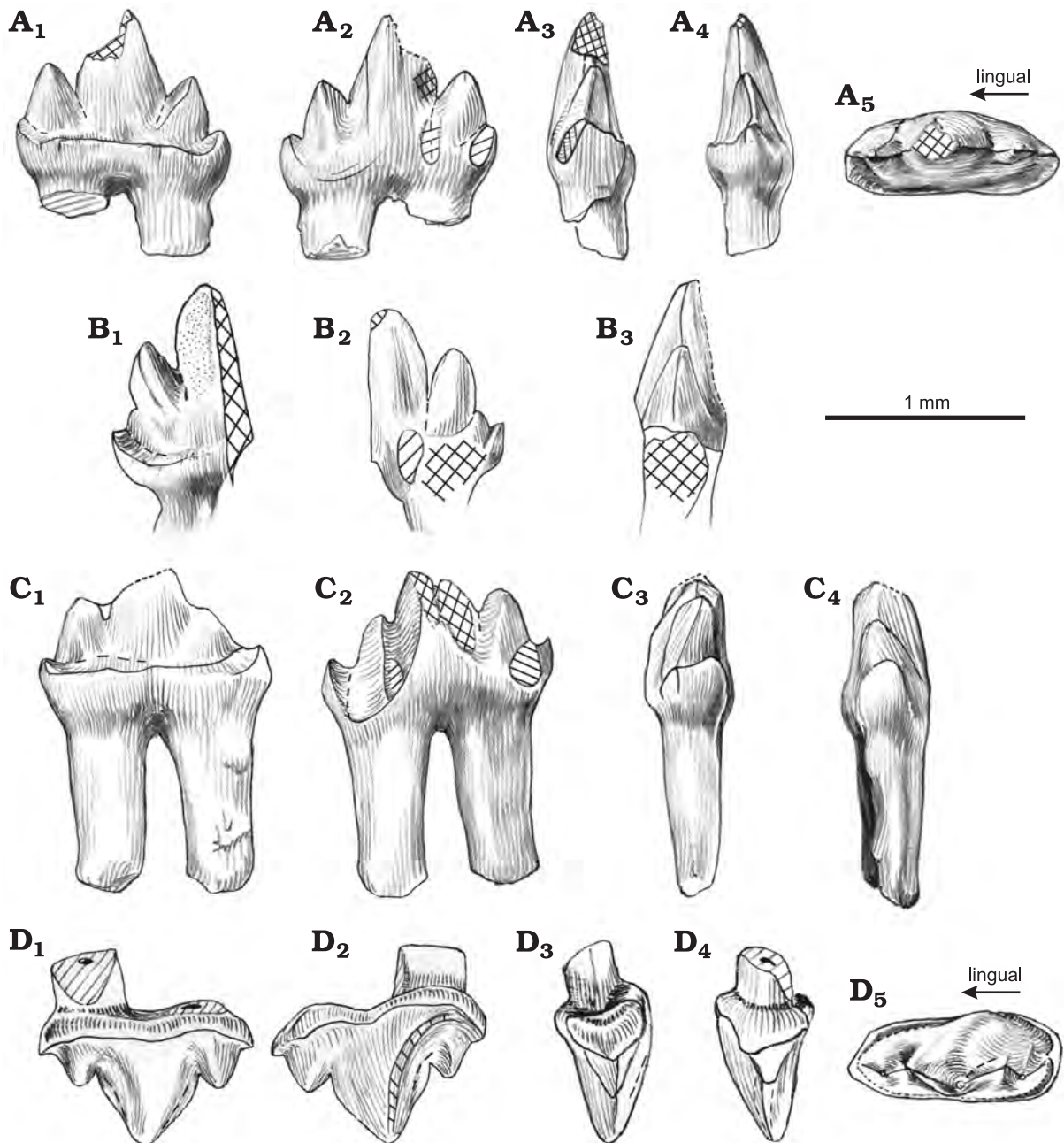
Fig. 4. *Phascolotherium simpsoni* sp. n. ("Amphilestidae") from the Middle Jurassic of Great Britain. All specimens from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian. **A**. M46513, right lower molar in lingual (A_1), labial (A_2), mesial (A_3), distal (A_4), and occlusal (A_5) views. **B**. M46036, right lower molar in lingual (B_1), labial (B_2), and mesial (B_3) views. **C**. M46503, right lower molar in lingual (C_1), labial (C_2), mesial (C_3), and distal (C_4) views. **D**. M46440, right upper molar in labial (D_1), lingual (D_2), mesial (D_3), distal (D_4), and occlusal (D_5) views. Arrows point anteriorly. Cross hatching refers to a broken surface, parallel hatching indicates wear, and dots indicate broken edges.

M46513 (right lower molar; L = 1.12 mm, W = 0.45 mm; Fig. 4A) has the size of the holotype, M46115. Cusp a is strongly convex labially; cusps b and c are intermediate between those of *Amphilestes broderipii* and *Phascolotherium bucklandi* in shape and direction; e and f are of unequal height, f being higher than e; they are nearly fused, with no sulcus between them. The cingulum is horizontal and finely crenulated. Wear has created a narrow groove between a and b (due to C) and an oval facet on f (due to A); this again recalls *Amphilestes*. Another wear surface may be present on the base of the distal face of c.

M46036 (right lower molar; L = 0.58 mm, W = 0.40 mm, as preserved; Fig. 4B) seems to be the mesial half of a large tooth similar to M 46513. The b cusp is high and upright. Wear has eroded the base of the tooth between a and b.

M46503 (right lower molar; L = 1.15 mm, W = 0.45 mm; Fig. 4C) is poorly preserved, but enough remains to show a near symmetrical configuration of the three main cusps in lingual view, b and c being closer to a than in M46513. A complete lingual cingulum, not rising in the middle, terminates in the e cusp mesially and the d cusp distally. Mesially, a narrow sulcus isolates a badly preserved f cusp; this mesial indentation is intermediate in depth between that of M46115 and that of M46513. Wear, heavier than in other specimens, has affected at least the distolabial part of the tooth. This tooth seems to be closer to *Amphilestes broderipii* according to the shape of the cusps and the closer approximation of b and c to a, but it may differ in the lesser height of the cusps, although this is uncertain owing to the wear.

Upper molars. — Upper molars, also from Kirtlington, may be identified by the presence of both labial and lingual cingula and other characteristics. These are of appropriate size and morphology to occlude with the lower molars of *Phascolotherium simpsoni*, and are referred to the species by analogy with the associated upper and lower dentition known for *Juchilestes* (Gao *et al.* 2010). They are described individually in the paragraphs that follow.

M46440 (right upper molar; L = 1.08 mm, W = 0.46 mm; Figs 3E and 4D) could well fit with the smaller lower molars M46115 and M46513. From the inclination of the partially preserved distal root and the shape of cusp A, M46440 is interpreted as a right molar. The crown is relatively lower than that of the lower teeth, and there is a labial cingulum as well as a lingual one; these cingula are narrow, smooth, and vaguely sinuous. An elevation of the cingula forms a cuspule (?E), directly mesial to B, but F is not individualized and no mesial indentation is detectable. D is slightly displaced lingually from the A–C line; it would probably lie lingual to E of the next tooth. All cusps are triangular in lateral view, even more so than on the lower molars described above. Cusp A is longer mesiodistally at the base, and B and C are relatively smaller than the corresponding cusps of lower molars belonging to *Phascolotherium simpsoni*. Surprisingly, assuming the specimen is a right tooth, the crown is wider distally than mesially, unlike amphilestid lower molars, and B is slightly larger than C. Cusp A bears a ridge on its lingual side, turning distally toward the base. This divides the lingual surface into a convex mesial part and a concave distal part. There were two roots, the distal one only basally preserved. Wear has flattened the lingual ridge of A, especially at its recurved base, creating a narrow elongated facet facing distally. The short lingual ridge of C is not worn.

M46762 (right upper molar; L = 0.85 mm, W = 0.37 mm; Fig. 5A) is smaller than M 46440, and its enamel is not as well preserved, but it is very similar and offers the same challenge as to its orientation. The differences with M46440 concern B and C, which are small and less detached from A, only the latter having a triangular shape in lateral view. Its lingual ridge and concavity are also less accentuated. There is no E cusp; D is again lingually placed, and the complete distal root is inclined backward. No wear facet is discernible, except perhaps on the cingulum above C. M46762 could be interpreted as a distal molar of the same taxon as M46440 (though the wear [?] above C would imply the presence of a more distal lower molar).

M46538 (?left upper molar; L = 0.95 mm, W = 0.40 mm; Fig. 5B) is of the same size as M46762, but with sharper cusps. The lingual cingulum is weaker and may even be incomplete mesially. Cusp E is absent, but there is a small labial cusp F, separated by a groove from the mesial ridge of B. D is less lingually placed than on M46440. The rounded ridge on A is present lingually. The distal root is vertical, long, and slender, and decreases in diameter apically. Perhaps this tooth is a deciduous premolar.

M46536 (?right upper molar; L = 1.12 mm, W = 0.50 mm; Fig. 5C), an upper molar broken by a vertical crack across A, is close to M 46440 in size and in the lingual convexity of A, but it has straighter labial crests and C seems to have been more vertically oriented and closely apposed to A. Cusp E is not individualized. The narrow cingulum on both sides of the tooth remains equal along its entire course. No wear is detectable. The attribution of this tooth remains debatable, given the characters noted above and also the contour of the crown view. An alternative possibility is that it is an upper molar of *Amphilestes* cf. *A. broderipii*.

DISCUSSION

Comparisons, lower molars. — Outside of the "amphilestids" from the Middle Jurassic of the UK, the closest form to *P. simpsoni* may be the Morrison (Late Jurassic) genus *Comodon* (= *Phascolodon* Simpson, 1925b), based on lower molars. The latter agrees with *P. simpsoni* in size, proportions and shape of cusps, situation of e and f, wear (groove between a and c), and smooth enamel. *Comodon* was said to "closely [resem-
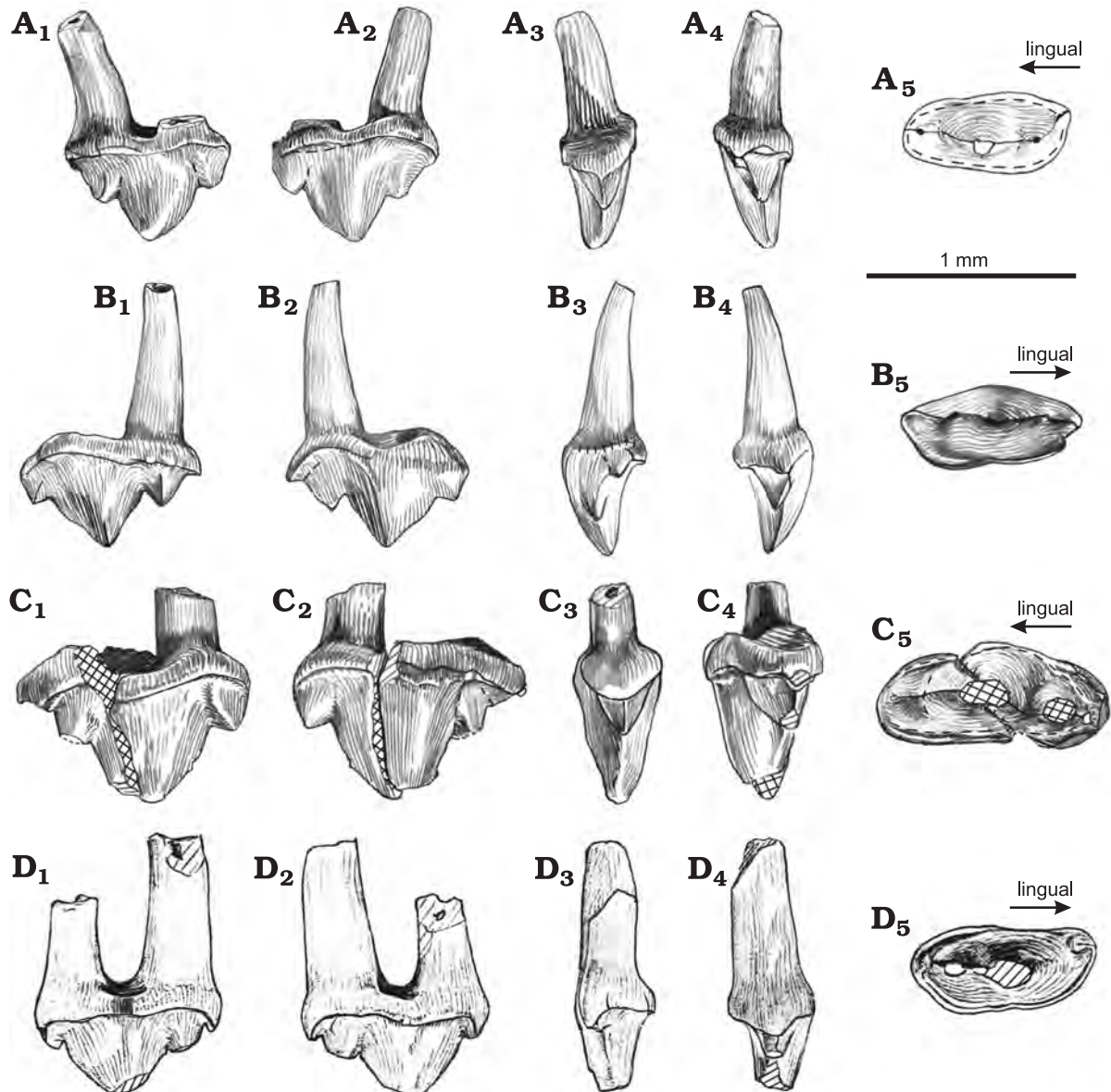
Fig. 5. "Amphilestidae" and ?"Amphilestidae" from the Middle Jurassic of Great Britain, upper molars. All specimens from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian. **A–C**. *Phascolotherium simpsoni* sp. n. **A**. M46762, right upper molar in labial (A_1), lingual (A_2), mesial (A_3), distal (A_4), and occlusal (A_5) views. **B**. M46538, left upper molar in labial (B_1), lingual (B_2), mesial (B_3), distal (B_4), and occlusal (B_5) views. **C**. M46536, right upper molar in labial (C_1), lingual (C_2), mesial (C_3), distal (C_4), and occlusal (C_5) views. **D**. Gen. et sp. indet., M46441, left upper molar in labial (D_1), lingual (D_2), mesial (D_3), distal (D_4), and occlusal (D_5) views. Arrows point anteriorly. Cross hatching refers to a broken surface and parallel hatching indicates wear.

ble] *Phascolotherium*" (Simpson 1925b, p. 335), but it "can be readily distinguished by the smooth enamel, by the character of the cingulum" [weaker in *Comodon*?], "and the reduction of the last molar" (Simpson 1929, p. 31); a slight curvature of the crown should be added (Sigogneau-Russell 2003a, p. 55, pl. 1, figs 6–8). However, the smooth enamel of the Kirtlington specimens reduces the gap between the two genera.

A lower molar from the Early Cretaceous of West Siberia (PM TGU 16/6 404 — not 401) was attributed by Averianov *et al.* (2005, p. 5, fig. 2G–I) to "Amphilestidae indet." It more closely resembles *Amphilestes* in the shape of the lateral cusps and the narrowness of the primary cusps; but it has only a slight anterior indentation and f is very weak. The roots are more widely separated than on the Bathonian teeth, suggesting the possibility that a replacement tooth may have developed in the space between them.

The partial lower tooth attributed by the same authors to *Kemchugia* (Averianov *et al.* 2005, p. 5, fig. 3; PM TGU 16/6-410) seems to have a low, divergent d cusp and a mesiodistal alignment of a and c as in

Phascolotherium, but the apparently intact anterior border seems to preclude the presence of a b cusp, or at least indicates that it was much smaller than c. This tooth could be a first molar, on which the b cusp is reduced as in *Gobiconodon borissiaki* Trofimov, 1978 (see Kielan-Jaworowska and Dashzeveg 1998) but not as on m1 of the Stonesfield specimens of *Amphilestes* or *Phascolotherium*.

Though described as family indet., the Early Cretaceous genus *Hakusanodon* Rougier *et al.*, 2007, based on a lower jaw, is shown within the "amphilestids" in the cladogram of these authors. It differs from *Amphilestes* and resembles *Phascolotherium* in the loss of anterior premolars. However, it differs from both Bathonian genera in that cusp a is slightly recumbent, b is taller than c, f and the mesial indentation are absent, and the lingual cingulum is represented only by mesial and distal segments. In addition, on OUM J.20079 of *Amphilestes*, b appears slightly wider — if not slightly higher — than c, and it is higher on M35000, attributed above to *Amphilestes* cf. *A. broderipii*. Furthermore, the variability of this character along the toothrow should be considered. None of the "family indet." specimens from the late Early Jurassic of Mexico (Montellano *et al.* 2008) resembles the Kirtlington specimens. Finally, *Juchilestes* lower molars differ from the teeth described above by the straighter disposition of the cusps, the absence of a lingual concavity, of a labial "bulging base of cusp a" (Rougier *et al.* 2007, p. 80), and the absence of cusp f.

The cladistic analysis of Gao *et al.* (2010) confirms that "Amphilestidae" are not monophyletic: the authors distinguish two groups, the first containing *Amphilestes* and *Phascolotherium*, representing stem taxa to *Tinodon* and the Trechnotheria; the second, a clade containing *Hakusanodon*, *Juchilestes*, *Comodon*, *Amphidon*, and *Aploconodon*, which is closer to gobi-conodontids.

This study, which reveals confusing combinations of similarities and differences in molar structure, underscores the fragility of current phylogenetic relations among taxa based on isolated teeth (for instance, a phylogenetically important area like the angular region of the lower jaw of *Amphilestes* is not preserved).

Occlusion (Fig. 6). — The traditional view of alternate occlusion among "amphilestids" rested originally on the observation by Mills (1971, p. 53) that "the dental occlusion of *Phascolotherium* is essentially of the *Kuehneotherium* type". In fact, a slight triangulation of a with b and c had been claimed for *Amphilestes* (Osborn 1888; Mills 1971; Crompton 1974); however, careful examination of OUM J.20079 following recent preparation (Sigogneau-Russell 2003a) showed that the tips of the cusps are in a straight line, though the base of cusp a projects labially because of its larger size; this results in the convexity of the labial margin of the lower tooth. Also, because a is much higher than b or c, it appears out of line if the tooth is not seen exactly from above. Nevertheless, two of our specimens belonging to *Amphilestes* cf. *A. broderipii* (M35000, M46744) are very shallowly concave on the lingual outline, thus suggesting a slight triangulation.

The identification of M46440 and others as upper molars of *Phascolotherium simpsoni* supports this alternate type of occlusion, in which the A cusp of the upper tooth would naturally bite into the embayment between two lower convexities. The ridge on the lingual side of A corresponds to the embrasure between two lower teeth, separating the occlusal domains of c

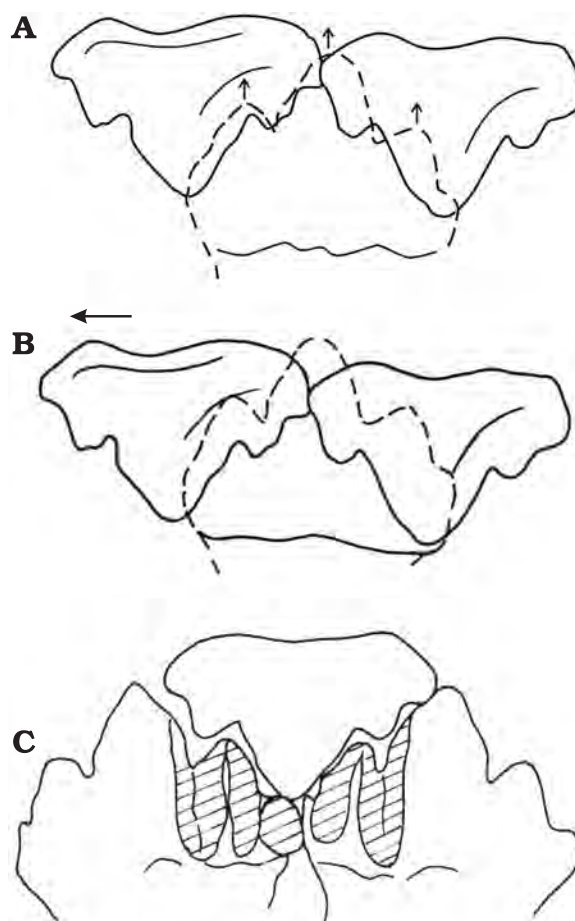Fig. 6. *Phascolotherium simpsoni* sp. n. from late Bathonian. Proposed occlusal relationships between upper (M46440 Old Cement Works Quarry, Kirtlington, Oxfordshire, UK) and lower (M46115, Watton Cliff, Dorset, UK) molars. **A**, **B**. Successive stages in upward movement of the lower tooth (dotted line). **C**. The facets (parallel hatching) produced by an upper tooth. Arrow points anteriorly.

mesially and b distally. Superposition of drawings shows that the cusps of M46440 are in correct position to cause wear such as that seen on M46503. Wear on lower molars takes the form of steeply inclined strips on the edges of the cusps and in the grooves between their bases. Fig. $6A_3$ shows the maximum potential position of the facets; individual differences may be ascribed to degree of wear and small variations in tooth position. The facets were presumably produced by the tips of upper cusps, when the lower teeth travelled upward and lingually as the jaws closed.

Upper molars. — Until recently, no "amphilestid" upper molar had been recognized with certainty: the Indian genus *Paikasigudodon* Prasad *et* Manhas, 2002, defined on an upper molar, has recently been referred to the family (Kielan-Jaworowska *et al.* 2004, p. 240) but these authors recognize this placement as "highly uncertain": the asymmetrical outline of the tooth, its minute cingular denticulations, the proportions of the cusps and the absence of D, the presence of accessory anterior and posterior cuspules, the quasi absence of a lingual cingulum (assuming that the specimen is an upper molar, an interpretation that is itself questionable) justify such doubts.

Averianov *et al.* (2005, p. 3) reidentified as a new "amphilestid" *Kemchugia magna* an upper molar (PM-TGU 16/6-401; Averianov *et al.* 2005, p. 5, fig. 2A–C) from the Early Cretaceous of Siberia, previously published in 2003 by Leshchinskiy *et al.* (2003, p. 351, fig. 1a–c) as Morganucodontidae indet. (PM-TGU 16/6-301). The authors distinguished this tooth from those of Morganucodontidae by "a more vertical and higher central cusp A and less height differential between cusps B and C" (Averianov *et al.* 2005, p. 4) with cingular cusp E less lingually situated; and from the Gobiconodontidae by the absence of an ectoflexus. Cusp E has possibly been misidentified (the real cusp E is visible lingually (Leshchinskyi *et al.* 2003, p. 351, fig. 1c). Moreover, the same relative size of A can be observed on M1–M2 of *Megazostrodon* or the eutriconodontan *Jeholodens* Ji *et al.*, 1999. In fact, identification of *Kemchugia* as an "amphilestid" rested partly on a referred, incomplete lower molar, PM-TGU 16/6-410, which shows (Averianov *et al.* 2005, p. 6, fig. 3) facets "1" (formed by occlusion of cusps C–a) and "2" (formed by occlusion of cusps c–A) as defined by Crompton (1971) on triangular-cusped teeth (and as such not applicable here), "consistent with the embrasure dental occlusion characteristic for amphilestids" (Averianov *et al.* 2005, pp. 4, 5, fig. 3). These facets could as well be identified as those figured by Mills (1971, p. 40, fig. 1) for the early stages of wear in *Morganucodon*. Moreover, the seemingly intact mesial border indicates that the b cusp was very small or absent, so that the tooth would not occlude with the upper molar. Finally, the anterior cuspules e and f**,** characteristic of "amphilestids", are unknown for this incomplete tooth, which could be a first molar in which the b cusp is reduced, as in *Gobiconodon borissiaki* (see Kielan-Jaworowska and Dashzeveg 1998). In any case, compared to the upper molars referred above to *Phascolotherium*, that of *Kemchugia* is wider distally, with higher cusps, a mesiodistally narrower A, upright B and C which are joined to A at a higher level, and strongly crenulated cingula. Finally, the lingual ridge of A is absent.

The upper molars of *Juchilestes* differ from those of *Phascolotherium simpsoni* in the same ways as do the lowers: by the straighter disposition of the cusps, the lack of a labial concavity in occlusal view, and the lesser lingual bulging of the cingulum. This supports the phyologenetic hypothesis of Gao *et al.* (2010), who recognized the clade including *Amphilestes* and *Phascolotherium* as distinct from another comprising *Juchilestes* and its relatives.

?Family **"Amphilestidae"** Osborn, 1888

Gen. et sp. indet.

(Fig. 5D)

One additional upper molar from the Old Cement Works Quarry, Kirtlington (Oxfordshire, UK; late Bathonian), M46441 (left upper molar; L = 0.92 mm, W = 0.45 mm; Fig. 5D), is of uncertain affinities; we describe it under this heading for lack of a definitive identification. Like the upper molars of *Phascolotherium simpsoni*, this tooth also bears a cingulum labially and lingually. It is similar in size to M46538, referred to *P. simpsoni,* but it is more asymmetrical, the small B cusp arising from the cingulum; A is then placed more anteriorly, as on premolars of morganucodontans. The cingulum is complete and lacks denticulations. E and F are absent; D is in line with A and C; the lingual ridge of A is not developed. The tips of the cusps are abraded and A may have been slightly reduced by wear. The roots are vertical and stouter than on M46538, the distal one being the largest. This tooth could be interpreted as an upper premolar (though lower premolars of *Amphilestes* and *Phascolotherium* are strictly symmetrical).

Family **Gobiconodontidae** Chow *et* Rich, 1984

Gobiconodontidae are distinguished from "Amphilestidae" by their more robust teeth and cranial elements, specialized anterior dentition, curving upper tooth row, and replacement of at least some molariforms (e.g., Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Meng *et al.* 2005; Yuan *et al.* 2009). Most gobiconodontid occurrences are of Early Cretaceous age, possible exceptions being *Klamelia* Chow *et* Rich, 1984, from the Late Jurassic of China (excluded from the family by Kielan-Jaworowska *et al.* 2004); and *Huasteconodon* Montellano *et al.*, 2008, represented by a remarkably small (upper molar length, 0.55 mm) fossil from the late Early Jurassic of Mexico. Kielan-Jaworowska *et al.* (2004) included in the Gobiconodontidae the type genus *Gobiconodon* and the Chinese genera *Hangjinia* Godefroit *et* Guo, 1999, and *Repenomamus* Li *et al.*, 2000. *Hangjinia* is defined on a lower jaw with partial teeth; *Repenomamus* has been more recently returned to its own family, Repenomamidae Li *et al.*, 2000, by Hu *et al.* (2005). Finally, *Meemannodon* Meng *et al.*, 2005 has been described from the Early Cretaceous of China, also based on a lower jaw.

Specimens from Kirtlington and Swyre form the basis for recognition of *Gobiconodon bathoniensis* sp. n., described below. Additional specimens not surely referable to the species, genus, or family are described under separate headings following treatment of *G. bathoniensis* sp. n.; a brief summary is presented at the end of the section on Gobiconodontidae.

Genus *Gobiconodon* Trofimov, 1978

Type species: *Gobiconodon borissiaki* Trofimov, 1978.

Gobiconodon bathoniensis sp. n.

(Figs 7A–C, 8A, B)

LSID urn:lsid:zoobank.org:act:222BC89E-E0B0-4690-968D-7E3287C5740D

Holotype: M46527**,** upper right molar (Figs 7A, 8A).

Etymology: From Latin *Bathonium*, in reference to the geological age (based on outcrop at Bath, UK).

Type horizon and locality: Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian.

Referred material. — M46083 and M46189, both upper left molars from Kirtlington; M46031, ?last upper right molar, from Swyre, Dorset, UK; late Bathonian.

Diagnosis. — Small-sized upper molars, whose main cusps show an "incipient triangular pattern, cusp A being placed more lingually than cusps B and C" (Kielan-Jaworowska and Dashzeveg 1998, p. 417), generally diagnostic of the genus *Gobiconodon*, and differing from the pattern seen in *G. luoianus* Yuan *et al.*, 2009. Differs from *G. hoburensis* (Trofimov, 1978), *G. borissiaki* Trofimov, 1978*, G. ostromi* Jenkins *et* Schaff, 1988, G. *hopsoni* Rougier *et al.*, 2001, and *G. zofiae* Li *et al.*, 2003, in that teeth in corresponding serial positions are narrower, with the occlusal contour triangular rather than rectangular, and the ectoflexus shallower (though this feature varies from M1 to M5 in the above species). Differs from *G. zofiae,* where cusps of molars are aligned antero-posteriorly, cusp D is said to be "degenerated" (Li *et al.* 2003, p. 1129), and E larger than B. Closest in size to *G. hoburensis* and *G. palaios* Sigogneau-Russell, 2003a. Differs from *G. hoburensis* with cusp A relatively higher and shorter, and lateral cusps better detached from A; last molar more reduced. Differs from *G. palaios* in shallower ectoflexus and D cusp more pointed in crown view. Differs from the other Jurassic form, *Huasteconodon* Montellano *et al.*, 2008, in its larger size, larger cusp C, occlusal shape, lesser ectoflexus, and roots narrower transversely, not visible in occlusal view.

Description. — The holotype, M46527 (right upper molar; L = 1.30 mm, W = 0.57 mm; occlusal angle = 160°; Figs 7A, 8A) shows a curvature of the crown in occlusal view, with the lingual edge evenly convex, the labial edge barely concave, the mesial end truncated, and the distal end pointed. Cusp A is narrow, sharp, centrally placed, and high relative to B and C; in side view, it has the shape of an equilateral triangle, as in the Mongolian species of *Gobiconodon*, *G. borissiaki*, and *G. hoburensis*. B is smaller and slightly more labially placed than C. The F cuspule, mesiolabial to B, is as large as the D cusp; the latter is fully labial, so that the C–D crest is oblique; the B–F region is even more bent labially. There is an encircling cingulum, wider on the labial side, and faintly crenulated in places. The mesial root is flat mesially, its greater diameter pointing obliquely toward the mesiolabial end of the crown. The distal root, which is broken, was flattened labiolingually and also obliquely disposed under the crown, so that the bases of the roots are closer lingually than
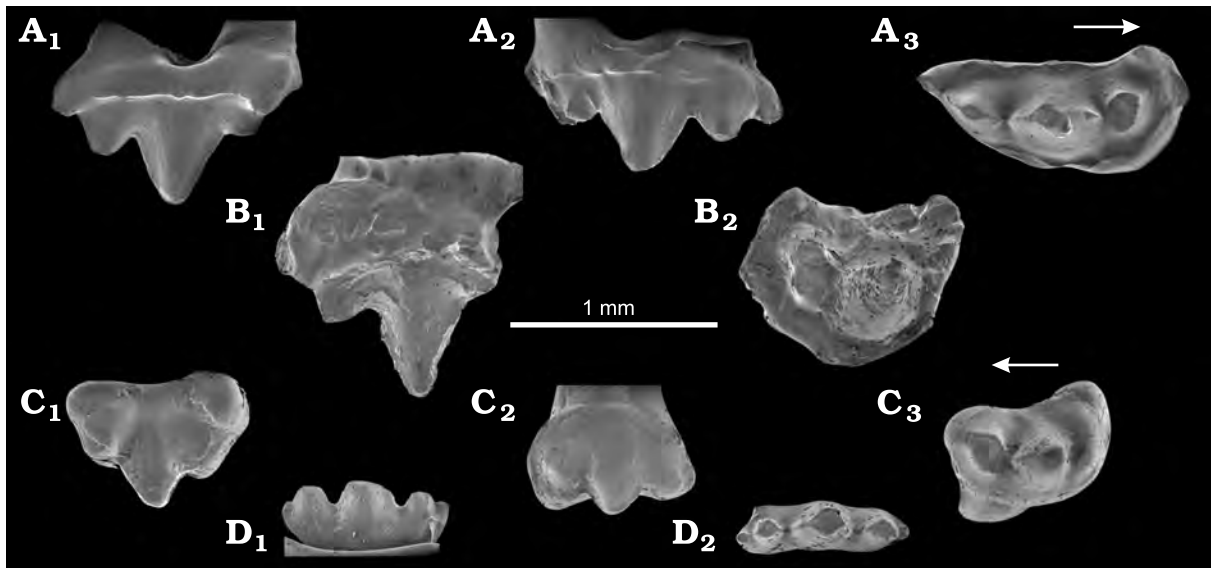
Fig. 7. Gobiconodontidae and Triconodontidae from the Middle Jurassic of Great Britain. **A–C**. *Gobiconodon bathoniensis* sp. n. **A**. Holotype M46527, Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian, right upper molar in labial (A_1), lingual (A_2), and occlusal (A_3) views. **B**. M46083, Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian, left upper molar in labial (B_1) and occlusal (B_2) views. **C**. M46031, Swyre, Dorset, UK; late Bathonian, right upper molar in labial (C_1), lingual (C_2), and occlusal (C_3) views. **D**. *Eotriconodon sophron* gen. et sp. n., holotype M46736, Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian, right lower molar in lingual (D_1) and occlusal (D_2) views. SEM photos; roots cropped as needed. Arrows points anteriorly.

labially. Wear facets are visible on the mesial faces of F and B (by contact with D of the succeeding tooth). Possible wear on the lingual cingulum would presumably be due to occlusion with lower molar cusp a or c, and wear on the cingulum distal to C would be due to occlusion with lower molar cusp a.

M46083 (left upper molar; L = 1.40 mm, W = 0.85 mm; angle = 165°; Fig. 7B) has cusps B and C abraded, and the distal part of the lingual edge broken off. It is similar to M46527 but the crown is proportionately broader and more curved in occlusal view than the holotype, with C displaced as labially as B, and F even more prominent labially. The labial cingular ledge is even wider; it is also more grossly denticulate with a higher cuspule distally. The lingual cingulum is again faintly undulating. The ectoflexus is deeper than on the holotype. The mesial root is stouter; the distal one has been broken off, but their bases are again closer lingually than labially. The enamel is only partially preserved, but it does seem that wear had heavily affected the mesial faces of F, B and A, and possibly the lingual cingulum; the tip of A remains intact. The greater curvature and more pronounced ectoflexus indicate that this tooth occupied a more distal position than the holotype.

M46189 (left upper molar; L = 1.05 mm, W = 0.52 mm; angle = 155°; Fig. 8B) is notably smaller than the two teeth described above; it is also proportionately narrower. The crown is badly eroded, and worn the same way as the holotype and M46083 (and M46563; see below, under Gobiconodontidae gen. et sp. indet.), with A remaining unworn, while B and C are heavily worn. The crown is again curved in occlusal view, with a truncated mesial end and a pointed D, the latter being more labial than C. There may have been two cingula but erosion has minimized the evidence. The mesial root has broken off; the distal root is flattened labio-lingually and the two root bases are again divergent. This tooth is interpreted as possibly a worn molar of a first generation, or a more anterior member of the series containing M46527 and M46083.

M46031 (right upper molar; L = 0.92 mm, W = 0.52 mm; angle = 137°; Fig. 7C) is puzzling: it is even shorter mesiodistally than the preceding tooth but relatively wider labiolingually. B and C are displaced labially, B more than C. F protrudes labially. B and C are equal in height and much lower than A, which is conical. D is rudimentary on the distal crest of C. All three main cusps are set close to each other. There is a trace of E mesial to B, in the shape of a wear facet. The lingual cingulum is not discernible but the enamel is missing at that level; labially, the cingulum was present at least distally and possibly also mesially. The crown was supported by a single root, wider mesially and furrowed with a faint sulcus lingually, as if formed by the union of two roots; its labial face has been broken away, exposing the pulp cavity. Again, B and C have been abraded, the tip of A remaining intact. Lingually, wear has affected the mesial crest of A, the
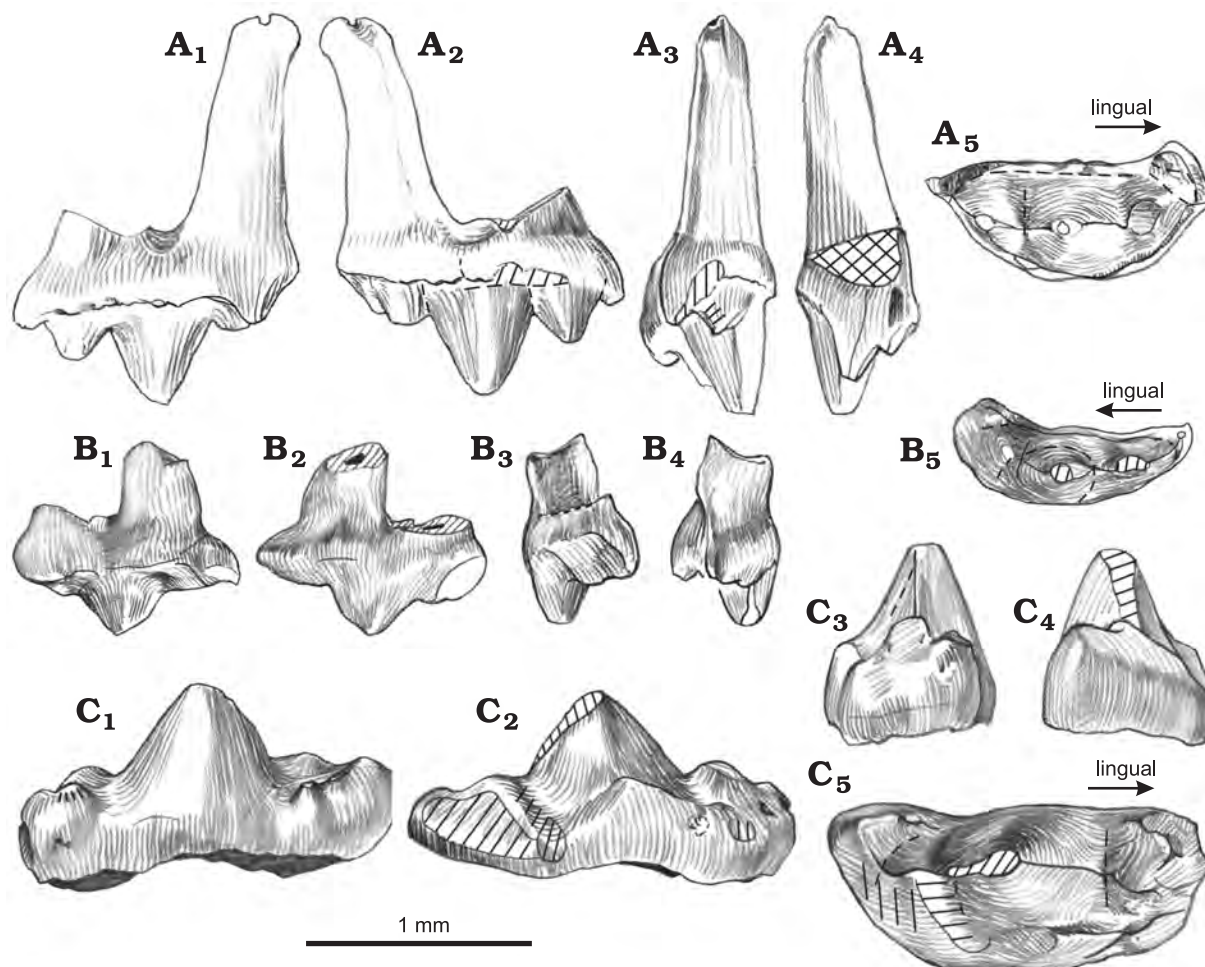
Fig. 8. Gobiconodontidae from the Middle Jurassic of Great Britain. All specimens from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian. **A**, **B**. *Gobiconodon bathoniensis* sp. n. **A**. Holotype M46527, right upper molar in labial (A_1), lingual (A_2), mesial (A_3), distal (A_4), and occlusal (A_5) views. **B**. M46189, left upper molar in labial (B_1), lingual (B_2), mesial (B_3), distal (B_4), and occlusal (B_5) views. **C**. *Gobiconodon* sp. indet., M46563, right lower molar in labial (C_1), lingual (C_2), mesial (C_3), distal (C_4), and occlusal (C_5) views. Arrows point anteriorly. Cross hatching refers to a broken surface and parallel hatching indicates wear.

mesial face of B as far as F, and the distal crest of C leading to a small D cusp. By the relative development of the two lobes and the general proportions recalling the M5 of *Gobiconodon hoburensis*, this tooth can be interpreted as a last upper molar, even though the latter is two-rooted in *Gobiconodon borissiaki* (Kielan-Jaworowska and Dashzeveg, 1998, fig. 1) and *G. zofiae* (Li *et al.* 2003).

Discussion. — These gobiconodontid upper molars are small, comparable in size to those of *G. palaios*, from the ?Berriasian of Morocco. In *G. zofiae* there are five lower molars but only four upper molars; in *G. luoianus* both upper and lower dentitions include five molars. M46031, if a last upper molar, could therefore be M4 or 5 (see summary and discussion in Yuan *et al.* 2009).

In *Gobiconodon zofiae,* M1 is narrower than M2–M3, and M3 is the broadest; the same is true in *G. borissiaki* and *G. hoburensis*. We have attempted to reconstruct the dentition in order of differences in width/length (Fig. 9A): M46189, M46527, and M46083 progressively increase in size and relative width, and might be M1–M3. Comparing this hypothetical series with *G. hoburensis* and *G.borissiaki,* we note that the teeth of *G. bathoniensis* are narrower, and M2 and M4 are smaller relative to M3, M2 having a shallower ectoflexus. The F cuspule is well defined, mesiolabial to B and projecting labially beyond the border, and the E cuspule is a widening of the cingulum mesial to B, at the mesial extremity of the tooth; the effect is that this mesial end is obliquely truncate. In *G. borissiaki* and *G. hoburensis,* E is represented by a ridge on B, running toward the mesial apex of the tooth, while F is weakly developed (Kielan-Jaworowska and Dashzeveg 1998, figs 1–4). Moreover, in *G. bathoniensis*, the lingual margin is convex, giving the teeth a triangular
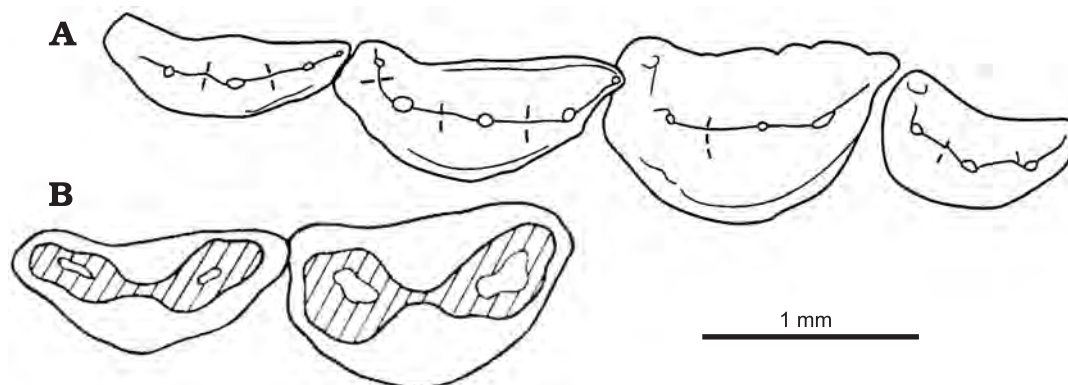
Fig. 9. *Gobiconodon bathoniensis* sp nov. from late Bathonian. **A**. Reconstructed left upper molar series; from left to right: M46189, M46527, and M46083 (Old Cement Works Quarry, Kirtlington, Oxfordshire, UK), M46031 (Swyre, Dorset, UK). **B**. Root pattern of M46527 and M46083.

shape, as in *G. palaios*; whereas in other species, the lingual margin is nearly straight, with a slight median concavity, and the mesial and distal margins are more transverse, so that the teeth are more quadrangular. The last molar of *G.borissiaki* and *G. hoburensis* shows various degrees of reduction of its distal part (least in *G. ostromi*). *G. palaios* is known by isolated molars that vary in relative width and probably represent more than one serial position (?M2, 3). It resembles *G. bathoniensis* not only in size, but also in having upper molars with narrow crowns that are triangular rather than quadrate, with the labiodistal end pointed. We also note that abrasion in *G. palaios* MNHN SA 119 (Sigogneau-Russell 2003a, p. 31, fig. 2d–e) is of the same type as on M46189 and M46083, with B and C cut off but A nearly intact; such a state of wear has not been illustrated in the other Cretaceous species. Finally, asymmetry of roots (Fig. 9B) has not been mentioned in the Cretaceous species except *G. palaios*.

In fact, the differences between *G. bathoniensis* and the Cretaceous species (except *G. palaios*) might provide grounds for generic separation. In any case, *G. bathoniensis*, wth teeth narrow and triangular, ecto-flexus faint, and labiodistal corner pointed, probably represents a primitive condition in *Gobiconodon*, only slightly modified in *G. palaios*; it is to be anticipated that other anatomical differences, in particular in the anterior dentition, would help to assess the specific distinction.

The upper gobiconodont tooth from the late Barremian of Spain, which is slightly larger than M46083, is described as possessing "cusps nearly subequal in height and reduced lingual cingulum […] occlusal outline more rounded than in *G. borrissiaki*, *G. hoburensis* and *G. ostromi*" (Cuenca Bescos and Canudo 1999, p. 41). The lingual side of the B cusp is broken, but the mesial end is pointed, and there is a small ?F, followed by a shallow ectoflexus. The most obvious difference from *G. bathoniensis* is that the tooth is broader distally and rounded, rather than pointed, and the lingual profile is less convex; B and C are said to be larger relative to A than in the previously known species. However, given the poor state of preservation of this tooth and the variation along the dental series already mentioned for other species of the genus, it is not possible to make a more detailed comparison.

Huasteconodon wiblei is known by a fragment of maxilla containing two molars and the alveoli of a third, from the late Early Jurassic of Mexico (Montellano *et al.* 2008). The teeth are about half the size of those of *Gobiconodon bathoniensis*, but they show some resemblances. They are narrow, in contrast to most Cretaceous species; the A cusp is more lingual than B and C; and D projects at the distolabial corner of the tooth, at the end of an oblique A–C–D ridge. There is a difference in the ectoflexus, which has the form of a deep indentation of the margin labial to cusp A.

Gen. et sp. indet.

(Figs 8C, 10)

The following three teeth (all from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian) differ from the upper molars of *Gobiconodon bathoniensis* in that the three main cusps are in line, the mesial area being oriented directly forward instead of being oblique. The outline is therefore oval rather than triangular. It is possible that they are gobiconodontid lower molars, and they are provisionally described as such. Alternatively, if uppers, they could represent a new genus of Gobiconodontidae.
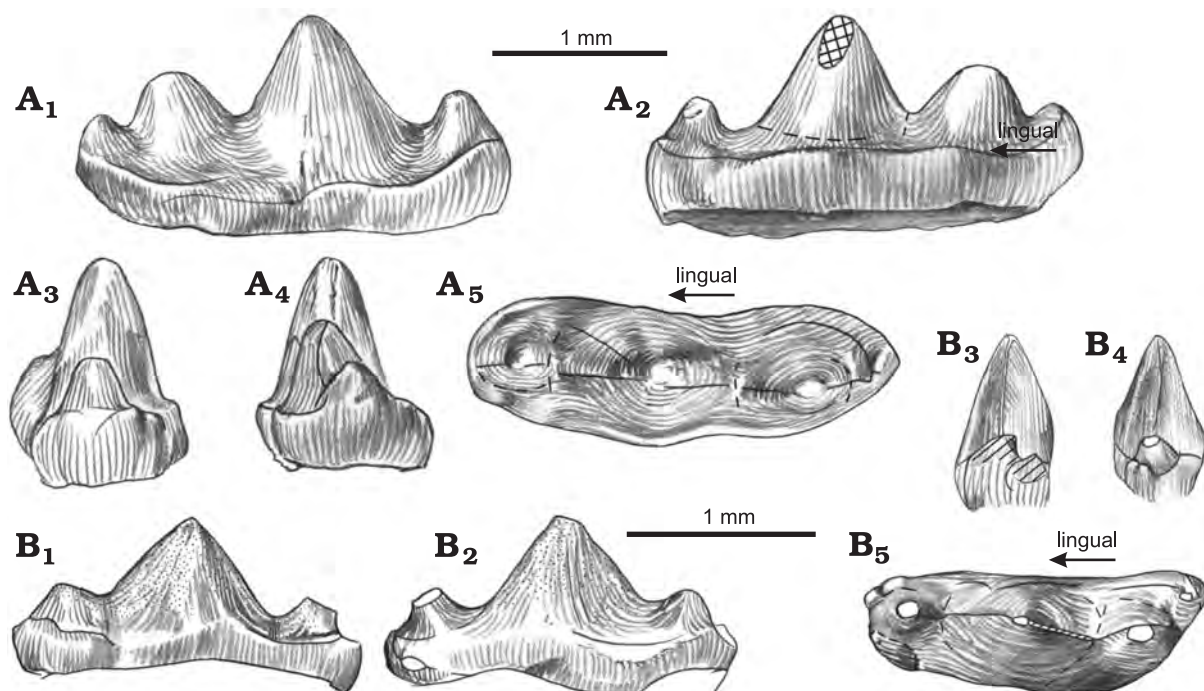
Fig. 10. Gobiconodontidae gen. et sp. indet., specimens provisionally identified as lower molars, from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian. **A**. M46815, left lower molar in labial (A_1), lingual (A_2), mesial (A_3), distal (A_4), and occlusal (A_5) views. **B**. M46300, left lower molar in labial (B_1), lingual (B_2), mesial (B_3), distal (B_4), and occlusal (B_5) views. Arrows point anteriorly. Cross hatching refers to a broken surface and parallel hatching indicates wear.

Description. — M46563 (?right lower molar; L = 1.72 mm, W = 0.75 mm; Fig. 8C) is similarly constructed to M46527, but reversed labio-lingually. It is less arched and relatively longer, the labial border is broadly convex, the distal end is pointed with d more lingual than c, the mesial end transverse; the lingual face is straighter than is the labial face of M 46527 and b is in line with a and c, so that the b–e–f-complex is directly anterior to a. Cusp a remains high but is relatively wider than in the upper teeth and less acute. A high labial cingular cusp protrudes at the mesial base of a, which was not individualized on the holotype upper tooth of *Gobiconodon bathoniensis* (M 46527). Most notable is the absence of a lingual cingulum; but the e and f cusps are well developed, and a tiny lingual cuspule is mesial to d. The pulp cavity is open. Strong wear affected the distal crest of cusp a, cusp b and even more cusp c, a groove having been cut between the latter and a, and extending to the labial cingulum, which is worn.

These features could have been interpreted as M46563 being a milk upper molariform, or rather a first generation upper molar, since gobiconodontid molars are known to be replaced (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998), but its size speaks against this interpretation. On the other hand, considered as a right lower tooth, M46563 resembles the lower molars of *Gobiconodon borissiaki* (Kielan-Jaworowska and Dashzeveg 1998, p. 419, fig. 1D) in the rectilinear arrangement of b, a and c, and the general outline (labially convex, lingually straight, distal end pointed); however, it differs in the small size of b and c relative to a, in the absence of an interlocking mesial groove, and in the presence of a labial marginal cusp. In any case, this specimen is too large to occlude with the upper molars of *G. bathoniensis*.

M46815 (left lower molar; L = 2.00 mm, W = 0.80 mm; Fig. 10A) is longer and relatively narrower than M46563, with low cusps. It appears to be an unerupted crown on which the enamel is incompletely developed and pitted. Cusps b and especially c are larger in comparison with M46563; b and d are slightly displaced lingually. The mesial border is rounded. There is a complete encircling cingulum but no cingular cusps, except mesially where one can detect incipient e and f cusps. No root is present, and the pulp cavity is fully exposed. No wear is discernible. If this tooth belongs to the same taxon as M46563, it may be from a more distal position in the dentition; or, given the absence of wear, a newly erupted tooth; in any case it is again too large to belong to *G. bathoniensis*.

M46300 (left lower molar; L = 1.48 mm, W = 0.64 mm; Fig. 10B) closely resembles M46563, except that it is smaller and relatively narrower. Cusps b and c remain small; d is displaced lingually. A labial cingulum
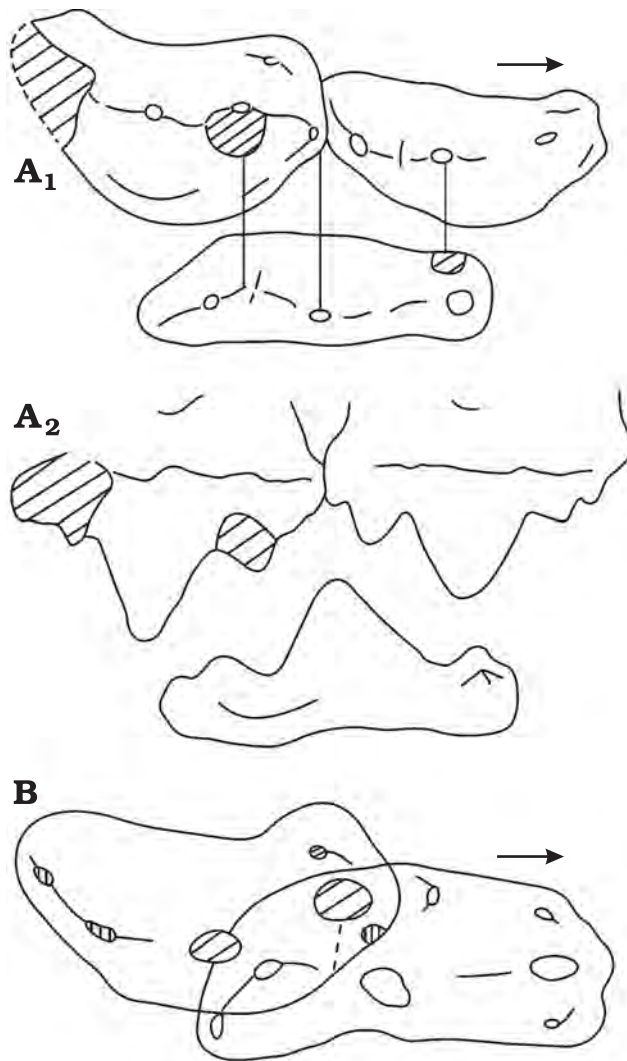
Fig. 11. *Gobiconodon bathoniensis* sp. n. from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian. **A**. Postulated lower molar M46300 in relation to upper molar M46083 (reversed) and M46527, in occlusal (A_1) and side (A_2) views. **B**. Postulated occlusion (occlusal view) between lower molar M46563 and a hypothetical upper tooth based on M46083.

is faintly indicated distally but lacks the cingulum cusp; the lingual cingulum is clearly developed with an elevation at the level of the mesial half of a. The top of b has been abraded and there appears to be a small facet on f; otherwise no wear is distinguishable, and the enamel is definitely pitted. The roots had not developed, therefore it was probably incompletely erupted (hence the pitted enamel?); its size makes it more likely to occlude with the uppers of *G. bathoniensis*.

Enamel pitting is known only in the Stonesfield material of the "amphilestid" *Phascolotherium* and was included by Simpson (1928) in its generic diagnosis. However, M46815 and M46300, both with pitted enamel, show little resemblance to the *Phascolotherium* teeth described in this paper: they differ from them in their asymmetry, the wider separation of the mesial cusp from the main cusp, as well as in the lowness of the crown. On the other hand, there is greater resemblance to the upper teeth of *Gobiconodon*, as noted above, but with differences suggesting that they could be lower teeth of this genus in spite of the lowness of the main cusp and presence of the labial cingulum.

Occlusion. — As a gobiconodont lower molar, M46300 would fit between the upper molars of *G. bathoniensis* M46527 and M46183. Superposition of drawings indicates occlusal relations (Fig. $11A_1$): the tip of cusp a would fit into the interdental embrasure between C and D anteriorly and E posteriorly. Cusp c occludes with B, accounting for a facet on the lingual surface of that cusp on M46563. The tip of the upper cusp A would pass between b and the more mesial d, meeting f at the end of the stroke. These relationships agree with those of *Gobiconodon borissiaki* and *G. hoburensis* described by Kielan-Jaworowska and Dashzeveg

(1998), taking into account the greater height of the cusps in the latter. We therefore speculate that M49300 may be a lower molar of *G. bathoniensis*. M46563, because of its resemblance to M49300, would therefore also be a lower molar, but presumably of a larger species. Its wear facets indicate the same occlusal relationships, with the exception that the facet on the labial side of c is much more extensive, reaching the peculiar marginal cusp. It would seem that the corresponding upper tooth (not represented in the available sample) had a much larger B cusp (Fig. 11B).

?Family **Gobiconodontidae** Chow *et* Rich, 1984

Gen. et sp. indet.

(Fig. 12A, B)

Description. — Three teeth (all from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian) are possibly gobiconodontid premolars. M46077 (left; L = 1.20 mm, W = 0.70 mm; Fig. 12A) is a relatively large tooth with an asymmetrical crown. In outline it is triangular, with lingual apex. The crown is dominated by a high, acute A cusp, recurved distally at the tip. This cusp bears, lingually, a strong vertical crest creating a concave distal half, while it is strongly convex labially. C is low relative
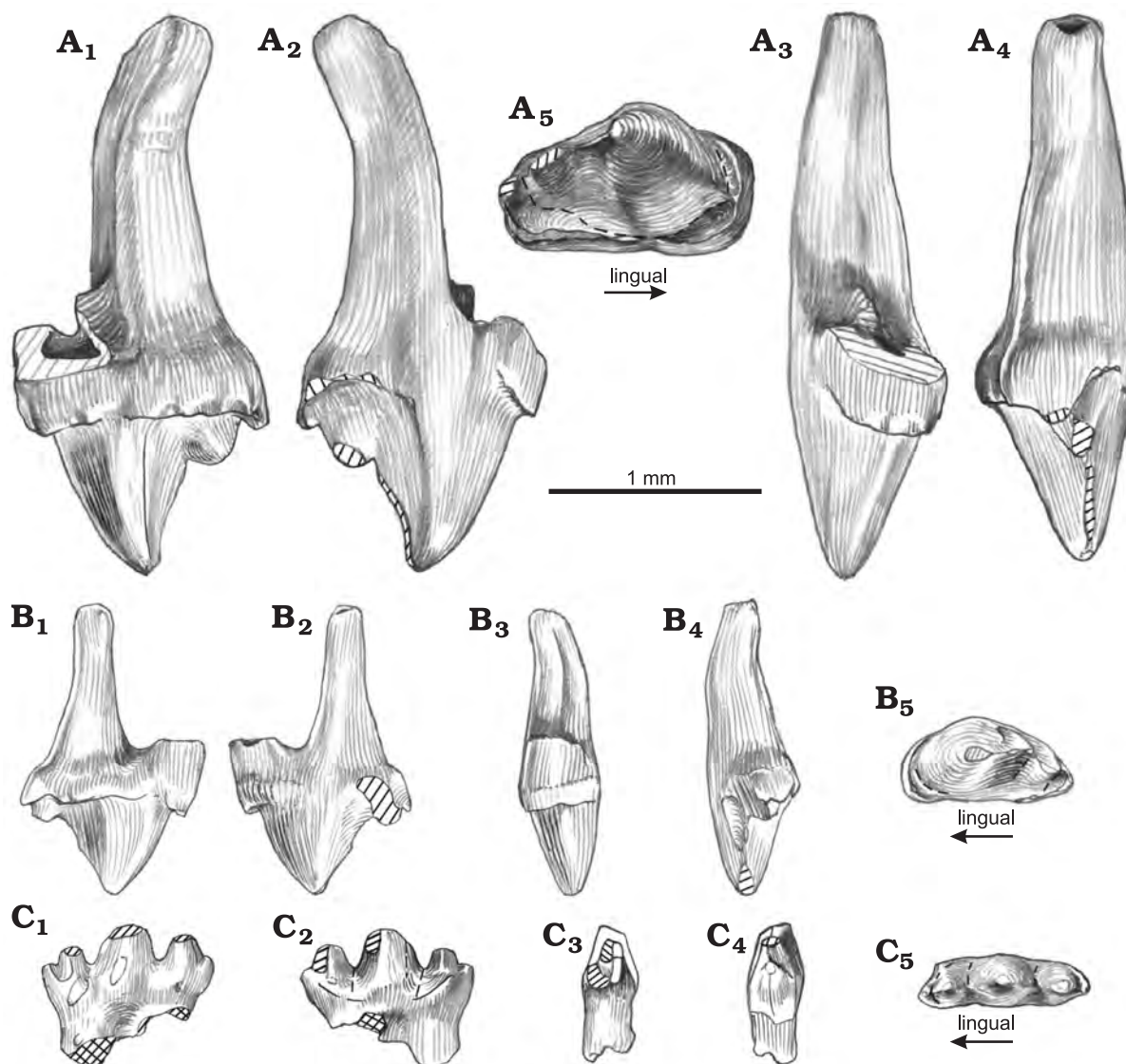
Fig. 12. Eutriconodonta and Triconodontidae from the Middle Jurassic of Great Britain. All specimens from the Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian. **A**, **B**. ?Gobiconodontidae, gen. et sp. indet. **A**. M46077, left upper premolar in labial (A_1), lingual (A_2), mesial (A_3), distal (A_4), and occlusal (A_5) views. **B**. M46597, right upper premolar in labial (B_1), lingual (B_2), mesial (B3), distal (B_4), and occlusal (B_5) views. **C**. *Eotriconodon sophron* gen. et sp. n., holotype M46736, right lower molar in lingual (C_1), labial (C_2), mesial (C_3), distal (C_4), and occlusal (C_5) views. Arrows point anteriorly. Cross hatching refers to a broken surface and parallel hatching indicates wear.

to A; there is no B cusp. A complete labial crenulated cingulum is prolonged mesially and expands in two slight bumps (E and F?) but with hardly an indentation between them. Distally the cingulum culminates in a D cusp and wraps around to encircle C lingually. There were two roots, which had a similar arrangement as on the gobiconodontid molars: the distal root, the only one preserved, is long, massive, flattened mesio-distally but obliquely orientated, lingually and distally; it diverged from the mesial root toward the labial side of the tooth. The mesial root was clearly smaller. A flange joins the bases of the roots, which were close together. The posterior crest of A and the tip of C are abraded; incipient wear is observable on the cingulum linguo-distally.

Because of its triangular shape and asymmetrical pattern, this tooth can only be an upper premolar. The absence of B and its low length/width ratio distinguish it from gobiconodontid molars. It somewhat resembles a last premolar of *Megazostrodon* (in particular, it has the same labial ledge above C as figured by Crompton (1974, p. 406, fig. 4C; p. 407, fig. 5A; pl. 2A); it could qualify as an upper premolar of *Gobiconodon bathoniensis*, although the marked labial convexity of A and the asymmetry of the roots may also suggest a trechnotherian premolar.

M46823 (L = 0.82 mm, W = 0.45 mm) is quite similar to, but much smaller than M46077, and cusp A is not posteriorly recurved. E and F are separated by a slight indentation; the labial cingulum points under the middle of A. The distal root is relatively shorter, and apparently no stronger than the mesial root (missing). Wear has touched the same areas as on M 46077, but more extensively and it extends to D.

M46597 (right; L = 0.90 mm, W = 0.45 mm; Fig. 12B) is morphologically very close to M46823, with A less convex labially and C more distant from A; the labial cingulum is also weaker. The two roots were subequal, but the distal one is disposed obliquely as in M46077. The distal side of C is worn vertically.

If these teeth have been correctly identified, they would indicate that the premolar dentition in the Bathonian gobiconodontids was less specialised than in the Cretaceous species (no premolar is preserved for *Huasteconodon*). Not only are the roots unfused, but the crown retains the structure characteristic of morganucodontans.

DISCUSSION: GOBICONODONTIDAE

The family Gobiconodontidae has been shown to have had an extensive geographical distribution, being recorded from Mongolia (Trofimov 1978; Kielan-Jaworowska and Dashzeveg 1998; Godefroit and Guo 1999; Rougier *et al.* 2001), North America (Jenkins and Schaff 1988; Montellano *et al.* 2008), Siberia (Maschenko and Lopatin 1998), Spain (Cuenca Bescos and Canudo 1999), China (Wang *et al.* 2001; Yuan *et al.* 2009), North Africa (Sigogneau-Russell 2003a), and southern Britain (Sweetman 2006). Its presence in the Bathonian of Kirtlington confirms an early origin of the family, as already suggested by the Mexican species (*Huasteconodon wiblei*; late Early Jurassic), since all other occurences date from the Cretaceous. This revives the suggestion already proposed (Sigogneau-Russell 2003a) that a megazostrodontid-gobiconodontid relationship may not be as far-fetched as it would seem: anterior molariform replacement, supposedly present in *Megazostrodon* (Gow 1986), exists in *Gobiconodon* (Jenkins and Schaff 1988; Wang *et al.* 2001; Luo *et al.* 2004). True, the specialisations of the anterior part of the lower jaw of the latter genus are not indicated in *Megazostrodon*, but we are ignorant of this anatomical region in the pre-Cretaceous Gobiconodontidae.

The presence of megazostrodontids as well as gobiconodontids on each side of the Tethys implies exchanges between Laurasia and Gondwana; such exchanges during the Jurassic have long been documented (Galton 1977; Rage 1988) and supported by palaeogeographic reconstructions (Barron *et al.* 1981; Smith *et al.* 1994). However, we are left to explain the absence of gobiconodontids in the Late Jurassic Morrison Formation of North America or the Early Cretaceous Purbeck Limestone Group, as well as in most Gondwanan Mesozoic localities.

Family **Triconodontidae** Marsh, 1887
Genus *Eotriconodon* gen. n.
LSID urn:lsid:zoobank.org:act:283D5F57-6AF4-49A3-B551-8EB4DBAF1795

Type species: *Eotriconodon sophron* sp. n.
Etymology: From Greek *eos*, dawn; in reference to the age of the new form with respect to most other triconodontids.

Distribution. — As for the type and only species.

Diagnosis. — As for the type and only species.

Eotriconodon sophron sp. n.
(Figs 7D, 12C)
LSID urn:lsid:zoobank.org:act:1FA19E1C-7C1C-40C9-84A4-BC0C03DF0F8C

Holotype: M46736, a right lower molar.
Etymology: From *sophron*, discrete.
Type horizon and locality: Old Cement Works Quarry, Kirtlington, Oxfordshire, UK; late Bathonian.

Diagnosis. — Similar to most triconodontids in having lower molars with three main cusps (a–c) mesiodistally aligned and subequal; distinct from all comparable taxa in its miniscule size, the absence of a lingual cingulum (derived), and the presence of cusps e and f, detached from b (primitive).

Description. — The only tooth in the Kirtlington collection attributable to the Triconodontidae is a tiny right lower molar, M46736 (L = 0.80 mm, W = 0.27 mm). It includes three main, subequal cusps, of

which the central (a) is just the largest; the mesial (b) is only slightly lower and shorter than c. These three cusps are mesiodistally aligned and widely separated. In crown view the labial margin is slightly convex owing to the larger size of a; the lingual margin is straight. The a cusp is constricted distally, especially on the labial side. Cusp b is preceded by two cuspules, e and f; e is columnar and is directly mesial to b, while f is more distally situated, forming a ledge labially under b; e and f are separated by a vertical groove. Cusp d is very small and in line with a, b, and c. There is no distinct labial cingulum, unless it is represented by cuspule f under b, and a ledge between a and c; more noteworthy is the fact that the lingual cingulum is also absent. Two roots were present, connected proximally by a flange. Intercuspal valleys are rounded, as if opposing cusps passed between them. The tips of the cusps have been abraded. An extended contact facet is clearly detectable mesially between e and f. Wear facets are also clearly indicated on the distal face of a and c, and less clearly on the mesial side of a and b: these facets determine which is the labial side, in spite of the latter having a basal ledge, while the lingual side lacks a cingulum (a lingual cingulum is almost universally present among other Triconodontidae and is found among other basal mammaliaforms and mammals). Some wrinkling of the enamel is visible at the labial crown base between a and f.

Discussion. — Crown morphology, especially the low cusp a and the relative proportions and disposition of the three main cusps, identifies M46736 as belonging to a triconodontid. A distal constriction of cusp a is observed in several triconodontids, especially *Priacodon* Marsh, 1887, which retains a degree of cusp inequality (Simpson 1929). Also, the valleys separating these cusps are rounded at the bottom to allow for the passage of upper cusps through them, as in other triconodontids. The fact that e and f are distinct cusps anterior to b could be considered as a primitive condition relative to that of Early Cretaceous triconodontids, where these cuspules are stylised and more or less fused distally to the body of the crown (Sigogneau-Russell 2003a); but the columnar shape of e also favours triconodontid affinity. However, M46736 is unlike most triconodontid lower molars in the absence of a lingual cingulum, a character shared with the highly derived *Alticonodon* Fox, 1969, with m1 of *Jeholodens*, and the Volaticotheriini (Gaetano and Rougier 2011). "Amphilestids" differ from *Eotriconodon* in the elevated, dominant cusp a, indicating a different mode of occlusion, but there is some resemblance in the interlocking cuspules e and f of *Phascolotherium cf. P. bucklandi* M46115. The first — and only preserved — molar of the triconodontid *Victoriaconodon* Montellano *et al.*, 2008, from the late Early Jurassic of Mexico, is of practically the same small size as M46736; but it differs in several respects that raise the question whether it belongs to the same family: b and c cusps are lower and smaller relative to a and less widely separated from it, with narrow and not V-shaped valleys; an e cusp is present but not an f; and there is a nearly complete lingual cingulum.

Martin and Averianov (2010) have recently described a triconodontid tooth from the Callovian of Kyrgyzstan, which they claimed to be the geologically oldest record for the family (*Victoriaconodon* was not mentioned). It consists of a very fragmentary lower right molar that is larger than the holotype of *Eotriconodon sophron*. Its main triconodontid character is the mesial embayment delimited by two vertical crests, of which the lingual one is said to be the more pronounced. The specimen is unique in apparently possessing a supernumerary cusp apposed to the distal crest of cusp a. Its taxonomic position requires confirmation from additional material.

The most recent addition to knowledge of early Triconodontidae is *Argentoconodon fariasorum* Rougier *et al.*, 2007, from the late Early or early Middle Jurassic Cañadón Asfalto Formation, Argentina. Originally compared with "Amphilestidae" on the basis of the holotype, an isolated molariform, *Argentoconodon* is now known by associated upper and lower dentitions. Phylogenetic analysis (Gaetano and Rougier 2011) places it in the Triconodontidae, within a clade containing *Volaticotherium* (from the late Middle or early Late Jurassic of China; Meng *et al.* 2006) and *Ichthyoconodon*, from the ?Berriasian of Morocco (Sigogneau-Russell 1995). Analysis by Gaetano and Rougier (2011) places volaticotheriines in the triconodontid subfamily Alticonodontinae, mainly known from North America (Cifelli and Madsen 1998; Cifelli *et al.* 1998) but also now represented in the Early Cretaceous of China (Kusuhashi *et al.* 2009).

Summing up, pre-Late Jurassic records of Triconodontidae are rare (four, including *Eotriconodon*) and poorly represented by fossils. Scarcity of triconodontids in Kirtlington suggests the possibility that we may be, in the Bathonian, close to the origin of the family, or at least to its eastern extension if the identification of *Victoriaconodon* is confirmed. Nonetheless, the absence of a lingual cingulum in *Eotriconodon,* a derived character, implies an earlier diversification of this family, as suggested by Gaetano and Rougier (2011).

CONCLUSIONS

Progress in understanding "triconodontan" evolution depends on the occurence of morphologically informative, associated dental and non dental material; peculiar isolated teeth cannot be safely referred to recognized taxa. Kielan-Jaworowska *et al.* (2004) list 14 "triconodont" genera (seven morganucodontans, seven eutriconodontans) based on isolated teeth, and our study increases this number. Some of the latter may belong to groups yet unknown. Only in the case of "amphilestids" can our material be closely compared with mandibular specimens from the Stonesfield Slate. Other comparisons are more distant, namely: gobiconodontids from the Early Cretaceous, triconodontids from the Late Jurassic–Early Cretaceous, and morganucodontids from the Early Jurassic. All we can hope for is that future discoveries will include osteological material and associated dentitions which will clarify the taxonomic position of the isolated teeth described above, hence help in understanding the evolutionary pathways followed by "triconodont" mammals.

Despite these difficulties, the some thirty teeth described in this paper are sufficient to provide a rough picture of the faunal composition. Although all are variants of the plesiomorphic triconodont molar pattern, they show great diversity. This is particularly so in the order Morganucodonta, of which six specimens are referable to four or perhaps five genera. Of these, *Wareolestes* Freeman, 1979 has been reinterpreted with a change of orientation of the type specimen. *Morganucodon tardus*, named herein, is morphologically conservative and in this sense may be regarded more as a survivor from the Early Jurassic, whereas *Cherwellia* and *Stylidens* (both also proposed on the basis of species named herein) are more divergent and appear to be more recently evolved; the poorly preserved M46194 may represent another taxon. The "Amphilestidae" are represented by seven lower molars which vary in details of cusp form, interlocking cuspules, and lingual cingulum. A new species, *Phascolotherium simpsoni*, is proposed. Four upper molars are referred to this species. A fifth upper tooth, M 46441, is of questionable affinities because of its asymmetry. Ten teeth are identified as representatives of the Gobiconodontidae, of which four upper molars form the basis for *Gobiconodon bathoniensis*, a new species closely resembling *G. palaios*, from the Early Cretaceous of Morocco. Three lower molars and three possible upper premolars are referred to the family. By contrast, the Triconodontidae are represented by only a single specimen of the new genus and species *Eotriconodon sophron*.

As previously mentioned (Sigogneau-Russell 2003c), the Kirtlington mammalian fauna does not show close faunal links with the sympatric younger (earliest Cretaceous) Purbeck mammalian fauna. Thus Triconodontidae are rare in Kirtlington and gobiconodontids are absent in Purbeck. The difference could be ecological, though the two assemblages are considered to have accumulated in lacustrine environments. On the other hand, both areas are likely to have had terrestrial links during the Late Jurassic. It is true that the presence, in Kirtlington, of a shuotheriid genus known also in China (Sigogneau-Russell 1998), and the occurence of strikingly similar volaticotheriine "triconodonts" in Argentina, Morocco, and China (Meng *et al.* 2006; Gaetano and Rougier 2011) suggest that we very poorly master the faunal peregrinations in these ancient times. Indeed, much remains to be discovered or explained concerning early mammalian evolution, and ever-hopeful cladists should consider exploring both the field and long-unopened drawers.

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NEW TRIBOSPHENIC MAMMALS FROM THE MUSSENTUCHIT LOCAL FAUNA (CEDAR MOUNTAIN FORMATION, CENOMANIAN), UTAH, USA

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Herein we describe two new tribosphenic mammals from the Cedar Mountain Formation of Emery County, Utah, USA. The fossils occur in a narrow stratigraphic interval near the top of the unit (Mussentuchit Member) and date to approximately the Early–Late Cretaceous boundary (early Cenomanian, ~97 Mya). The specimens were recovered from screen-washing bulk rock samples. Both taxa are based on isolated teeth; from the limited morphology represented, both lack obvious specializations of the two major therian groups, Metatheria and Eutheria, and for present purposes they are regarded as basal tribosphenidans. *Dakotadens pertritus* sp. n. is the more abundant of the two and is closely related to a previously known species from the overlying (upper Cenomanian) Naturita Formation. *Culicolestes kielanae* gen. et sp. n. is notable in its large size (similar to *Pariadens mckennai* from the same fauna) relative to most other pre-Campanian tribosphenidans. The mammals of the Mussentuchit Local Fauna, now fully described on the basis of available fossils, represent one of the most diverse assemblages known from the Mesozoic, including some 22 taxa. Tribosphenidans, however, are neither abundant nor diverse, and include only six recognized species; most Late Cretaceous assemblages of North America include twice as many. Four of these are marsupialiforms and the remaining two, described herein, are considered basal tribosphenidans. Both eutherians and deltatheroidans, known from earlier and later faunas on the continent, are lacking. Triconodontids (Eutriconodonta) and spalacotheriids (basal Trechnotheria) make up nearly a third of mammalian diversity in the Mussentuchit Local Fauna, and account for about 40% of mammalian fossils identified to species level. Spalacotheriids (four taxa) are particularly abundant relative to both older (Albian) and younger (late Cenomanian onward) assemblages, suggesting some taphonomic or paleoecologic bias.

Key words: Cretaceous, Mammalia, Tribosphenida, Cedar Mountain Formation.

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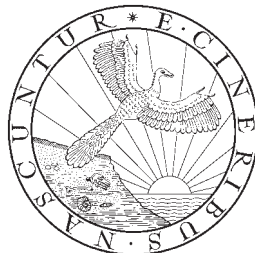
INTRODUCTION

The record of Cretaceous mammals in North America, long notorious for its patchiness and extended hiatuses (*e.g.*, Clemens *et al.* 1979), has improved substantially in recent decades (Kielan-Jaworowska *et al.* 2004). Notably, sampling from the Albian has increased (see Davis and Cifelli 2011; Cifelli and Davis 2015, and references therein), and the early part of the Late Cretaceous (late Cenomanian–Santonian) is now represented by several assemblages from southern Utah (see Eaton 1993, 1995, 2013 and references therein). Lying in between and approximating the Lower–Upper Cretaceous boundary, the uppermost unit (Mussentuchit Member of Kirkland *et al.* 1997) of the Cedar Mountain Formation has yielded a diverse suite of vertebrates, the Mussentuchit Local Fauna (Cifelli *et al.* 1999). The fauna is notable in that it includes a number of elements characteristic of later Cretaceous assemblages, together with surviving members of archaic clades (Cifelli *et al.* 1997). Mammals, for example, include such early-appearing clades as plagiaulacidan multituberculates, spalacotheriid "symmetrodonts", and triconodontids, as well as cimolodontan multituberculates and some of the earliest representatives of Marsupialiformes, which dominate Campanian–Maastrichtian assemblages of North America (Eaton and Nelson 1991; Eaton 1993; Cifelli and Madsen 1998, 1999; Eaton and Cifelli 2001; Cifelli 2004).

Herein we describe two new tribosphenidans from the Mussentuchit Local Fauna, completing the mammalian assemblage as based on available fossils. Though they are represented by fragmentary remains (isolated teeth, often incomplete) and are of uncertain affinities, the new tribosphenidans increase known taxonomic and morphologic diversity of the mammalian assemblage from the Mussentuchit Local Fauna, and prompt comparisons with earlier and later faunas.

Institutional abbreviations. — MNA, Museum of Northern Arizona, Flagstaff, Arizona, USA; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA; UALVP, University of Alberta Laboratory of Paleontology, Edmonton, Alberta, Canada; URBAC, Uzbek/Russian/British/American/Canadian Joint Palaeontological Expeditions (currently housed at San Diego State University, San Diego, California, USA).

METHODS, TERMINOLOGY, AND CONVENTIONS

All specimens described herein were obtained through underwater screen-washing and associated fossil recovery techniques (Cifelli *et al.* 1996). Scanning electron micrographs of specimen casts were obtained at the OMNH using a Denton Vacuum Desk II sputter coater (Denton Vacuum LLC, 1259 North Church Street Building 3, Moorestown, New Jersey 08057, USA) and a LEO 1450VP SEM (Carl Zeiss NTS LLC, One Corporation Way, Peabody, Massachusetts 01960, USA). Tooth measurements (all in millimeters) were taken with a Reflex Microscope (see MacLarnon 1989, Consultantnet Ltd, 94 High Street, Linton, Cambridge, CB21 4JT, UK), as defined by Lillegraven and McKenna (1986). Dental terminology (Fig. 1) mainly follows Kielan-Jaworowska *et al.* (2004, p. 412, fig. 11.1); where necessary, we provide references illustrating other
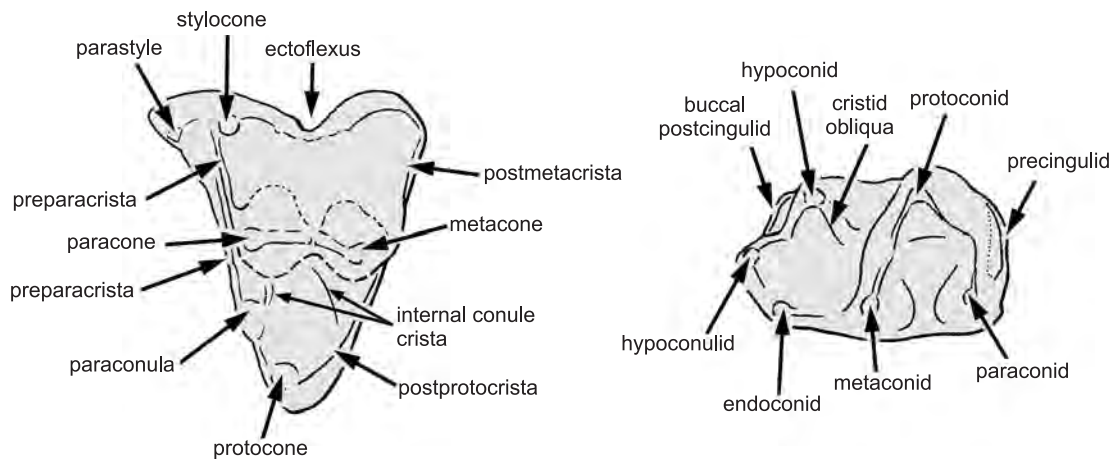
Fig. 1. Terminology for mammalian molars, based on the marsupialiform *Kokopellia juddi* (from Cifelli 2004).

structures and introduce new terms in the text. Unless otherwise specified, our implicitly comparative descriptions refer to basal tribosphenidan morphology, as approximated by taxa such as *Aegialodon* (Kermack *et al.* 1965), *Kielantherium* (Dashzeveg and Kielan-Jaworowska 1984; Lopatin and Averianov 2006), *Kermackia* (Slaughter 1971), and *Potamotelses* (Fox 1972).

We recognize Tribosphenida (McKenna 1975; = Boreosphenida of Luo *et al.* 2001; see Rougier *et al.* 2007; Davis 2011a) in a restricted sense, and exclude australosphenidans, which may have independently evolved a similar molar pattern (Luo *et al.* 2001, 2002; Martin and Rauhut 2005; Luo 2007; Davis 2011b). The taxa described herein join a growing roster of Cretaceous mammals having tribosphenic molars (sensu Simpson 1936) but lacking obvious apomorphies of living therian groups. Bryan Patterson, first to recognize this primitive structural grade, coined the accurate (but long-winded) moniker "therian mammals of uncertain infraclass affinities but of metatherian-eutherian grade" (Patterson 1956, p. 13) to describe them. Later, Butler (1978) formally placed then-known taxa in the Tribotheria, a paraphyletic assemblage. Though he later abandoned the name (Butler 1990), the term "tribothere" has survived (*e.g.*, Sigogneau-Russell 1995; Kielan-Jaworowska *et al.* 2004). In order to avoid unwanted taxonomic implications, we refer to these taxa as basal tribosphenidans. Within Tribosphenida, we follow Vullo *et al.* (2009) in recognizing Marsupialiformes as a stem-based group including fossil taxa more closely related to crown Marsupialia than to Deltatheroida. With reference to other mammals of the Mussentuchit Local Fauna, we follow Gaetano and Rougier (2011) in restricting Eutriconodonta Kermack *et al.*, 1973 to taxa more closely related to *Triconodon* than to Cladotheria McKenna, 1975; and we refer to spalacotheriid "symmetrodonts" as basal trechnotherians (*e.g.*, Li and Luo 2006).

Our original descriptions and formal proposal of new scientific names, below, constitute nomenclatorial acts governed by the International Commission on Zoological Nomenclature (ICZN) Code of Nomenclature. Accordingly, we have registered this paper and contained nomenclatorial acts in ZooBank, the official registry designated by ICZN. The identifiers for the publication and taxa carry a "LSID" prefix and appear following the citation for this paper (above) and each new name (below), respectively. ZooBank can be accessed at http://zoobank.org/.

Measurement abbreviations. — ANW, anterior (mesial) width (trigonid width of lower molars); AP, anteroposterior (mesiodistal) length; POW, posterior (distal) width (talonid width of lower molars).

GEOLOGIC SETTING AND AGE

Specimens described herein were collected in the course of a long-term, large-scale microvertebrate collecting program in the Cedar Mountain Formation between 1990 and 2002. The fossils were recovered from OMNH localities V213, V234, V235, V239, V240, V695, V794, and V868 (Fig. 2). Stratigraphic positions for the sites are given in Cifelli *et al.* (1999). All are on public lands administered by the US Bureau of Land
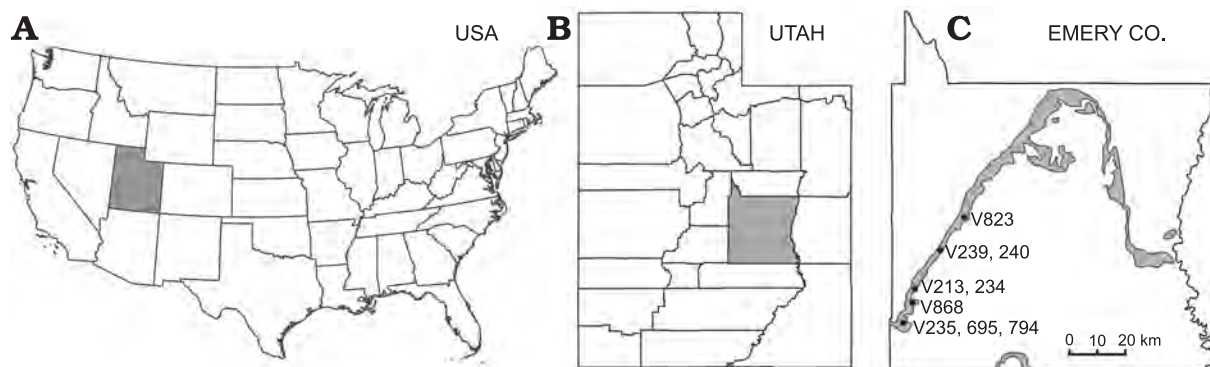
Fig. 2. Study area in Emery County, Utah, USA, showing outcrop of the Cedar Mountain Formation and approximate positions of fossil localities. Maps of USA (**A**) and Utah with counties (**B**) from FreeVectorMaps.com; outcrop belt and locality positions (**C**) after Cifelli *et al.* (1999).

Management, which also manages locality data associated with the fossils. The sites, which include representation of several different depositional facies (Goldberg 2000), are closely spaced geographically and lie in a restricted stratigraphic interval near the top of the Cedar Mountain Formation. Multiple, concordant radiometric dates indicate that the Mussentuchit Local Fauna dates to about 97 Mya (Cifelli *et al.* 1997; Cifelli *et al.* 1999; see also Garrison *et al.* 2007) and is of early Cenomanian age, close to the Albian–Cenomanian (Early–Late Cretaceous) boundary, which is currently placed at 100.5 Mya (Gradstein *et al.* 2012; Cohen *et al.* 2013).

SYSTEMATIC PALEONTOLOGY

Mammalia Linnaeus, 1758

Tribosphenida McKenna, 1975

Family incertae sedis

Genus **Dakotadens** Eaton, 1993

Type species: *Dakotadens morrowi* Eaton, 1993.

Referred species. — The type, and *Dakotadens pertritus* sp. n.

Distribution. — Cenomanian, Utah.

Dakotadens pertritus sp. n.

(Figs 3, 4, Table 1)

LSID urn:lsid:zoobank.org:act:879DE202-E0DA-4D75-BB50-5F2772A86C86

Holotype: OMNH 33247, left upper molar lacking the protocone.

Etymology: *Pertritus*, Latin, very worn, in allusion to the heavy occlusal and apical wear that characterizes known molars of the species.

Type locality: OMNH locality V695, Emery County, Utah, USA.

Type horizon: Mussentuchit Member, Cedar Mountain Formation (97.0 ± 0.1 Ma, Cifelli *et al.* 1999; see Garrison *et al.* 2007).

Referred material. — OMNH 25617 (OMNH locality V235), distobuccal corner of left Mx; 27641 (OMNH locality V794), left Mx lacking mesiobuccal corner; 25813 (OMNH locality V239), left last upper

Table 1. Dental measurements (in mm) of *Dakotadens pertritus* sp. n. (*, holotype).

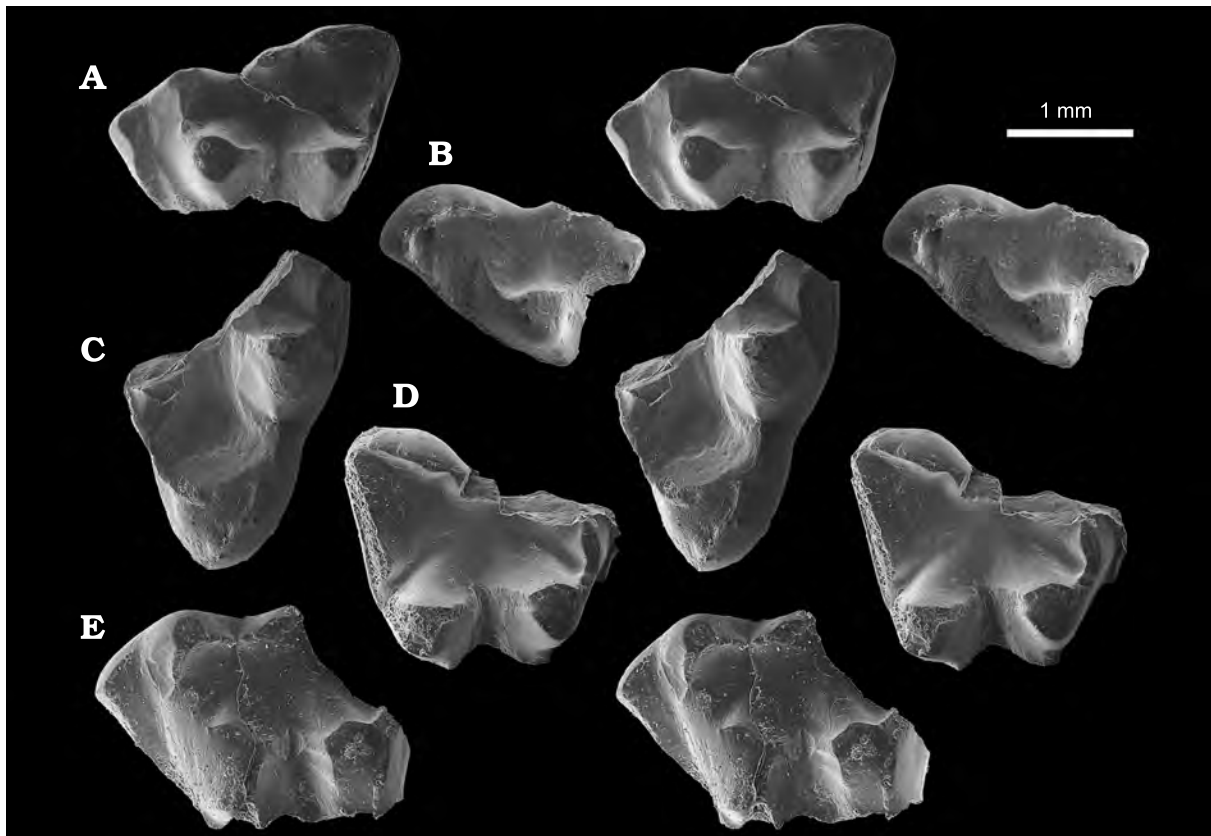| Specimen	Tooth	AP	ANW	POW
OMNH 33247*	Mx	2.42	–	–
OMNH 25798	mx	2.4	1.41	1.29
OMNH 27544	m1	2.54	1.22	1.17
OMNH 33997	m1?	–	1.28	–
OMNH 30588	mx	–	–	1.38
OMNH 24148	mx	–	–	1.4
OMNH 25803	mx	–	–	1.26

Fig. 3. *Dakotadens pertritus* sp. n., upper molars. All specimens are from the Mussentuchit Member, Cedar Mountain Formation (Cenomanian), Emery County, Utah, USA. **A**. OMNH 33247 (holotype), OMNH locality V695, LMx lacking the protocone in occlusal stereopair. **B**. OMNH 25813, OMNH locality V239, left last upper molar lacking the protocone in occlusal stereopair. **C**. OMNH 27641, OMNH locality V794, LMx lacking the mesiobuccal corner in occlusal stereopair. **D**. OMNH 27640, OMNH locality V794, RMx lacking the protocone and mesiobuccal corner in occlusal stereopair. **E**. OMNH 27644, OMNH locality V794, LMx lacking the protocone and distobuccal corner in occlusal stereopair.

molar lacking the protocone; 27640 (OMNH locality V794), right Mx lacking the protocone and mesiobuccal corner; 27509 (OMNH locality V695), mesiobuccal corner of right Mx; 27644 (OMNH locality V794), left Mx lacking the protocone and distobuccal corner; 26731 (OMNH locality V695), fragment of Mx; OMNH 25798 (OMNH locality V239), left ?last lower molar; 27544 (OMNH locality V695), left m1; 33998 (OMNH locality V794), talonid of right mx; 25627 (OMNH locality V234), talonid of left mx; 33997 (OMNH locality V794), trigonid of right m1?; 30588 (OMNH locality V794), talonid of right mx; 24148 (OMNH locality V213), talonid of right mx; 25803 (OMNH locality V239), talonid of right mx.

Diagnosis. — Similar to *D. morrowi*, but smaller with higher molar crowns. The paracone and metacone are closer together than in *D. morrowi*, with the centrocrista V-shaped in buccal view; protocone mesiodistally shorter. The stylocone is the largest stylar cusp when present (lacking on the last upper molar); differs from *D. morrowi* in that cusps in the C and D positions are less developed. The postmetacrista has a distinct notch at the base of the metacone; this notch is poorly developed or lacking in *D. morrowi*. Lower molars have a greater talonid/trigonid height differential, with relatively narrower talonid, and the protoconid is significantly taller than the metaconid and paraconid; cusp f is less developed, not forming a strong precingulid as seen in *D. morrowi*. All cusps of upper and lower molars show a distinctive pattern of heavy apical and occlusal wear.

Description. — Upper molars (Fig. 3) generally have short, robust cusps with heavy apical and occlusal wear. The paracone and metacone are subequal in height; the former cusp is slightly more voluminous and more heavily worn, suggesting that it may have been slightly taller than the metacone when unworn. The paracone is wider than the metacone, both mesiodistally and buccolingually. The metacone is more angular (*i.e.*, it has a pyramidal appearance, with planar faces, in occlusal view) than the paracone, which is more rounded and bulbous; both cusps have well-defined keels on their lingual faces, owing to wear. The
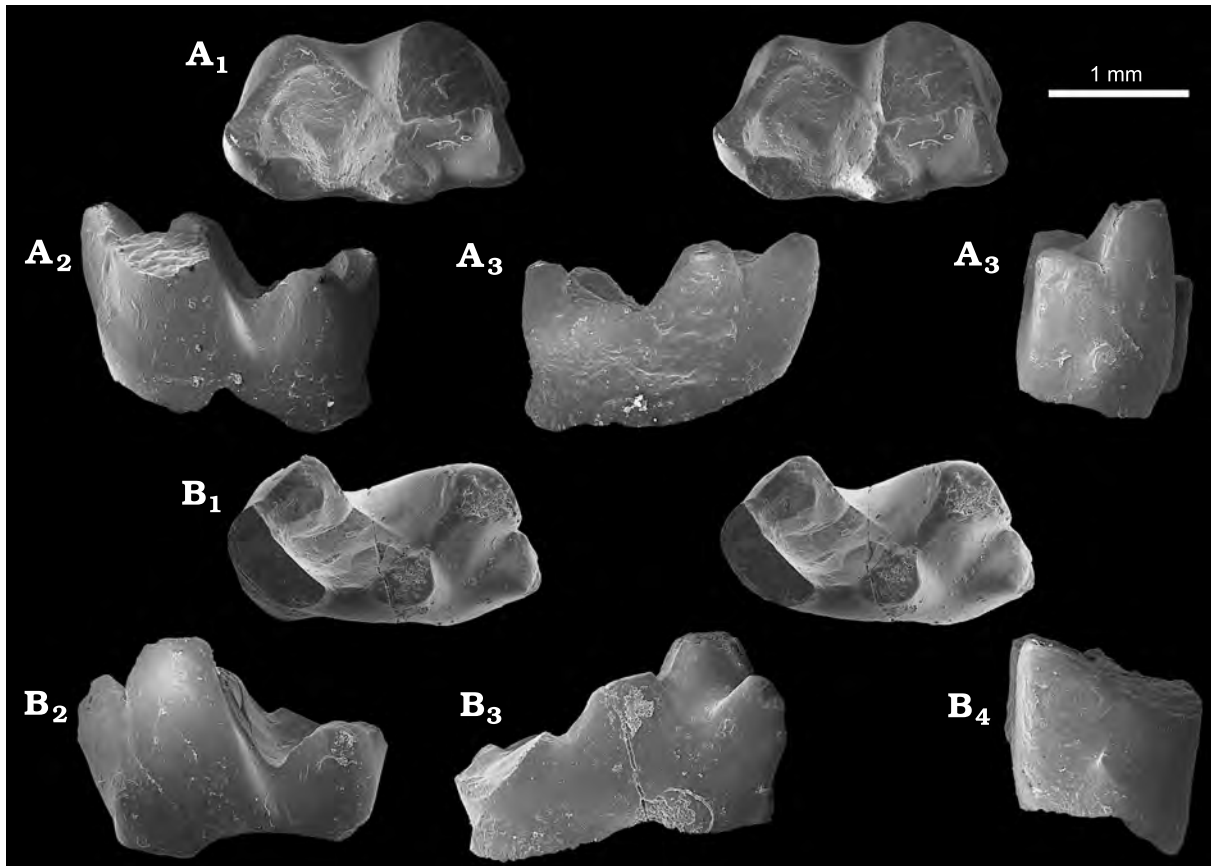
Fig. 4. *Dakotadens pertritus* sp. n., lower molars. All specimens are from the Mussentuchit Member, Cedar Mountain Formation (Cenomanian), Emery County, Utah, USA. **A**. OMNH 25798, OMNH locality V239, Lmx in occlusal stereopair (A_1), buccal (A_2), lingual (A_3), and mesial (A_4), views. **B**. OMNH 27544, OMNH locality V695, Lm1 in occlusal stereopair (B_1), buccal (B_2), lingual (B_3), and mesial (B_4) views.

paracone and metacone have separate bases and are slightly inclined mesially and distally, respectively; the centrocrista (crest joining the apices of paracone and metacone; Davis 2007, p. 219, fig. 2A) shows light wear. A stylocone is present directly buccal to the paracone except for the last upper molar (OMNH 25813, Fig. 3B), which bears instead a series of cuspules in the position of the stylocone. The stylocone is inflated and bulbous, with heavy apical wear; it is connected to the paracone by a preparacrista that bears a weak notch. In OMNH 25813, the preparacrista fades out and terminates halfway between the paracone and parastyle. A parastyle is present directly mesial to the stylocone position (the photos shown in Fig. 3B are rotated counterclockwise from anatomical position, such that the parastyle appears to lie lingual to the stylocone), and is lingually connected to a mesial cingulum, which is presumably the buccal extension of the preprotocrista. The parastylar lobe of the stylar shelf is about half the width of the metastylar lobe. A weak ectoflexus is developed distal to the stylocone and mesial to stylar cusp C. Stylar cusps C and D (Clemens 1979, p. 200, fig. 11-1) are present but are variable in their development. Stylar cusp C is distal to the deepest point of the ectoflexus, and cusp D is directly buccal to the metacone. Both stylar cusps C and D are situated along the buccal edge of the stylar shelf. Stylar cusps C and D are small but distinct, roughly equivalent in size, bulbous, and joined by a faint ridge in OMNH 33247 (Fig. 3A); they appear to be similar but slightly weaker on OMNH 27640 (Fig. 3D; cusp C is broken on this specimen). As with all the cusps, stylar cusps C and D tend to show apical wear, despite the fact that they do not directly occlude with opposing structures on the lower molars (see discussion in Clemens 1979). The postmetacrista is notched at its junction with the metacone. This notch extends buccomesially across the stylar shelf, giving the metastylar region the appearance of a pennant extending backward and outward from the mesial part of the stylar shelf.

OMNH 27641 (Fig. 3C), a left upper molar lacking the paracone and most of the stylar shelf, is noteworthy because it preserves the protoconal region. The protocone is rounded lingually and has a steep buccal surface, forming the lingual face of a deep trigon basin. No metaconule per se is present, although there is a faint notch

where the postprotocrista terminates at the metacone. A somewhat better though still questionable case can be made for the presence of a paraconule, represented by a swelling and buccally-extending keels lingual to the paracone. Much of the damage to the tooth crown evidently occurred postmortem, though it is clear that occlusal wear is present. Notably, the presence of a deep and extensive facet on the postmetacrista suggests strong reliance on postvallum-prevallid shear (supported also by the length and development of the post-metacrista on OMNH 27640, Fig. 3D). The protocone of OMNH 27641 differs from those on non-ultimate molars referred to *D. morrowi* (Eaton 1993, p. 108, fig. 4A, B, D, E) in being shorter mesiodistally.

Lower molars, like the uppers, are characterized by short, robust cusps and typically show heavy apical wear. The trigonid/talonid height differential exceeds that of *D. morrowi* but is less than in comparable taxa such as *Kielantherium*, and the talonid is broad, being subequal to the trigonid in width. The paraconid and metaconid are most broadly separated and weakest on OMNH 27544 (Fig. 4B), suggesting that it is a first molar. The trigonid is more mesiodistally compressed on OMNH 25798 (Fig. 4A). The paraconid is not lingually displaced, as is typically the case for Late Cretaceous marsupials (Clemens 1979), nor is it appressed to the metaconid, as often occurs among early eutherians (*e.g.*, Kielan-Jaworowska *et al.* 1979, 2004). The paraconid and metaconid are subequal in height and volume, though the metaconid is more severely worn in available specimens. The cristid obliqua originates below the notch in the protocristid (the crest connecting protoconid and metaconid; Kielan-Jaworowska *et al.* 2004, p. 412, fig. 11.1B), and a distal metacristid (Fox 1975, p. 424, fig. 4) is lacking. The talonid basin is bowl-like and deep. The hypoconulid differs in development, orientation and placement, as a result of either individual or positional variation. In some cases (*e.g.*, OMNH 25798) it appears to be slightly displaced lingually; in others (*e.g.*, OMNH 30588) it is more centrally placed. No buccal postcingulid is present. Near the mesial base of the crown, cusp f is variable in its development, either as a small knob (OMNH 27544) or as a ridge that extends buccally along the base of the protoconid (OMNH 25798).

Comments. — Although nowhere abundant, *Dakotadens pertritus* is among the more cosmopolitan of species from the upper Cedar Mountain Formation, being known from six different sites (see discussion in Goldberg 2000). Its molars are notable in the robust construction of cusps and strong apical wear, suggesting a divergence in diet from most other early tribosphenidans.

In addition to the hypodigm of *D. morrowi*, Eaton (1993) mentioned two additional upper molars referable to the genus, as *Dakotadens* sp. We identify both of these as ultimate molars. Neither is surely conspecific with MNA V6318, the ultimate upper molar Eaton (1993, p. 108, fig. 4G) referred to *D. morrowi*: MNA V6025 (Eaton 1993, p. 108, fig. 4O) apparently has a much smaller parastylar region (that of MNA V6318 is broken) and a more rounded protocone; while MNA V5345 (Eaton 1993, p. 108, fig. 4N) is considerably larger, with a more mesiodistally expanded protocone. The only one of these to preserve the mesiobuccal part of the crown more-or-less intact is MNA V6025, in which the parastyle is much shorter than that of OMNH 25813, described above as a partial ultimate upper molar of *D. pertritus*. MNA V5345 appears to be too large to belong to *D. pertritus*; MNA V6318 and OMNH 25318 (ultimate upper molars referred to *D. morrowi* and *D. pertritus*, respectively) are comparable, but known parts do not overlap sufficiently for comparison. We provisionally agree with Eaton (1993) that at least two (and perhaps three) species of *Dakotadens* (or close relative[s]) are present in the Naturita Formation (previously considered to be the Dakota Formation; see Young 1960; Carpenter 2014).

Genus *Culicolestes* gen. n.

LSID urn:lsid:zoobank.org:act:00D3168A-523D-40FC-A92A-9FBEF4B948E1

Type species: *Culicolestes kielanae* sp. n., monotypic.

Etymology: Culico- (*culex*, Latin, gnat or midge), for species of *Culicoides* (commonly called "cedar gnats"), the unforgettable companions to field parties working in the study area during mid-May–early-July; and -lestes (Greek, meaning robber or plunderer, a commonly-used suffix for genera of small predatory mammals).

Distribution. — As for the type and only species.

Diagnosis. — As for the type and only species.

Culicolestes kielanae gen. et sp. n.

(Fig. 5)

LSID urn:lsid:zoobank.org:act:4FF5387E-2377-4E1B-BD21-CDF580FD01F0

Holotype: OMNH 25809, left upper molar missing the distal stylar shelf and some cusp apices.
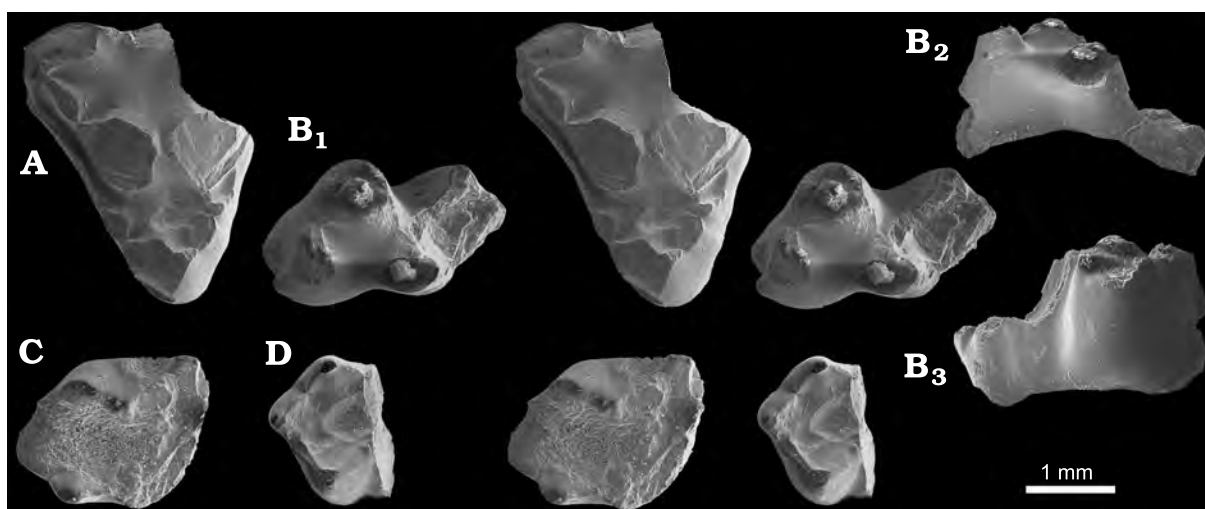
Fig. 5. *Culicolestes kielanae* gen. et sp. n. All specimens are from the Mussentuchit Member, Cedar Mountain Formation (Cenomanian), Emery County, Utah, USA. **A**. OMNH 25809 (holotype), OMNH locality V239, LMx missing distal stylar shelf and cusp apices in occlusal stereopair. **B**. OMNH 26727, OMNH locality V695, Rmx missing lingual part of talonid in occlusal stereopair (B_1), lingual (B_2), and buccal (B_3) views. **C**. OMNH 26441, OMNH locality V235, talonid of Lmx in occlusal stereopair. **D**. OMNH 25625, OMNH locality V234, talonid of Rmx in occlusal stereopair.

Etymology: For the late Zofia Kielan-Jaworowska (1925–2015), in recognition of her contributions to knowledge of Cretaceous mammals.

Type locality: OMNH locality V239, Emery County, Utah, USA.

Type horizon: Mussentuchit Member, Cedar Mountain Formation (97.0 ± 0.1 Ma, Cifelli *et al.* 1999; see Garrison *et al.* 2007).

Referred material. — The type, and OMNH 26727 (OMNH locality V695), right lower molar missing lingual part of the talonid; OMNH 25625 (OMNH locality V234), talonid of right lower molar; and 26441 (OMNH locality V235), talonid of left lower molar.

Tentatively-referred specimens. — OMNH 25830 (OMNH locality V240), talonid of right lower molar; and OMNH 25802 (OMNH locality V239), talonid of left lower molar.

Diagnosis. — Most similar to *Dakotadens* among comparable taxa, differing in: larger size; upper molars with preparacrista extending mesially, toward the parastyle (rather than buccally, toward the stylocone, as in *Dakotadens* and most other basal tribosphenidans); conules and internal cristae more distinct (presumed apomorphies); paracone and metacone share a common base; trigon basin not as deep; stylar shelf wider (mesially, at least). Lower molars are larger than and distinct from those of *Dakotadens* in having a strong, cusp-like f (developed as a narrow ridge in *Dakotadens*), a strong e cusp (weak or absent in *Dakotadens*), and a greater trigonid/talonid height differential.

Description. — The single known upper molar, OMNH 25809 (Fig. 5A) is battered and incomplete: the paracone and metacone are broken off near their bases and the metastylar region is missing. The tooth is distinctive in the fauna by virtue of its large size (ANW = 3.71) and robust construction. The mesial part of the stylar shelf, at least, is broad, suggesting that the specimen represents a tooth in the middle of the molar series. The bases of the paracone and metacone are well joined, and judging from the bases, the cusps may have been subequal. The preparacrista is deeply notched near the base of the paracone and again at its mesiobuccal termination, mesial to the stylocone and nearly at the mesiobuccal corner of the tooth, which is broken (the development of a parastyle is uncertain). Judged by its base, the stylocone was robust and developed mesiodistally; it forms a noticeable bulge on the buccal side of the crown. The ectoflexus appears to have been shallow. The inflection of enamel in the ectoflexus suggests that a low cusp was likely present in the C position. The protocone is small (both mesiodistally and buccolingually) relative to the condition generally seen in Late Cretaceous marsupialiforms (Clemens 1979; Kielan-Jaworowska *et al.* 2004). The preprotocrista extends mesiobuccally past the base of the paracone and terminates at the broken mesiobuccal corner of the tooth. The extent of the postprotocrista is uncertain owing to breakage, but it appears to have terminated near the break, approximately in mesiodistal alignment with the paracone and metacone. Both paraconule and metaconule are present near the bases of paracone and metacone, respectively; the specimen is worn but internal conular cristae can be distinguished. The trigon basin is well marked but not as deep as in *Dakotadens*.

Lower molars are referred to *Culicolestes kielanae* on the basis of size, similar construction (robust cusps) to the upper molar, and morphological appropriateness (small protocone on upper molars with corresponding open trigonid and narrow, small talonid on lowers). The most complete specimen, OMNH 26727 (ANW = 1.71; Fig. 5B), preserves most of the crown except the lingual part of the talonid; major cusp apices are broken. The trigonid is open lingually, with the paraconid placed well mesial to (and distinct from) the metaconid. No determination can be made as to the relative height of paraconid and metaconid. The paraconid is slightly buccal to the metaconid. Its mesiolingual face forms a keel that terminates in a pronounced cusp e, which in turn overlies a concavity that presumably fit with the hypoconulid of the preceding tooth. Buccally, a prominent cusp f is present adjacent to the concavity and below the level of cusp e (cusps e [mesiolingual] and f [mesiobuccal] are variably-developed, basal cuspules on lower molars of early mammals and close relatives; see Crompton and Jenkins 1968, p. 432, fig. 2B, C).

The distal wall of the trigonid bears a distal metacristid that is continuous with the cristid obliqua. The talonid appears to have been somewhat narrower than the trigonid (as also seen in OMNH 26441; Fig. 5C), and the trigonid was elevated well above the level of the talonid.

Comments. — *Culicolestes kielanae*, known only by a few fragmentary teeth, is notable in its large size, in this respect rivaling *Pariadens mckennai* (also poorly known), the largest marsupialiform in the Mussentuchit Local Fauna (Cifelli 2004). The species are otherwise dissimilar: lower molar cusps of *C. kielanae* are low, rounded, and rapidly reduced by apical and occlusal wear; those of *P. mckennai* are tall, sharp, and support well-developed shearing crests. *P. mckennai* further differs in its greater height of the paraconid and metaconid; better-differentiated, taller talonid cusps; and (as in other marsupialiforms) the presence of a buccal postcingulid. Upper molars of *P. mckennai* are not known, but those of closely-related *P. kirklandi* from the Naturita Formation (Eaton 1993, p. 119, fig. 8A–D) differ from *Culicolestes* in having a much larger (buccolingually and mesiodistally) protocone and in having well separated paracone and metacone (bases of the two cusps are united in *Culicolestes*).

<div align="center">

Gen. et sp. indet.

(Fig. 6)

</div>

Included specimens. — Upper molariforms and parts thereof: OMNH 26449, protocone (OMNH locality V235); OMNH 26729, buccal portion of tooth, preserving paracone and metacone, and the metastylar lobe (OMNH locality V695); OMNH 30532, also buccal part of a tooth crown with paracone, metacone, and metastylar lobe (original fossil lost in quarrying; specimen preserved as a natural mold and casts made from that mold; OMNH locality V695); OMNH 33238, complete except for metacone (OMNH locality V695); and OMNH 33052, in which paracone and metacone are broken at their bases and the distal stylar shelf is missing.

Description. — These specimens vary in size and morphology and probably represent multiple taxa. They are described together because we are uncertain as to their identity and because they share fundamental points of similarity: the protocone is small, the mesial part of the stylar shelf is developed as a crest or cingulum only, and the stylocone is lacking or, when present, is placed mesial (rather than buccal) to the paracone.

OMNH 33238 (Fig. 6A) is the most complete of these teeth. The metacone is broken, but judging from the size of the base, the paracone was clearly much larger than the metacone. Their cusp bases are well joined, forming a united mound in the center of the crown. The paracone is conical and virtually unworn, save for minor apical wear, with a keel present only on the distal face (postparacrista; a preparacrista is absent). A small parastyle is developed mesial to the paracone. No stylocone is present; a faint cingulum runs along the buccal wall of the paracone, and is developed into a minute cuspule at the distobuccal base of that cusp. Distally, the stylar shelf is broad, with a well-developed metastylar region. The postmetacrista is oriented distobuccally at an angle less than 135° (from a horizontal passing through the approximated positions of the apices of paracone and metacone) and is incompletely preserved, but it was notched near its junction with the metacone; distobuccal to this, a faint swelling is present near the metastylar angle of the crown. The protocone is remarkable for its weak development, both mesiodistally and buccolingually. It forms a salient point, with its buccal face being virtually planar (a trigon basin as such is not developed) and sloping deeply toward the bases of the paracone and metacone. A very faint bulge hints at the presence of a paraconule, but the metaconule is absent and the protoconal cristae end at the bases of the paracone and metacone.

OMNH 26729 (Fig. 6B) is similar but smaller. Although it is less complete than OMNH 33238, it adds some morphological details. The metacone is significantly shorter than the paracone and the postmetacrista
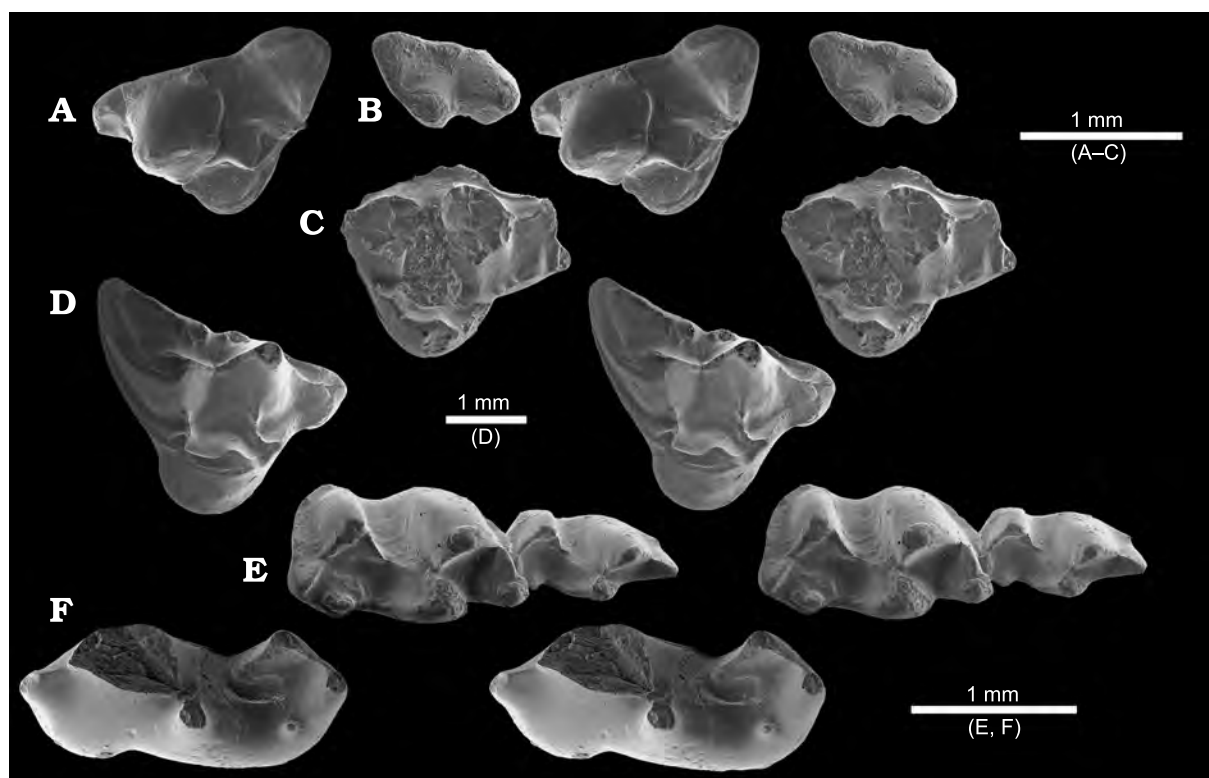
Fig. 6. Theria incertae sedis (**A**, **B**), and Marsupialiformes (**C–F**). **A–C** and **F** are from the Mussentuchit Member, Cedar Mountain Formation (Cenomanian), Emery County, Utah, USA; units and localities for D–E are listed below. **A**. OMNH 33238, OMNH locality V695, left upper molariform, occlusal stereopair. **B**. OMNH 26729, OMNH locality V695, right upper molariform fragment, missing protocone and mesial stylar shelf, occlusal stereopair. **C**. cf. *Sinbadelphys schmidti*, OMNH 33082, OMNH locality V868, right DP3, occlusal stereopair. **D**. *Protolambda florencae*, OMNH 68824, OMNH locality V1209, Hell Creek Formation (Maastrichtian), Carter County, Montana, USA, right dP3, occlusal stereopair. **E**. *Alphadon eatoni*, OMNH 27380, OMNH locality V798, North Horn Formation (Maastrichtian), Emery County, Utah, USA, left dp3–m1, occlusal stereopair. **F**. cf. *Kokopellia juddi*, OMNH 33972, OMNH locality V868, right dp3, occlusal stereopair.

is oriented somewhat more buccally than is the case in OMNH 33238. Light apical wear is present on both paracone and metacone; occlusal wear is evident on the postmetacrista and centrocrista, but the enamel is lightly frosted and occlusal wear cannot be definitively established elsewhere. A faint rim is present along the buccal margin of the stylar shelf in the metastylar region; as with OMNH 33238, a weak cuspule is present distobuccal to the base of the paracone.

Comments. — The striking features of these specimens (paracone much larger than metacone, small protocone, conules weak or lacking, mesial stylar shelf and stylocone lacking) are reminiscent of *Picopsis*, described by Fox (1980), and *Tirotherium*, described by Montellano-Ballesteros and Fox (2015), both from the Santonian Milk River Formation of southern Alberta. A similar specimen is also described by Davis *et al.* (2016, this volume) from the coeval Eagle Formation of northern Montana, and we offer complementary comments here. (In the text that follows, we collectively refer to these upper molariforms as "*Picopsis*-like".) Yet in these same features, these fossils resemble deciduous premolars, in particular, DP3 of metatherians. Fox (1980) made point-by-point comparisons between the holotype upper molariform of *Picopsis pattersoni* Fox, 1980 (UALVP 15100) and DP3 of marsupials, regarding the former as distinct and as representing a permanent molar. Like the upper molariforms of *Picopsis* and *Tirotherium*, the specimens described under this heading do show some differences when compared with DP3 of "typical" Late Cretaceous marsupialiforms such as *Protolambda florencae* (Clemens, 1966) (Fig. 6D; see Clemens 1966 for illustrations of other taxa). For example, in *P. florencae*, the protocone is relatively larger and the protoconal cingula extend past the metacone and paracone, respectively; conules and internal conular cristae are present; the paracone and metacone are more nearly equal in size; the postmetacrista is oriented distobuccally; and a crest descends along the mesial face of the paracone, terminating at the parastyle. On this basis, we recognize at least one marsupialiform DP3, OMNH 33082 (perhaps belonging to *Sinbadelphys schmidti* Cifelli, 2004), from the

Mussentuchit Member of the Cedar Mountain Formation (Fig. 6C). Yet this does not prove, nor even suggest by default, that the specimens described under this heading, as well as upper molariforms referred to *Picopsis* and *Tirotherium*, are permanent teeth (molars). Knowledge of deciduous teeth belonging to early marsupialiforms and basal tribosphenidans is poor; among other metatherians, DP3 of the deltatheroidan *Sulestes karakshi* Nessov, 1985 (URBAC 04-149, Averianov *et al.* 2010, p. 307, fig. 2C, D), at least, departs from the pattern typical of North American marsupialiforms. More broadly, great morphological disparity among deciduous teeth of Cretaceous tribosphenidans is suggested by *Slaughteria eruptens*, regardless of how many deciduous teeth the holotype contains (contrast Winkler *et al.* 2011 with Davis 2011a). Based on their size, the upper molariforms referred to *Tirotherium aptum* Montellano-Ballesteros *et* Fox, 2015 are reasonably interpreted as DP3 of the two species of *Aquiladelphis* from the same fauna (Fox 1971; Davis 2007).

The principal concern with recognition of *Picopsis*-like teeth as representing upper molars is that, in our opinion, there are no plausible lower molars (which tend to be much more abundant than uppers in fossil assemblages) from any of the assemblages in which the uppers have been found. In our view, the trigonid ascribed to *Picopsis pattersoni* (UALVP 15101, Fox 1980, p. 1491, fig. 1F–J) and the lower molariforms referred to *Tirotherium aptum* (UALVP 29423, 29417, 29422, Montellano-Ballesteros and Fox 2015, p. 80, fig. 2) can be readily identified as marsupialiform dp3 by their low, poorly formed, and widely separated paraconid and metaconid; and by the strongly developed talonid, which is broader than the trigonid and which bears three distinct cusps (hypoconid, hypoconulid, and entoconid) enclosing a well-formed talonid basin. An example from the Cedar Mountain Formation is OMNH 33972 (Fig. 6F), which we provisionally refer to *Kokopellia juddi*. In most features, it is similar to dp3 of Late Cretaceous marsupialiforms such as *Alphadon eatoni* (Fig. 6E). If, as Montellano-Ballesteros and Fox (2015) propose, *Picopsis*-like teeth represent upper molars specialized for carnivory, emphasizing postvallum-prevallid shearing (see Muizon and Lange-Badré 1997), then upper molars with a reduced protocone, reduced stylocone, and hypertrophied postmetacrista should co-occur with lowers that have a strongly developed paracristid (the crest connecting paraconid to protoconid; Kielan-Jaworowska *et al.* 2004, p. 412, fig. 11.1B), with a large paraconid (compared to metaconid) and a small, narrow talonid. This is well illustrated by specimens referred to the North American deltatheroidan *Nanocuris improvida* Fox, Scott, and Bryant, 2007 (see Wilson and Riedel 2010). We know of no such lower molars from units in which *Picopsis*-like teeth have been reported.

Summing up, *Picopsis*-like upper molariforms show some differences from known marsupialiform DP3. Yet there remains ambiguity as to whether these molariforms are deciduous or permanent, and that ambiguity will remain until more informative specimens come to light (some alternative affinities, such as molariform eutherian premolars, are explored elsewhere in this volume, Davis *et al.* 2016). We regard the specimens as indeterminate, and we regard the taxa based on them (*Picopsis pattersoni* and *Tirotherium aptum*) as nomina dubia.

DISCUSSION

This paper completes alpha-level systematic treatment of mammals from the Mussentuchit Local Fauna, as based on specimens now in hand (6680 specimens cataloged to date in the OMNH collection, 1586 of which are referable to Mammalia). The mammalian assemblage includes three triconodontids, nine multituberculates, four spalacotheriid trechnotherians, and six tribosphenidans, for a total of 22 recognized taxa (Table 2). Although many species (for example, the two described herein) are poorly known, it is reasonable to conclude that the assemblage is well sampled (also see Goldberg 2000): mammalian diversity exceeds that of virtually all other Mesozoic faunas known. Of those from the Cretaceous of North America, for example, diversity easily eclipses that of the most completely-sampled Judithian assemblages (15–17 species), and rivals the best-known local faunas of Lancian age (23–33 species, data from Kielan-Jaworowska *et al.* 2004). Taxon-by-taxon comparisons to other faunas are limited by the fact that multituberculates, which are dominant elements in Cretaceous faunas of North America (*e.g.*, Clemens and Kielan-Jaworowska 1979; Kielan-Jaworowska *et al.* 2004; Wilson *et al.* 2012), have not yet been fully described from Early Cretaceous (Albian) faunas of the continent. At the genus level, two taxa are shared with Albian assemblages (the triconodontids *Astroconodon* and *Corviconodon*, Cifelli *et al.* 1998; Cifelli and Madsen 1998) and seven (the multituberculates ?*Mesodma*, *Bryceomys*, *Cedaromys*, and cf. *Paracimexomys*; the basal trechnothere

Table 2. Mammals of the Mussentuchit Local Fauna. Unidentified taxa are included where they appear to represent unnamed species.

Eutriconodonta Kermack *et al.*, 1973
   Triconodontidae Marsh, 1887
      Astroconodon delicatus Cifelli *et* Madsen, 1998
      Corviconodon utahensis Cifelli *et* Madsen, 1998
      Jugulator amplissimus Cifelli *et* Madsen, 1998
Multituberculata Cope, 1884
   ?Plagiaulacidae Gill, 1872
      Gen. et sp. indet.
   Neoplagiaulacidae Ameghino, 1890
      ?*Mesodma* sp. Jepsen, 1940
   Family incertae sedis
      Janumys erebos Eaton *et* Cifelli, 2001
      cf. *Paracimexomys perplexus* Eaton *et* Cifelli, 2001
      Dakotamys robisoni (Eaton *et* Nelson, 1991)
      Bryceomys intermedius Eaton *et* Cifelli, 2001
      Cedaromys bestia (Eaton *et* Nelson, 1991)
      Cedaromys parvus Eaton *et* Cifelli, 2001
      Ameribaatar zofiae Eaton *et* Cifelli, 2001
Trechnotheria McKenna, 1975
   Spalacotheriidae Marsh, 1887
      Spalacolestes cretulablatta Cifelli *et* Madsen, 1999
      Spalacolestes inconcinnus Cifelli *et* Madsen, 1999
      Spalacotheridium noblei Cifelli *et* Madsen, 1999
   ?Spalacotheriidae Marsh, 1887
      Gen. et sp. indet.
Tribosphenida McKenna, 1975
   Family incertae sedis
      Dakotadens pertritus sp. n.
      Culicolestes kielanae gen. et sp. n.
Metatheria Huxley, 1880
   ?Stagodontidae Marsh, 1889
      Pariadens mckennai Cifelli, 2004
   Family incertae sedis
      Adelodelphys muizoni Cifelli, 2004
      Kokopellia juddi Cifelli, 1993
      Sinbadelphys schmidti Cifelli, 2004

Spalacotheridium; the basal tribosphenidan *Dakotadens*; and the marsupialiform *Pariadens*) with younger faunas (Cifelli and Madsen 1999; Eaton and Cifelli 2001; Cifelli 2004).

At higher taxonomic levels, tribosphenidans of the Mussentuchit Local Fauna differ from Albian assemblages in being dominated by marsupialiforms. This is consistent with the pattern in younger Cretaceous faunas of North America, although the Mussentuchit assemblage lacks the remarkable morphologic and taxonomic diversity seen among marsupialiforms of the Campanian–Maastrichtian (Cifelli 2004). And, although negative evidence must be interpreted cautiously, it is worth noting that eutherians and deltatheroidans, known from both older and younger faunas in North America (Kielan-Jaworowska *et al.* 2004; Davis and Cifelli 2011; Cifelli and Davis 2015), have not been identified among tribosphenidans of the Mussentuchit Local Fauna. Lastly, molars of the two tribosphenidans described herein, *Dakotadens pertritus* and *Culicolestes kielanae*, as well as previously-described *Pariadens mckennai*, depart from the primitive pattern common among Early Cretaceous taxa (*e.g.*, the "Trinity therians", Davis and Cifelli 2011) in being larger, with more robust construction and more rounded cusps, suggesting exploitation of different food resources. One poorly-known species from the Cloverly Formation, *Argaliatherium robustum*, is similar, suggesting that such diversification had begun by the Albian (Cifelli and Davis 2015). Numerous mammals in this size range (for present purposes, arbitrarily defined as having molars with an AP of ≥ 2.5 mm) and having robust, rounded cusps are encountered among marsupialiforms of Aquilan–Lancian faunas of North America (Kielan-Jaworowska *et al.* 2004).

Given the relatively large numbers of mammalian fossils and species recovered from the upper Cedar

Mountain Formation, tribosphenidans cannot be regarded as either abundant or diverse: the total of six recognized species (which account for only 11% of mammalian fossils identified to species level) is comparable to diversity from the more poorly sampled Albian faunas of North America (five species from the Cloverly Formation, Wyoming and Montana, and eight from the Trinity Group, Texas and Oklahoma, Cifelli and Davis 2015); and is less than typically seen among Late Cretaceous assemblages, such as the Santonian–Campanian Milk River fauna (some 14 species, Kielan-Jaworowska *et al.* 2004). A major factor at play with regard to the Mussentuchit Local Fauna involves archaic groups, the triconodontids (eutriconodontans) and spalacotheriids (basal trechnotheres). These persisted into the Santonian–Campanian, as rare occurrences of one or two species (Fox 1969, 1976; Cifelli and Madsen 1986; Eaton 2013; Eaton and Cifelli 2013). In the Mussentuchit Local Fauna, by contrast, triconodontids and spalacotheriids collectively make up almost a third (seven of 22) of mammalian species, and the spalacotheriids (which are rare in Albian faunas of North America) account for almost 40% of mammalian fossils identified to species level. These differences suggest some taphonomic or paleoecologic bias. Further data, including better sampling of younger (Turonian) faunas (currently under study by JEC) and systematic treatment of North America's Albian multituberculates, will be required to address the issue.

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DINOSAURS OF THE GOBI: FOLLOWING IN THE FOOTSTEPS OF THE POLISH-MONGOLIAN EXPEDITIONS

PHILIP J. CURRIE

The Polish-Mongolian Palaeontological Expeditions collected many partial and complete dinosaur skeletons from the Nemegt Formation of Mongolia between 1964 and 1971. Under the leadership of Zofia Kielan-Jaworowska, the specific localities of fifty of these quarries were recorded on published maps. In recent years, more than half of these quarries have been relocated for the collection of additional data and even missing parts of some specimens. They have been included in a database that contains more than six times the original number of specimens. The larger, more precise database will ultimately be useful for identifying and interpreting the stratigraphic and geographic distributions of specific dinosaur taxa. However, at this stage it only confirms a preservational bias that favors the recovery of specimens of the tyrannosaurid *Tarbosaurus* with greater frequency than any herbivorous dinosaurs.

Key words: Dinosauria, Polish-Mongolian Palaeontological Expeditions, Upper Cretaceous, Nemegt Formation.

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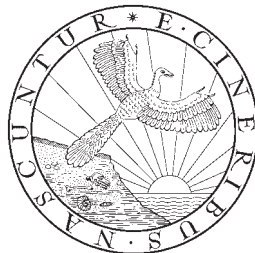
INTRODUCTION

Some of the most famous and influential scientific expeditions were the central Asiatic expeditions (1922–1930) of the American Museum of Natural History (Andrews 1932). Under the leadership of Roy Chapman Andrews, the multidisciplinary team became best known for their palaeontological discoveries, including many important localities in the Gobi Desert of China and Mongolia, and spectacular fossils that included the first recognized dinosaur eggs plus now famous dinosaurs like *Alectrosaurus olseni*, *Oviraptor philoceratops*, *Protoceratops andrewsi*, *Psittacosaurus mongoliensis*, and *Velociraptor mongoliensis*. The expeditions, which ended in 1930, attracted worldwide attention, and inspired a series of large-scale expeditions from the Soviet Union (USSR) in 1946, 1948 and 1949 (Lavas 1993). In addition to collecting at some of the sites discovered by the AMNH expeditions, the Soviet expeditions discovered some spectacular Late Cretaceous sites farther to the West that have produced one of the richest dinosaur faunas known. They called one site the "Dragon's Tomb," and it yielded more than 60 tonnes of articulated dinosaur skeletons, including partially mummified remains of the hadrosaur *Saurolophus*, and skeletons of the tyrannosaur now known as *Tarbosaurus*. The accomplishments of both the American and Russian expeditions in Mongolia became well-known in Soviet Bloc countries in the years following the Second World War. An agreement between the Mongolian and Polish scientific academies put a youthful and energetic Zofia Kielan-Jaworowska in charge of setting up and leading a series of expeditions to the central Asian country (Kielan-Jaworowska 2013). The Polish-Mongolian Paleontological Expeditions (1964–1971) went on to become one of the greatest and most productive expeditions in the history of vertebrate palaeontology. They not only collected some of the best specimens that had been discovered in the Gobi Desert up to that time, but they kept good records of what, when, where, and how they collected specimens. The specimens were quickly prepared and within two years of starting the expeditions, the first scientific papers were released in international, peer-reviewed scientific journals. Their publications, both scientific and popular, were in English, which gave them the broadest audience and the greatest international attention. Although none of the scientists were well-known outside of their limited fields of research expertise in Europe, they quickly became internationally renowned for their work on Cretaceous vertebrates from Mongolia. This is especially true when it came to Zofia Kielan-Jaworowska's research on Cretaceous mammals, the research on Cretaceous dinosaurs by Halszka Osmólska and Teresa Maryańska, the stratigraphic/ sedimentological analyses by Ryszard Gradziński and Tomasz Jerzykiewicz, and the research of virtually everyone who was part of this incredible team of researchers. On the Mongolian side, Rinchen Barsbold also climbed to international fame as a dinosaur researcher. Long after their last expedition in 1971, their work endures through specimens (particularly the holotypes of many species) in Poland and Mongolia, through their pivotal research projects, and through the information they collected in the field. In spite of the fact that the world was not so technologically advanced when the PMPE were underway, they nevertheless established the gold standard for how expeditions should be run. The purpose of this article is to show how their attention to detail has allowed us to return to their dinosaur quarries and collect more data that will help us to better understand the palaeobiology of dinosaurs and the animals that lived with them.

A chance reading of "All About Dinosaurs" (Andrews 1953) was in fact the reason that I decided to become a vertebrate palaeontologist. Andrews, based on his experiences as the leader of the Central Asiatic Expeditions (Andrews 1932), described how they had found the first dinosaur fossils in the Gobi Desert of Mongolia. Not surprisingly, I was also fascinated by subsequent expeditions that collected dinosaurs in the Gobi (Rozhdestvenskii 1960, Colbert 1968, Kielan-Jaworowska 1969). Throughout my student years, I never thought it would be possible for me to go to the either China or Mongolia because of the international political conditions. However, when I started to collect dinosaurs as a professional in Alberta, Canada in 1976, it became evident that the Cretaceous dinosaurs of Alberta and Mongolia were inter-related. This increased my desire to study the Asian fossils and sites, and a few years later I had an opportunity to do an expedition to central Asia. Initially our team at the newly created Tyrrell Museum of Palaeontology tried to secure an agreement with Mongolia, and I contacted Zofia Kielan-Jaworowska for advice. We had met in 1981 at the Mesozoic Terrestrial Ecosystems Conference in Warsaw, where I remembered being pleasantly surprised by how much she looked and behaved like a younger version of my own grandmother (Ruth Brander, 1903–1983). When I contacted Zofia about the potential project in Mongolia in the summer of 1983, she was in Malcolm McKenna's field camp in Wyoming; I went there to speak with her directly. She was very happy to talk about the Polish-Mongolian Palaeontological Expeditions, and freely provided advice and contacts.

In the long run, we were unable to secure an agreement with Mongolia, but went instead to the Chinese Gobi Desert as the Canada-China Dinosaur Project, 1986–1990 (Currie 1991, Grady 1993). Ultimately, I was also able to work in Mongolia, as a member of "Dinosaurs of the Gobi" (Nomadic Expeditions, 1996–2007, 2011) and as part of the Korea-Mongolia International Dinosaur Project (2006–2010, 2012). One of the greatest thrills of my life was when Zofia joined us in 2002 with her husband Zbigniew Jaworowski and granddaughter Zofia (Zosia) Jaworowska (Kielan-Jaworowska 2013). In addition to our normal program of work, we visited Polish-Mongolian expedition sites with her at Hermiin-Tsav (I and II), Khulsan, and Nemegt (Central and Northern Sayrs, Red Monadnocks, Southern Monadnocks), and she helped to unravel the mysteries of some of the locality information. During the evenings, she would share stories of the Polish-Mongolian expeditions around the supper table.

For many years, I have led interdisciplinary field projects in which we search for new dinosaur specimens (isolated bones, skeletons, bonebeds) and sites, and document and collect what we find. During the dinosaur renaissance of the 1970s, I realized that arguments about the physiology and palaeoecology of dinosaurs depended to a large extent on the reliability of records of specimens that had been collected previously (Sternberg 1950), and whether or not preservational or collecting biases existed. For example, Bakker (1972) maintained that evidence existed in Dinosaur Provincial Park (Alberta, Canada) for dinosaurian predator/prey ratios, and that these ratios showed that carnivorous dinosaurs in the Late Cretaceous were warm-blooded. He reasoned that the predators made up less than 10% of the known specimens, and that there were collecting biases that favoured the collection of all theropod skeletons but not all specimens of the more common herbivorous dinosaurs. This would therefore suggest that the actual predator/prey ratio was as low as 5%. Other researchers countered that there were no collecting biases, and that every well-preserved dinosaur was excavated. Because of these insoluble debates, two other priorities were added into my field programs — all articulated/associated dinosaur skeletons were documented, regardless of whether or not they were collected. Furthermore, old dinosaur sites were identified and documented whenever we found them so that we could improve the geographic and stratigraphic resolution of the provenance data associated with the older finds. In this way, we have strongly increased the sample size of dinosaur occurrences in the Park while minimizing the biases, and have produced some interesting results (Currie and Russell 2005).

Virtually every major dinosaur-hunting expedition to the Mongolian part of the Gobi Desert (Lavas 1993) has collected in what is now referred to as the Nemegt Formation. The formation has yielded the most diverse Late Cretaceous dinosaur fauna known (Weishampel *et al.* 2004) with the exception of the Dinosaur Park Formation of Canada (Currie and Koppelhus 2005). The Nemegt sites are inherently interesting palaeoecologically because of the faunal similarities with the Late Cretaceous faunas of Alberta (Currie and Koppelhus 2005). A program of collecting and documentation similar to the approach in Dinosaur Provincial Park was adopted in the Nemegt Formation of Mongolia because of its richness. Furthermore, previous work in the Nemegt Formation had revealed what appeared to be an ecologically skewed predator/prey ratio, and it was necessary to investigate the possibility that this represented a collecting bias. Overall, individuals of the tyrannosaurid *Tarbosaurus* clearly outnumbered individuals of any genus of herbivorous dinosaur from the same formation (Osmólska 1980). Consequently every articulated specimen encountered in the field has been documented and/or collected, including specimens vandalized by poachers (Currie 2012), and historic dinosaur quarries have been relocated and incorporated into the database whenever possible (Currie 2009). Quarries in the Baruungoyot Formation were included in the study because this formation is found at most of the same localities as the Nemegt Formation (and therefore included on the same maps). Furthermore, the two formations were not initially considered separate, and it is not always clear which formation a given specimen came from. Finally, the Baruungoyot and Nemegt formations overlap in time, and their sediments inter-finger (Eberth *et al.* 2009; Fanti *et al.* 2012).

Of the dinosaurs excavated in Mongolia during the twentieth century, those of the Central Asiatic Expeditions are mostly from the Djadokhta Formation. The positions of Soviet/Russian sites (from 1946 to present) were not recorded on maps, and we have not been able to field-identify more than a few of their quarries because specific locality data and/or photographs are rarely included in their publications. Exceptions include the famous Dragon's Tomb at Altan Uul II, and one Soviet site in Nemegt Central Sayr that was incidentally marked on the Polish-Mongolian maps (Fig. 1). Many Russian (Kurochkin and Barsbold 2000), Soviet and Mongolian quarries have been identified by the excavations with their associated quarry garbage (usually including tin cans and glass jars with Cyrillic stamps or labels) and/or bulldozer tracks. However, determining which dinosaur came from which excavation is currently not possible.
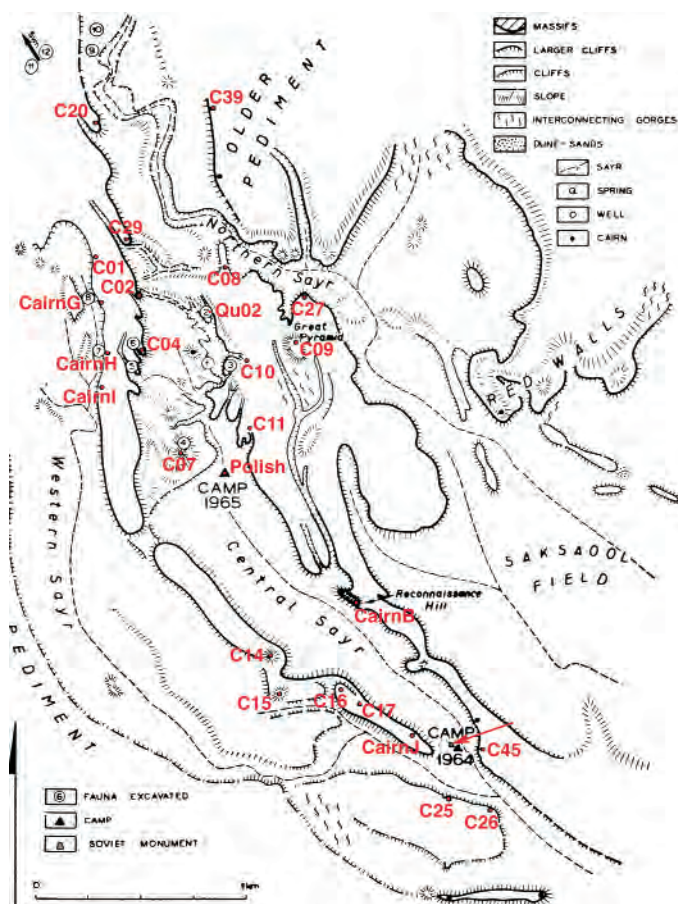
Fig. 1. Gradziński's map of the central and western part of Nemegt showing how the cairns used for triangulation were numbered as they were found and recorded by GPS. These data were used to modify the map slightly by adjusting the depiction of geography to better match GPS coordinates and by adding labels in red. Then the modified map was uploaded into a GIS program (initially it was Ozi Explorer, but more recently it has been MacGPS Pro) so that the expected coordinates could be calculated for all of the quarries that had not been found. Abbreviations: C, cairn; Qu02, quarry 2 of the PMPE plus an earlier Soviet excavation of a *Tarbosaurus* skeleton. Modified from original map by Gradziński *et al.* (1969, fig. 2).

The Polish-Mongolian Paleontological Expeditions were meticulous in recording where their specimens were collected. The topographic maps of Mongolia that were available to the expeditions (both then and now) were inadequate for meaningful documentation, and therefore the Polish geologists became proficient in producing maps of the primary collecting localities. These were essentially hand-drawn, although reference points were provided by constructing stone cairns (Fig. 2) for triangulation. The maps (Gradziński *et al.* 1969; Gradziński 1969; Gradziński and Jerzykiewicz 1974) drawn at the various Mongolian dinosaur localities have been the prime resource for finding and identifying original quarries. The Polish-Mongolian Expeditions collected more than 100 dinosaur skeletons between 1963 and 1971 (specimens and specimen records in ZPAL). By the definition adopted here, a skeleton may include as few as a half dozen bones provided they are from the same individual (for example, all specimens of *Elmisaurus rarus* Osmólska 1981), although some are virtually complete. Of these, 55 were recovered from the Baruungoyot and Nemegt formations, and most were included on the maps (Table 1).

Table 1. Abbreviations: AU2, Altan Uul 2; AU3, Altan Uul 3; AU4, Altan Uul 4; Khu, Khulsan; Nem, Nemegt; TsKh, Tsagan Khusuu.

Names	Specimen #	Quarry #	Collected	Discovered by
Saurolophus angustirostris	ZPAL MgD-I/087	AU2001		
Saurolophus angustirostris	ZPAL MgD-I/158	AU2001		
Saurolophus angustirostris	ZPAL MgD-I/166	AU2001		
Saurolophus angustirostris	ZPAL MgD-I/168	AU2001		
Tarbosaurus bataar	ZPAL MgD-I/005	AU3001	1965	Skarżyński
Deinocheirus mirificus	MPC-D100/018	AU3002	1965	Kielan-Jaworowska
Tarbosaurus bataar		AU3003	1965	Rachtan
Quadrupedal dinosaur		AU4001	1965	Kuczynski
Carnivorous dinosaur		AU4002		
Tarchia gigantea	ZPAL MgD-I/049	AU4003		

| Names	Specimen	Quarry #	Collected	Discovered by
Opisthocoelicaudia skarzynskii	ZPAL MgD-I/048	AU4004	1965	Gradziński
Tarchia gigantea	ZPAL MgD-I/043	AU4005	1964	Walknowski
Tarbosaurus bataar	ZPAL MgD-I/044 and 45	AU4006	1964	
Tarchia gigantea	ZPAL MgD-I/042	AU4007	1965	Lefeld
Gallimimus bullatus		AU4008		
Tarbosaurus bataar	ZPAL MgD-I/031	AU4009	1964	
Tarchia gigantea		AU4010		
Tarbosaurus bataar		AU4011		
Tarbosaurus bataar	ZPAL MgD-I/046	AU4012		
Breviceratops kozlowskii	ZPAL MgD-I/118	Khu001		
Hulsanpes perlei (could also be Khu08)	ZPAL MgD-I/173	Khu002	1970	
Breviceratops kozlowskii	ZPAL MgD-I/116	Khu004		
Breviceratops kozlowskii	ZPAL MgD-I/117	Khu005		
Tarchia kielanae	ZPAL MgD-I/111	Khu006		
Small theropod		Khu008		
Tylocephale gilmorei	ZPAL MgD-I/105	Khu010		
Saichania chulsanensis	MPC-D100/151	Khu011	1971	found in 1970
Tarbosaurus bataar	ZPAL MgD-I/029?	Nem001	1964	
Tarbosaurus bataar		Nem001A	1964	Borsuk-Białynicka
Tarbosaurus bataar	ZPAL MgD-I/029?	Nem002	1965	Maryańska
Tarbosaurus bataar		Nem003	1965	Barsbold
Gallimimus bullatus	ZPAL MgD-I/010	Nem004		
Gallimimus bullatus	ZPAL MgD-I/007	Nem005		
Nemegtosaurus mongoliensis	ZPAL MgD-I/009	Nem006	1965	Kuczynski
Gallimimus bullatus	ZPAL MgD-I/011	Nem007		
Homalocephale calathocercos	MPC-D100/051	Nem008	1965	Kielan-Jaworowska
Gallimimus bullatus	ZPAL MgD-I/015	Nem009		
Tarbosaurus bataar		Nem010		
Gallimimus bullatus	ZPAL MgD-I/008	Nem011		
Tarbosaurus bataar	ZPAL MgD-I/004	Nem012	1965, 1970	Małecki
"Coeluroid"		Nem013		
Gallimimus bullatus	ZPAL MgD-I/094	Nem014	1970	
Prenocephale prenes	ZPAL MgD-I/104	Nem019	1970	Osmólska
Gallimimus bullatus		Nem020		
Gallimimus bullatus	ZPAL MgD-I/033	Nem021		
Barsboldia sicinskii	ZPAL MgD-I/110	Nem023	1970	
Tarbosaurus bataar	ZPAL MgD-I/178	Nem024	1970	
Gallimimus bullatus		Nem025		
Bagaratan ostromi	ZPAL MgD-I/108	Nem026	1970	Kielan-Jaworowska
Saurolophus angustirostris	MPC-D , ?ZPAL MgD-I/170	Nem027	1970	
Saurolophus angustirostris	ZPAL MgD-I/157	Nem028	1970	
Tarbosaurus bataar	ZPAL MgD-I/109	Nem029	1970	
Tarbosaurus bataar		Nem030		
Tarbosaurus bataar	ZPAL MgD-I/175?	Nem031	1970	
Gallimimus bullatus	ZPAL MgD-I/001	TsKh001	1964	Skarżyński
Tarbosaurus bataar	ZPAL MgD-I/003	TsKh002	1964	Gwidon Jakubowski
Gallimimus bullatus	MPC-D100/011	TsKh003	1964	Kielan-Jaworowska
Tarbosaurus bataar		TsKh004	1965	Gradziński and Skarżyński
Tarbosaurus bataar		TsKh005	1964	Dovchin
Gallimimus bullatus	ZPAL MgD-I/024	TsKh006		
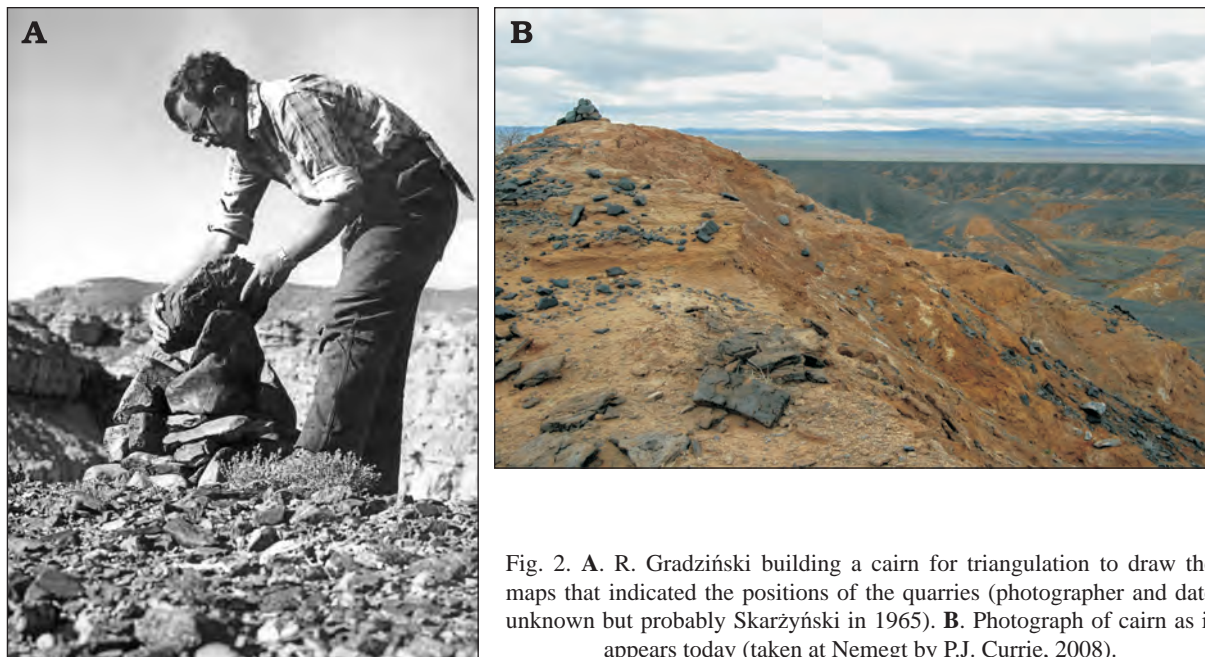
Fig. 2. **A**. R. Gradziński building a cairn for triangulation to draw the maps that indicated the positions of the quarries (photographer and date unknown but probably Skarżyński in 1965). **B**. Photograph of cairn as it appears today (taken at Nemegt by P.J. Currie, 2008).

The published maps of Baruungoyot/Nemegt dinosaur quarries include Altan Uul III (sketch map only, Gradziński *et al.* 1969, fig. 6), Altan Uul IV (Gradziński *et al.* 1969, fig. 4), Khulsan (Gradziński and Jerzykiewicz 1972, fig. 4), Nemegt Central Sayr (Gradziński *et al.* 1969, fig. 2), Nemegt/Khulsan (Gradziński and Jerzykiewicz 1974, fig. 1), Nemegt Northern Sayr (Gradziński and Jerzykiewicz 1972, fig. 1), the southeastern part of Nemegt (Gradziński and Jerzykiewicz 1974, fig. 3), and Tsagaan Khushuu (sketch map only, Gradziński *et al.* 1969, fig. 8). There are variants of these maps in other publications related to the Polish-Mongolian expeditions. They were drawn with varying degrees of accuracy, and finding some of the quarries, even when field photographs supplement the maps, has not always been possible. The sketch map of Hermiin Tsav I and II (Gradziński and Jerzykiewicz 1972, fig. 6) does not show the positions of any quarries.

Abbreviations. — AMNH, American Museum of Natural History, New York, USA; AU, Altan Uul; HT, Hermiin Tsav; Khu, Khulsan; KID, Korea-Mongolia International Dinosaur Project; MPC, Paleontological Center of the Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; Nem, Nemegt; PMPE, Polish-Mongolian Palaeontological Expeditions; Saurol, *Saurolophus*; Tarb, *Tarbosaurus*; TsKh, Tsagaan Khushuu; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Fig. 3. **A**. View northeast across the Northern Sayr of Nemegt at the Polish-Mongolian camp in 1970. **B**. Same view in 2010. Photos by W. Maczek (A) and P.J. Currie (B).

MATERIAL AND METHODS

Initially quarries were located either fortuitously, or by hiking with a copy of the relevant map in hand. The project of relocating Nemegt Formation quarries started in 1999, and coordinates taken that year with a handheld GPS proved to be highly inaccurate (because of signal scrambling) and had to be checked and retaken in subsequent years. The identification of old camps (Fig. 3), cairns used for triangulation, graffiti (Fig. 4), and places where specimens were crated (Fig. 5) helped immensely in finding some quarries. Although some quarries were easily found because of their size and the presence of plaster, wood, nails, and
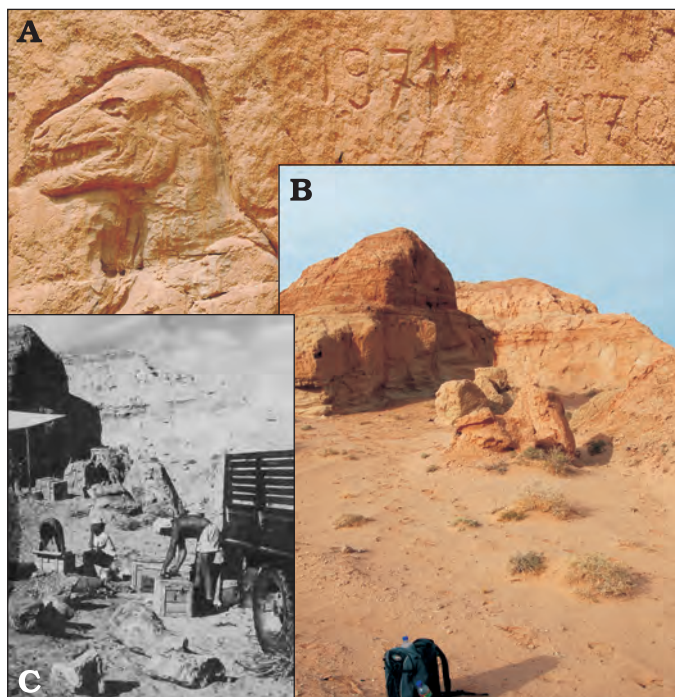
Fig. 4. "The Café" at Altan Uul IV, where the remains of *Opisthocoelocaudia* and other specimens were brought down from the upper level and crated. **A**. "The Café" was close to Polish-Mongolian camps in 1965, 1970 and 1971, and the walls are adorned with signatures, dates, and even bas-relief drawings like this *Tarbosaurus*. Note the dates 1971 and 1970 to the right of the *Tarbosaurus*. **B**. Dinosaur bones being crated (photo taken looking north by ?Gradziński, 1965). **C**. The same view in 2009, with the graffiti-covered wall in shadow. Photos A and C taken by P.J. Currie.

other paraphernalia (Fig. 6), others were only found after considerable effort. Copies of field photographs were obtained from the Institute of Paleobiology and the personal collection of Zofia Kielan-Jaworowska. Information on the backs of the photos was scanty, but was supplemented with information from Kielan-Jaworowska and Skarżyński. Copies of these photographs were taken into the field and used to identify some of the quarries. One quarry (AU4004, *Opisthocoelicaudia*), which should have been found easily because of its size, eluded us for several years, and was only found after Gradziński sent additional photographs of "the Café" (where the specimen was crated for transport, Fig. 5) and several points between AU4004 (Fig. 7) and "the Café".

For identifying specific quarries, the original map numbers have been retained, but a prefix has been added for each site: For example, "Nem001" is quarry 1 on the Nemegt map of Gradziński *et al.* (1969). The cairns marked on the maps were assigned numbers, and coordinates were taken for each cairn when it was found. Using MacGPS Pro 10.4 and Photoshop CS6, the coordinates of the cairns and known quarries were overlain on the hand-drawn maps. In some cases the points overlapped the maps perfectly when shrunk to the same scale. However, the maps tended to be less accurate toward the edges, where reference points were more dispersed. The maps were selectively distorted on a computer so that the reference points overlapped the known GPS points. Coordinates were then calculated for the quarries that had not been found yet. These were put into the handheld GPS, and used with varying degrees of success to try to find some of the missing quarries. In some cases this was possible, but most of the time the quarries still could not be located with certainty. Although not as accurate as those obtained for the field-checked quarries, the coordinates calculated from the maps (Table 2) are still useful.

The spellings of Mongolian geographic and stratigraphic names follow those of Benton *et al.* (2000), and the chronostratigraphic framework is from Jerzykiewicz and Russell (1991).

RESULTS

The positions of the Polish-Mongolian camps were identified by photographs (Fig. 3), the alignments of rocks that encircled tents and parking areas for the trucks, garbage pits that include jars, cans and broken porcelain from Poland, and sometimes by graffiti carved into the surrounding rocks. Finding the campsites (Table 2) was often the first step in confirming positions on the maps so that cairns and quarries could be identified. Furthermore, we often used the same campsites while we were in those areas.
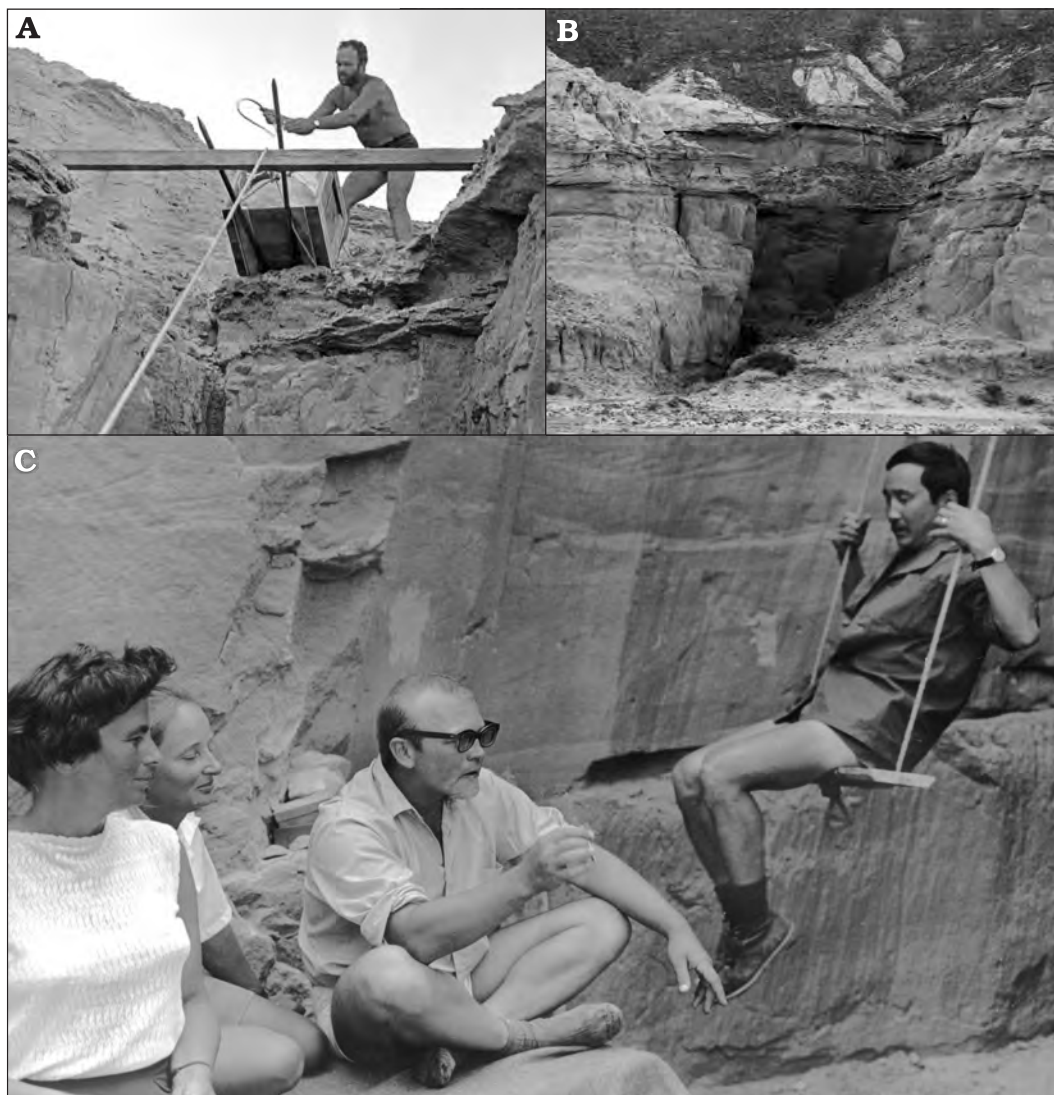
Fig. 5. "The Café 2" across the sayr from the 1970 and 1971 Nemegt camps of the PMPE. Specimens were lowered from a ledge above for crating inside the notch in the wall, which is shaded most of the day. **A**. Skarżyński preparing to lower a crate. **B**. "The Café" as it appeared in 2010. The patch of white that can be seen on the back wall of the quarry is a metal plaque placed there by Skarżyński in September 2008 when he was involved with a Polish wind-sailing expedition across the Gobi Desert. **C**. A historic meeting in "the Café" of the leaders of the Polish-Mongolian and Russian-Mongolian expeditions. This photograph shows Zofia Kielan-Jaworowska, Halszka Osmólska, V.I. Zhegallo and Rinchen Barsbold. Photos A and C taken by W. Maczek, and B was photographed by P.J. Currie.

Even though the first mapping cairns were built more than half a century ago, the majority of them are still standing. Each cairn is built where it can be seen from at least two other cairns, and most are high on the slopes close to the edges of canyons. They are generally less than a metre high, and are usually made of durable "Gobi stones" that are fist-sized or larger (Fig. 2). Khulsan proved to be an exception because hard stones are not as accessible, and it was necessary to use the field notes and sketches of Jerzykiewicz to sort out where many of the cairns were. Some of the cairns at each locality were undercut by erosion, and some have disappeared for no apparent reason (the stones may have been used for other purposes, for example). Another problem is that many additional cairns have been built over the years, often by poachers who are using them to mark specimens of interest.

Altan Uul I is the most eastern of the four sites on the south flank of the mountain known as Altan Uul. It was discovered by the Soviet expeditions in the 1940s, but received its present name from the Polish-Mongolian expeditions (Gradziński *et al.* 1969). Although Polish-Mongolian teams apparently visited the site in 1964, 1965 and 1971, no map was ever published to show the distribution of fossils, and the *Tarbosaurus* specimen (ZPAL MgD-I/038) collected there in 1964 is fragmentary and incomplete.
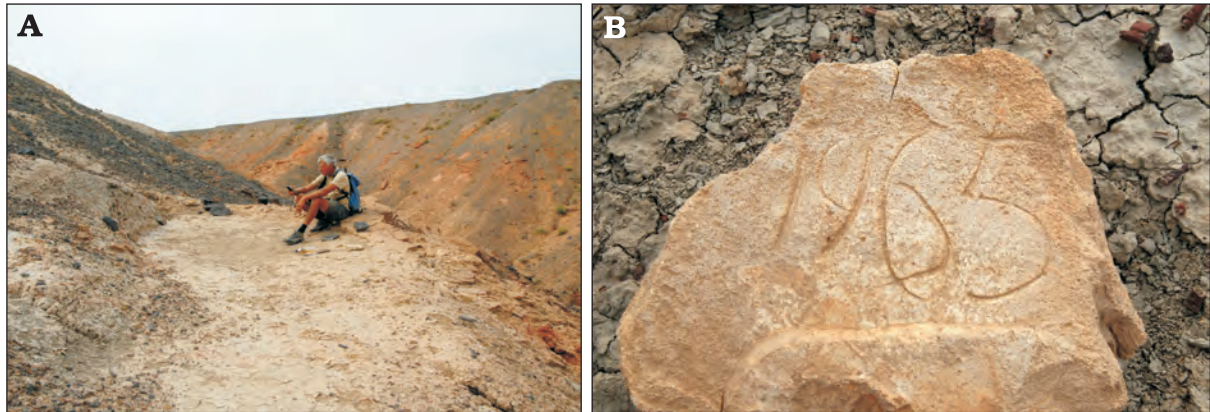
Fig. 6. Quarry AU4001 as it looked when it was re-located in 2010. Confirmation as to quarry identity came from a slab of plaster that, when turned over, revealed the date 1965. Pieces of lumber, plaster, and nails were found on the quarry floor, and a road went from the quarry up the hill toward the 1965 upper camp. Photo by E.B. Koppelhus (**A**) and by P.J. Currie (**B**).

Table 2. GPS coordinates (datum is WGS84) for Polish-Mongolian quarries and associated points of interest expressed in degrees and minutes. The first two columns were field-checked, whereas the third and fourth columns are calculations derived from the maps for Altan Uul4 and Nemegt. This could not be done for some maps because they were either too inaccurate, or not enough GPS points were taken to calibrate the maps. Note that AU4009, AU4010, AU4012 were field checked but there was no evidence (i.e. plaster, wood, nails, photographs, bone) to confirm that these quarries have been correctly identified. Nem011 (an ornithomimid tail and hind limbs) was never marked on the maps of Gradziński *et al.* (1969) and Gradziński and Jerzykiewicz (1972). See text for information on Saurol26, Saurol40, Tarb58 and Tarb68, all of which were marked on the Polish-Mongolian quarry maps even though they were not assigned quarry numbers. Abbreviations: AU2, Altan Uul 2; AU3, Altan Uul 3; AU4, Altan Uul4; calc, calculated; Khu, Khulsan; low, lower camp in 1965; Nem, Nemegt; Saurol, *Saurolophus*; Tarb, *Tarbosaurus*; TsKh, Tsagan Khusuu; up, upper camp in 1965.

	North actual	East actual	North calc	East calc
AU2001	43°36.192'	100°33.663'		
AU3001	43°34.358'	100°29.017'		
AU3002	43°33.987'	100°28.959'		
AU4001	43°35.263'	100°26.729'		
AU4002			43°35.469'	100°26.935'
AU4003			43°35.278'	100°26.762'
AU4004	43°36.157'	100°27.317'		
AU4005			43°34.932'	100°26.500'
AU4006			43°34.893'	100°26.484'
AU4007			43°35.200'	100°27.163'
AU4008	43°35.830'	100°27.426'		
AU4009	43°36.183'	100°27.364'		
AU4010	43°36.073'	100°27.162'		
AU4011			43°36.275'	100°27.355'
AU4012	43°36.087'	100°27.133'		
Khu011	43°30.419'	101°07.646'		
Khu013	43°29.607'	101°07.492'		
Nem001	43°30.157'	101°03.156'		
Nem001A	43°30.152'	101°03.154'		
Nem002	43°30.280'	101°03.152'		
Nem003	43°30.157'	101°03.218'		
Nem004			43°29.959'	101°03.062'
Nem005			43°30.149'	101°02.869'
Nem006			43°30.208'	101°02.871'
Nem007			43°30.190'	101°02.743'
Nem008			43°30.322'	101°02.706'
Nem009			43°30.939'	101°02.719'
Nem010			43°30.994'	101°02.736'
Nem012	43°31.089'	101°01.783'		

	North actual	East actual	North calc	East calc
Nem013			43°31.690'	101°02.613'
Nem014	43°31.744'	101°02.691'		
Nem019	43°32.366'	101°02.112'		
Nem020			43°32.290'	101°02.190'
Nem021			43°30.779'	101°02.752'
Nem023	43°31.799'	101°02.396'		
Nem024	43°31.743'	101°02.486'		
Nem025			43°32.375'	101°02.270'
Nem026			43°31.204'	101°02.991'
Nem027	43°31.485'	101°02.507'		
Nem028	43°31.513'	101°02.755'		
Nem029	43°31.689'	101°01.927'		
Nem030	43°31.233'	101°01.887'		
Nem031	43°31.591'	101°01.786'		
Saurol26	43°30.157'	101°03.037'		
Saurol40	43°30.202'	101°03.045'		
Tarb58	43°30.213'	101°03.063'		
Tarb68	43°30.283'	101°03.143'		
TsKh001	43°28.924'	100°21.640'		
TsKh002	43°28.911'	100°21.777'		
Café 1965	43°35.948'	100°27.430'		
Café 1970	43°30.803'	101°02.763'		
Camp Au4 1965up	43°34.968'	100°26.368'		
Camp Au4 1965low	43°35.718'	100°27.403'		
Camp Khu 1971	43°29.983'	101°07.482'		
Camp Nem 1964	43°29.202'	101°04.008'		
Camp Nem 1965	43°29.892'	101°03.218'		
Camp Nem 1970	43°30.853'	101°02.797'		
Camp TsKh 1964	43°29.022'	100°22.123'		

In 1948, a Soviet expedition discovered a spectacular site that they called the "Dragon's Tomb". They excavated seven skeletons of *Saurolophus*, and parts of at least three *Tarbosaurus* skeletons. Many of the hadrosaurs have associated skin impressions, sometimes covering the entire flank of the body (Bell 2012). Although the PMPE never did any major excavations at Altan Uul II, they apparently visited the site from time to time and collected several specimens that are now in Warsaw (Table 1). The "Dragon's Tomb" still has many specimens of *Saurolophus* and *Tarbosaurus*, but has been heavily vandalized in recent years by poachers.

Altan Uul III was worked by the PMPE in 1964 and 1965 (Gradziński *et al.* 1969; Kielan-Jaworowska 1969). Their expeditions recovered two partial skeletons of *Tarbosaurus bataar* (one of which is ZPAL MgD-I/5 from AU3003), and the holotype of *Deinocheirus mirificus* (numbered initially as ZPAL MgD-I/6, but eventually transferred to Ulaan Baatar as MPC-D100/018). The latter was discovered by the Polish leader, Zofia Kielan-Jaworowska, and for a long time was one of the most enigmatic dinosaurs known because it consisted only of gigantic front limbs. The exact position of the shallow quarry had been forgotten over the years, even though it was marked on the sketch map of Altan Uul III (Gradziński *et al.* 1969, fig. 6). The published photographs (Kielan-Jaworowska and Dovchin, 1969) showed the bones in the quarry, but there were no clues about the surrounding terrain. However, I finally managed to get one photograph in Warsaw that showed some of the landscape (Fig. 8), and after years of looking for the quarry I found it during the 2008 KID Expedition. We picked up some additional fragments of vertebrae and gastralia of the *Deinocheirus*, but they were insufficient to resolve the relationships of this enigmatic dinosaur. However, interest in this dinosaur was so strong that word of the re-discovery of the quarry spread worldwide. The fallout was that I was notified of a poached specimen of *Deinocheirus* in Europe, which turned out to be the same individual as a damaged specimen we had collected at Bugeen Tsav in 2009. This in turn led to the recognition of another *Deinocheirus* specimen that we had collected at Altan Uul IV in 2007. After almost half a century, we finally knew that *Deinocheirus* was a large and unusual ornithomimosaur (Lee *et al.* 2014). I wrote to Zofia to let her know that there were finally several specimens of *Deinocheirus*, and that it was an even stranger
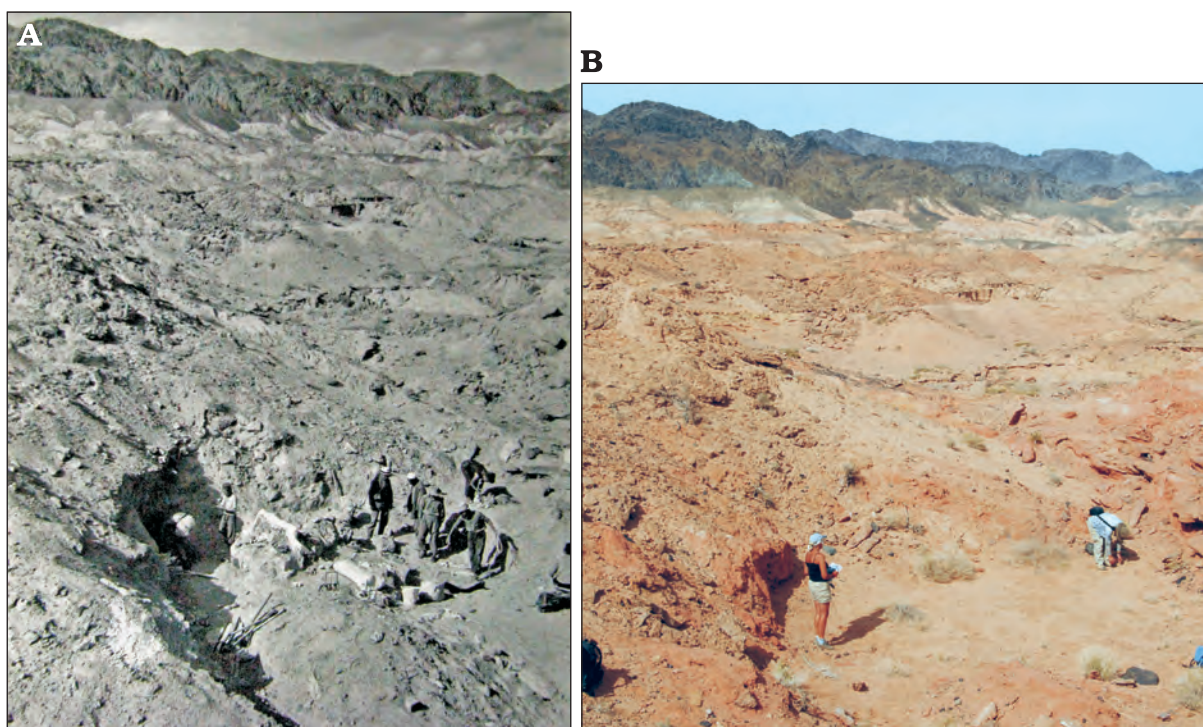
Fig. 7. Quarry AU4004 (IV on Altan Uul 4 map of Gradziński *et al.* 1969) where *Opisthocoelocaudia* was collected in 1965. Differences in the proportions of the photographs result from differences in the focal lengths of the camera lenses used. Upper photograph was taken by W. Skarżyński in 1965, whereas lower photograph was taken from North 43°36.150', East 100°27.305' by P.J. Currie in 2009.

animal than we had thought. Unfortunately she was not well by the time that the paper came out, and I never learned if she knew of the resolution of the mystery of the dinosaur she had discovered in 1965.

One other quarry was found at Altan Uul III (AU3001), but the excavation site of AU3003 remains unknown. Additional skeletons of an ankylosaur (ZPAL MgD-I/113), *Gallimimus* and *Tarbosaurus* were collected from AU3 in 1965 and 1971, but were never marked on any of the published maps.

Altan Uul IV was first explored by the Polish-Mongolian expedition of 1964 (Gradziński *et al.* 1969), although excavations were not undertaken until subsequent expeditions in 1965, 1970 and 1971. The material collected included the holotype of *Opisthocoelicaudia*, four ankylosaurs, one ornithomimid and five partial *Tarbosaurus*. Two of the Polish camps, half of the twelve quarries (Table 2), and many of the mapping cairns were rediscovered and pinpointed using GPS in 2006 and 2008.

One of the specimens excavated by the 2006 KID expedition was a large *Tarbosaurus* (Tarb32, MPC-KID022) from a place in Altan Uul IV that was impossible to access by vehicle. Consequently, the specimen had to be dragged out of the badlands using manpower. Interestingly, we discovered several years later that the Polish-Mongolian *Opisthocoelicaudia* quarry (AU4004) was nearby, and that they had similarly dragged that specimen down the same trail 41 years earlier. The spot where we loaded the specimen onto our truck was in fact the Café used by the PMPE to crate and load the sauropod skeleton.

Hermiin Tsav is a spectacularly beautiful site that yields dinosaur skeletons from both the Baruungoyot and Nemegt formations. It was originally discovered in 1969 by Barsbold, who worked there with the Joint Russian-Mongolian Palaeontological Expedition the following two years. The PMPE also worked at Hermiin Tsav in 1970 and 1971, but focused mostly on the Baruungoyot Formation. Although two distinct regions (Hermiin Tsav I, Hermiin Tsav II) are cited in the Polish literature (Gradziński and Jerzykiewicz 1972), they are lithologically similar and both include exposures of both formations. Unfortunately, the sketch map does not show the quarry locations. However, *Gobipteryx* eggs and embryos (Elżanowski 1981) were recovered from a single site at Hermiin Tsav I. One locality at the western end of the exposures (near a prominent natural feature called "the Gate") yielded abundant eggs of this animal and may have been the site where the embryos were found in 1971.

Khulsan was initially worked by the PMPE in 1970 and 1971 (Gradziński and Jerzykiewicz 1972), but has more recently been under heavy pressure from poachers. It has some of the best exposures of the
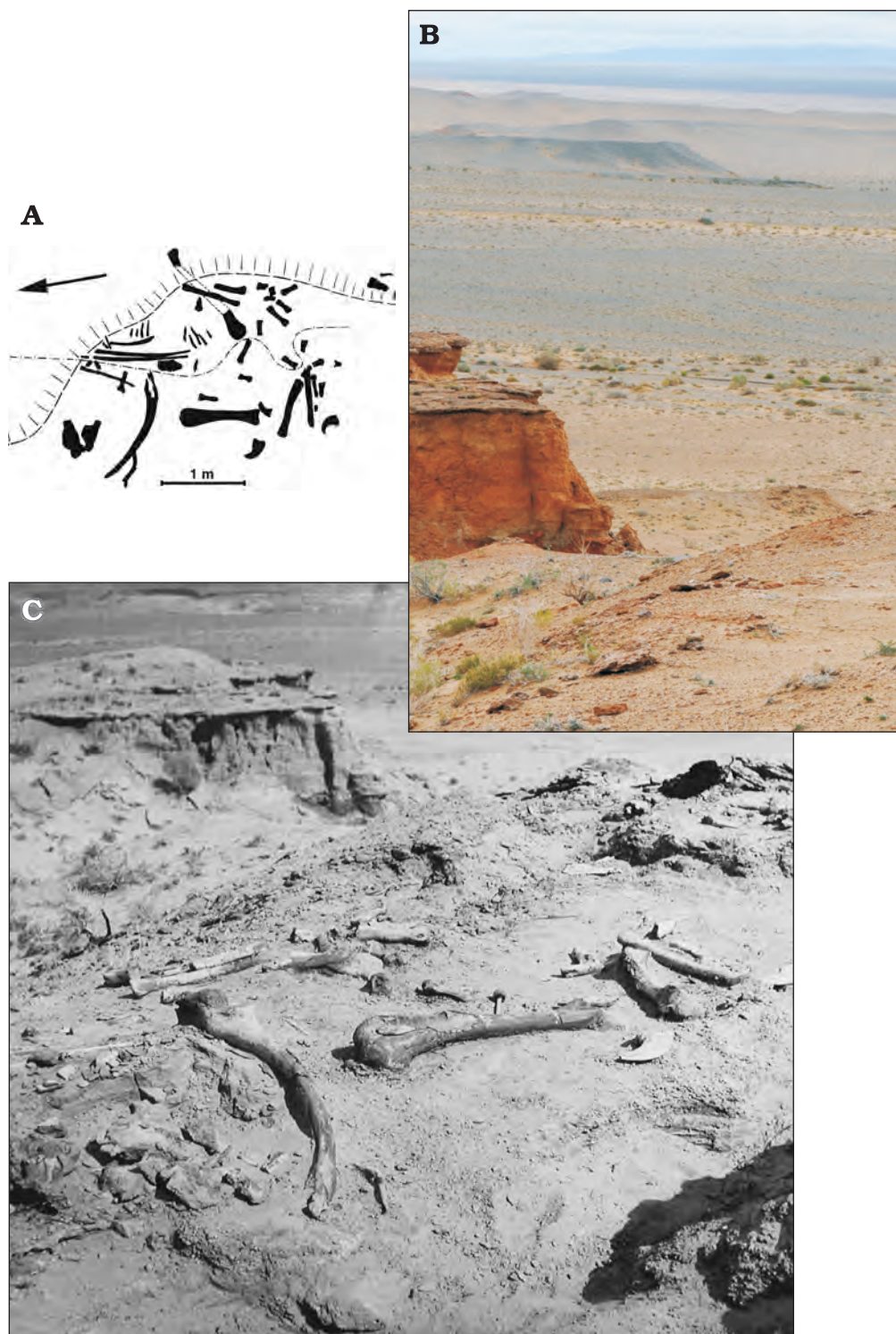
Fig. 8. Quarry AU3002 (II on Altan Uul 3 map of Gradziński *et al.* 1969) from which the holotype of *Deinocheirus mirificus* was recovered in 1965. **A**. Quarry map showing the distribution of bones (fig. 30 of Gradziński 1970). **B**. Photograph taken in 2008 by P.J. Currie from west side of quarry. **C**. Photograph taken by R. Gradziński in 1965 before the bones were removed from the quarry.

Baruungoyot Formation, which yielded two ankylosaurids, one pachycephalosaurid, three protoceratopsids, and one small theropod skeleton for the PMPE. In addition it yielded numerous, nicely preserved microvertebrates, including a spectacular concentration of mammal skulls that was referred to as Eldorado (Khu013). Presumably the *Gobipteryx* material described by Elżanowski (1974, 1977) also came from the same site, because we recovered *Gobipteryx* eggs from Eldorado in 2011. Generally speaking, the dinosaurs at Khulsan
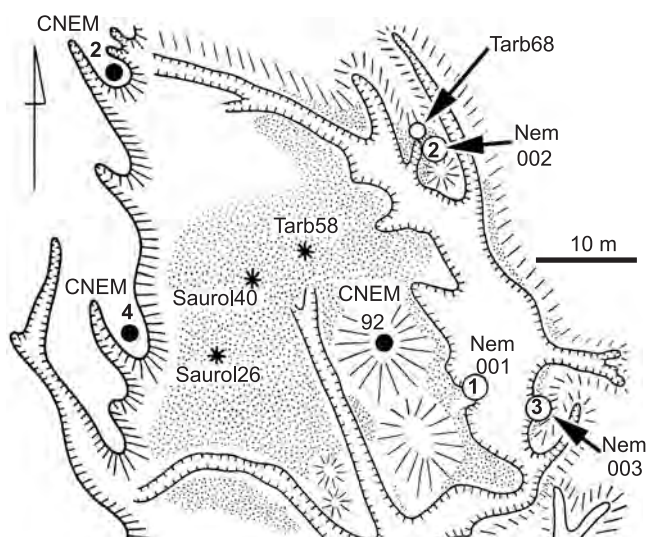
Fig. 9. Map of the northern part of Central Sayr of Nemegt Locality showing distribution of cairns (black dots), quarries (open circles) and weathered skeletons (asterisks). The quarry numbers have been modified by the addition of "Nem" to signify that they are from the Nemegt locality, and the cairns have been numbered and coordinates established with GPS. Abbreviations: CNEM, cairn from Nemegt locality; Nem, Nemegt locality; Saurol, *Saurolophus*; Tarb, *Tarbosaurus*. Modified from Gradziński (1970, fig. 33).

tend to be relatively small, and the soft sediments erode rapidly. The quarry that yielded the holotype of the ankylosaur *Saichania chulsanensis* (Khu011) is still easily seen, however.

The beds at Nemegt were originally found in 1946 by the Soviet Paleontological Expeditions, and were subsequently worked by the same group in 1948 and 1949. Polish-Mongolian expeditions to this locality started in 1964, and resulted in the production of the first maps of the complex badlands (Gradziński *et al.* 1969, Gradziński 1970). These are the most extensive badlands exposing the Nemegt Formation, and have also yielded the most numerous and diverse specimens. The transition with the Baruungoyot is also well exposed at Nemegt, and in recent years at least one taxon (*Nemegtomaia barsboldi*) has been identified in both formations (Fanti *et al.* 2012). The Polish-Mongolian quarries include four hadrosaurs (one of which is the apparently rare *Barsboldia*), two pachycephalosaurids, ten ornithomimids, one sauropod (the holotype of *Nemegtosaurus mongoliensis*), and ten *Tarbosaurus*. Nemegt quarries 1 and 2 on the Gradziński (1970, fig. 33) map are both double quarries. Nem001 and Nem001A can be identified in the photographs of the site, and show evidence of being quarried at the same time (there are nails on the floors of both excavated areas). It is possible that one of the two "quarries" was flattened out to prepare the crate for packing the specimen. Gradziński (1970) identified the quarry next to Polish quarry Nem002 (Fig. 9) as being one of the Soviet Paleontological Expedition excavations. Bone left behind in the quarry is clearly part of a vertebral column of a large *Tarbosaurus* that is designated as Tarb68 (Currie 2009). Also marked on the map were three weathered dinosaur skeletons, which were still visible in 1999 and were designated as Saurol26, Saurol40 and Tarb58 (Fig. 9). The last two specimens were partially excavated by poachers in 2003, and it seemed that Gradziński's assessment that they were weathered specimens was correct. However, we were very surprised when we returned in 2004 to find that the poachers had returned to Tarb58 to dig deeper. They found the skull underneath its body, encased it in a thin layer of plaster and burlap, and then attempted to turn it over. Unfortunately, they had done a poor job of jacketing the specimen and it collapsed. Rather than trying to fix the damage they had done, they simply hacked out all of the teeth and left the rest of the specimen in the hole. We salvaged large portions of the back of the skull and some of the forelimb elements. Nem003 is another small *Tarbosaurus* that was found by Barsbold in 1965. When the quarry was re-discovered in 2011, a 275 mm-long right jugal was recovered; because it would have been part of the original specimen that was excavated, it will assist in determining which of the *Tarbosaurus* specimens in Warsaw came from this quarry.

Nemegt is a huge area containing many quarries that are difficult to find. Of the 25 dinosaur quarries on the maps, a dozen still have not been found. These quarries mostly yielded small specimens (the holotypes of *Homalocephale calathocercos* and *Nemegtosaurus mongoliensis*, several specimens of *Gallimimus*, and an isolated vertebra of *Tarbosaurus* for example) that would not have required the excavation of large holes. Quarry Nem012 was a *Tarbosaurus baatar* found by Malecki in 1965, but only the leg was excavated that year. The balance of the skeleton was collected in 1970. When we visited the quarry in 2008, we were surprised to find that poachers had found and partially excavated another *Tarbosaurus* skeleton (Tarb49) only 15 m away at a slightly lower level. Quarry Nem024 (Fig. 10) was well-photographed, but nevertheless was difficult to find because of its position on a ledge above the valley floor. When Nem030 was re-found in
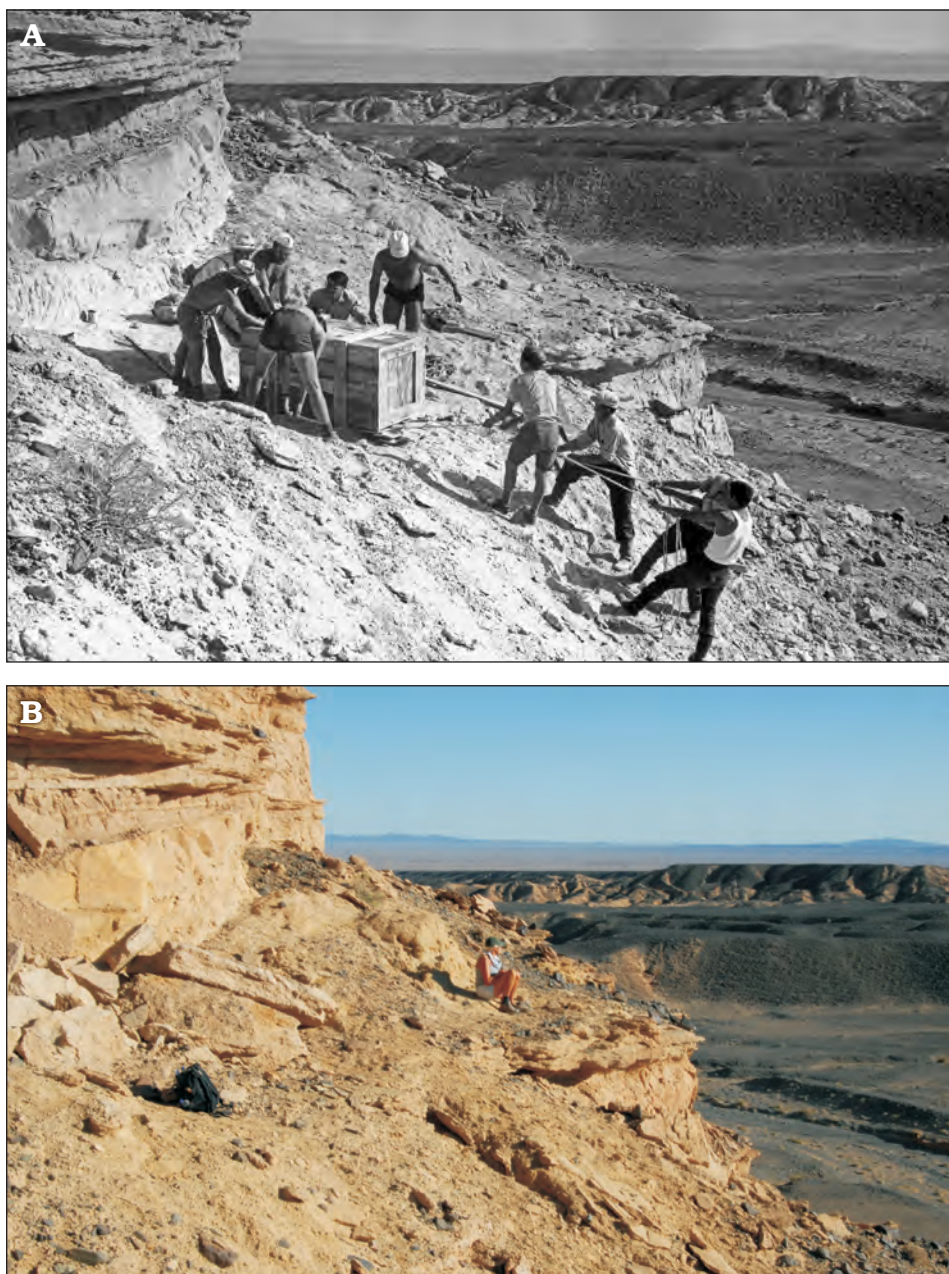
Fig. 10. Quarry Nem024, looking south down the Northern Sayr. **A**. Specimen being removed in 1970 (photo by W. Maczek). **B**. A similar view in 2010 (photo by P.J. Currie).

2009, there were bones of both *Tarbosaurus* and *Saurolophus* on the quarry floor, suggesting that parts of two individuals had been collected.

Tsagaan Khushuu is a much smaller area, but still gave the 1965 Polish-Mongolian Expedition a total of seven quarries, one of which was a concentration of turtles, whereas there were three quarries each of *Gallimimus* and *Tarbosaurus*. Two of the quarries (TsKh001) and (TsKh002) have been pinpointed.

DISCUSSION AND CONCLUSIONS

Precise locations (with GPS coordinates that can be returned to year after year) are now known for 32 of the PMPE quarries that were marked on maps of Altan Uul, Khulsan, Nemegt and Tsagaan Khushuu (Tables 1, 2). In spite of numerous attempts to find the rest of the sites in the Baruungoyot and Nemegt formations,

Table 3. Dinosaur faunal composition for the Nemegt Formation of Mongolia at the time of the PMPE compared with what is known at present. The PMPE numbers include specimens listed in Table 2, plus specimens in the ZPAL collections. The "present" numbers include the PMPE specimens and data/specimens collected by the Dinosaurs of the Gobi and KID expeditions, but almost none of the specimens collected by the AMNH, Japanese-Mongolian, Mongolian, Russian-Mongolian or Soviet-Mongolian expeditions.

Taxon	PMPE #s	PMPE %	Present #	Present %
Sauropoda	2	3.1	34	9.3
Ornithomimidae	18	28.1	105	28.9
Deinocheiridae	1	1.6	4	1.1
Tyrannosauridae	23	36.0	123	33.8
Other theropods	5	7.8	21	5.8
Ankylosauridae	8	12.5	26	7.1
Hadrosauridae	5	7.8	46	12.6
Pachycephalosauridae	2	3.1	5	1.4
Total	64	100	364	100

eighteen still have not been seen. Nevertheless, the approximate positions of these quarries can be determined from the maps (Table 2) and new clues may still lead to their discovery.

More precise documentation and additional work has not significantly changed the Nemegt Formation results of the PMPE of 1964, 1965, 1970, and 1971. The PMPE collected skeletons and partial skeletons of 64 dinosaurs from the Nemegt Formation (Table 3). The relative abundances of the families of dinosaurs have not changed appreciably (Table 3), most of older values falling within ±3% of those calculated from the larger sample that is available now. The numbers of hadrosaurids and sauropods have increased by more than 3% in the larger sample, whereas the number of ankylosaurs has decreased by more than 3%. The differences between the relative abundances of various dinosaur taxa found by the PMPE and what is now known are relatively trivial, and show that as far as dinosaurs were concerned, there were no collecting biases that favoured one type of dinosaur over any other.

Amongst the theropod dinosaurs, there are no changes in the order of abundance. Tyrannosaurids (*Tarbosaurus* makes up the vast majority of the tyrannosaurid numbers, and *Alioramus* continues to be rare) dominate over all other taxa, and compose almost a third of the dinosaurs found in the Nemegt Formation. Ornithomimids (mostly *Gallimimus*, but also *Anserimimus* and a possible new taxon under study) are almost as common. The ornithomimosaur *Deinocheirus* has quadrupled in numbers but remains one of the rarest elements of the fauna. *Therizinosaurus* was not recovered by the PMPE, and is represented by only a single claw in the enlarged sample of mapped specimens (and therefore was not included in Table 3). Other theropods (avimimids, dromaeosaurids, elmisaurids, oviraptorids, and troodontids) continue to be rare, and collectively make up less than 10% of the fauna.

Amongst the herbivores (ignoring the possibility that ornithomimosaurs and oviraptorids may have been at least facultative herbivores), the collections made by the PMPE would suggest that ankylosaurids are more common than hadrosaurids, and that sauropods are rare in the Nemegt fauna. Osmólska (1980) suggests that hadrosaurs were almost as common as *Tarbosaurus*. However, it is not clear from either the mapped or catalogued specimens where that statistic would have come from, and it is possible that it was a field observation. Regardless, the enlarged sample suggests that hadrosaur skeletons are less abundant than those of *Tarbosaurus*. The increased sample size (Table 3) also suggests that hadrosaurids (primarily *Saurolophus*) were the most common herbivores, that sauropods were almost as common, and that ankylosaurs were the third most abundant large herbivores. Pachycephalosaurids continue to be relatively rare. With the exception of Altan Uul 2 (where hadrosaurs clearly dominate in the Dragon's Tomb), the dominance of *Tarbosaurus* skeletons seems to be a common denominator in all sites where the Nemegt Formation is exposed.

The fact that *Tarbosaurus* continues to account for about a third of the dinosaur quarries is one of the most remarkable and puzzling aspects of the Nemegt Formation. It would be impossible to have a sustainable ecosystem that is dominated by such a large and clearly predatory dinosaur. In other ecosystems where tyrannosaurids were the top predator (for example, in Dinosaur Provincial Park, Currie and Russell, 2005), they normally comprise about 5% of the faunas. The suspicion that a preservational bias is at least partially responsible for the high incidence of *Tarbosaurus* in the Nemegt Formation is confirmed by comparison with a different preservational regime, the ichnite record. Dinosaur footprints are very common (numbering

in the thousands) in the Nemegt Formation (Currie *et al.* 2003), and are usually recovered from specific levels at the tops of fining-upward sequences in which skeletons are common near the bases. The footprint and bone levels are interleaved throughout the formation. Footprints suggest that the most common dinosaurs were hadrosaurs, that sauropods were also relatively common, and that tyrannosaurids were rare. Less than 5% of the footprints belong to tyrannosaurids.

Much thought has been put into trying to account for the disproportionately high number of *Tarbosaurus* skeletons recovered from the Nemegt Formation (Young 2011). The more frequent recovery of skeletons in high energy deposits (sheet flooding), rather than in more typical fluvial deposits, may indicate that there were commonly recurring adverse weather conditions that may have affected populations of carnivores more than herbivores. Another possibility is that tyrannosaurids were so thorough in cleaning up the carcasses of other dinosaurs that hadrosaurs and many other herbivores are under-represented because there was nothing left of a carcass for preservation. A third possibility that has been suggested is that high sedimentation only occurred at a certain season when *Tarbosaurus* was concentrated in the area. These hypotheses unfortunately suffer from any lack of evidence to prove or refute them. More than a hundred sites (including those found by the PMPE) have been identified where *Tarbosaurus* skeletons have been found; the next step is to undertake a thorough taphonomic/sedimentologic study to look for common patterns in these quarries that might explain why this dinosaur is preferentially preserved over herbivorous forms.

Although the skeletons of another theropod group (the Ornithomimosauria) are almost as common as *Tarbosaurus*, *Gallimimus* and other ornithomimosaurs were presumably omnivorous (Lee *et al.* 2014) or herbivorous (Kobayashi *et al.* 1999), and so their abundance is easier to understand. Ornithomimid footprints have also been recovered, but other small theropods, ankylosaurids, pachycephalosaurids and other taxa still have not been identified in the ichnological record.

Although the new, more precise data acquired about the PMPE dinosaur quarries has not given any greater insight into the Nemegt fauna, sedimentologic/stratigraphic studies currently underway will benefit from the greater resolution. This in turn will give us a better understanding of the temporal distribution of dinosaurs that are found within the Nemegt Formation. Above all else, the results of the PMPE show the importance of documenting the information at a fossil site. And even though it is easier to take a GPS reading and take a digital photograph than it was for the geologists of the PMPE to hand draw a map, it is unfortunately still not something that is consistently done for every specimen.

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FIRST FOSSIL MAMMALS FROM THE UPPER CRETACEOUS EAGLE FORMATION (SANTONIAN, NORTHERN MONTANA, USA), AND MAMMAL DIVERSITY DURING THE AQUILAN NORTH AMERICAN LAND MAMMAL AGE

BRIAN M. DAVIS, RICHARD L. CIFELLI, and JOSHUA E. COHEN

Mammalian faunas in North America experienced dramatic change during the Cretaceous, with earlier faunas characterized by eutriconodontans, symmetrodontans, and unspecialized therians giving way to a major diversification of therian lineages by the Campanian–Maastrichtian. The Aquilan North American Land Mammal Age (NALMA), originally based on the well-studied fauna of the Milk River Formation (Santonian) of southern Alberta, records the start of this transition. Notable are first appearances of pediomyoid marsupialiforms and the eutherian *Paranyctoides*, and last occurrences of eutriconodontans and symmetrodontans. The Campanian Wahweap Formation has yielded a similar fauna, but until now the John Henry Member of the Straight Cliffs Formation was the only other unit of known Santonian age from which fossil mammals have been recovered, leaving this transitional interval represented by limited sampling. The Eagle Formation in central and northern Montana is considered to be laterally equivalent to the Milk River Formation, with northernmost exposures correlated to the upper Santonian, based on palynomorphs and magnetostratigraphy. Here, we describe the first fossil mammals known from the Eagle Formation. A relatively small rock sample yielded a rich, diverse assemblage including two genera of spalacotheriid symmetrodonts, several "alphadontid" marsupialiforms and the large pediomyoid *Aquiladelphis*, and at least two eutherians including *Paranyctoides*. Multituberculates, to be described separately, are also abundant and diverse. The Eagle Formation assemblage is broadly similar in composition to that from the Milk River Formation, but shares the spalacotheriid *Spalacotheridium* with older units, including the Straight Cliffs Formation from southern Utah. These initial results provide another biostratigraphic data point linking Santonian faunas across a broad latitudinal range, and encourage reevaluation of the Aquilan NALMA.

Key words: Mammalia, Late Cretaceous, Symmetrodonta, Tribosphenida, Aquilan, Eagle Formation.

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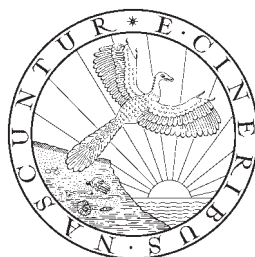
INTRODUCTION

Late Cretaceous terrestrial faunas are unquestionably the most thoroughly studied and best known assemblages of the North American Mesozoic. In particular, numerous studies documenting the diversity and ultimate turnover of communities at the K-Pg event have given us incredibly fine-scale details of the rise and fall of dinosaurs and mammals (Archibald and Fastovsky 2004; Cifelli *et al.* 2004; Wilson 2005, 2013, 2014; Sprain *et al.* 2015). Slightly older assemblages of Campanian age (83.6–72.1 Mya, Gradstein *et al.* 2012) are also well represented; in particular, faunas of the Kaiparowits (Utah) and Dinosaur Park (Alberta) formations have been heavily sampled (see reviews in Currie and Koppelhus 2005 and Titus and Loewen 2013, and references therein). Among therian mammals, the Campanian–Maastrichtian interval documents a substantial diversification event. Marsupialiform groups such as pediomyoids and "alphadontids" become highly diverse and are by far the most abundant therians in the latter part of the Late Cretaceous (Clemens 1966; Lillegraven 1969; Montellano 1992; Johanson 1996; Kielan-Jaworowska *et al.* 2004; Davis 2007; Williamson *et al.* 2012; Eaton and Cifelli 2013). Eutherians, on the other hand, exhibited little known diversity during the Early Cretaceous (Cifelli 1999a; Davis and Cifelli 2011; Cifelli and Davis 2015) and disappeared from the record before reemerging in the Santonian (Fox 1970) and reaching a moderate diversity by the close of the Period (Kielan-Jaworowska *et al.* 2004; Archibald *et al.* 2011). Some recent molecular analyses (*e.g.*, Meredith *et al.* 2011) have proposed that this Cretaceous diversity included the origin of crown Placentalia.

The mammalian record for the entire Early Cretaceous of North America is represented by only a handful of assemblages, many of which await full description. Of these, the best known are the historically important fauna from the Trinity Group of Oklahoma and Texas, and the contemporaneous Cloverly Formation in Montana and Wyoming (Patterson 1956; Butler 1978; Jenkins and Schaff 1988; Cifelli 1999a; Davis and Cifelli 2011, references therein; Cifelli and Davis 2015). The therian mammals are generally plesiomorphic; though these faunas are characterized by the classic "Theria of metatherian-eutherian grade" (Patterson 1956), it is likely that both metatherians and eutherians achieved unappreciated morphological and taxonomic diversity by the Albian (Cifelli and Davis 2015). Spalacotheriid symmetrodontans are present but poorly known in the Early Cretaceous of North America (Patterson 1955; Cifelli *et al.* 2014); they would explode in number and diversity by the Cenomanian, as evident in the well-sampled Cedar Mountain Formation in southern Utah (Cifelli and Madsen 1999), and persist as uncommon faunal elements until the early Campanian (Cifelli and Madsen 1986). Eutriconodontans were also diverse during the Early Cretaceous, represented by *Gobiconodon* and numerous alticonodontine triconodontids (Patterson 1951; Jenkins and Schaff 1988; Cifelli *et al.* 1998, 1999); this group is rare during the Late Cretaceous (Fox 1969; Cifelli and Madsen 1998), and is last recorded in the Santonian (Fox 1976; Eaton 2013).

The composition of North American mammalian faunas changed dramatically during the Cretaceous. Unfortunately, sampling during the first part of the Late Cretaceous (Cenomanian–Santonian) is uneven and generally poor, resulting in an incomplete understanding of this transition. Nearly all of our knowledge of this interval comes from sites in southern Utah (see summaries in Kielan-Jaworowska *et al.* 2004; Eaton and Cifelli 2013), with the best-studied faunas hailing from the Cedar Mountain and Dakota formations (Albian–Cenomanian and upper Cenomanian, respectively). Of note are the diversity of metatherians (Cifelli and Eaton 1987; Cifelli 1993, 2004; Eaton 1993, 1995, 2009; Cifelli and Muizon 1997) and the apparent absence of eutherians, a pattern in contrast with that observed in Asia (Archibald and Averianov 2005; Chester *et al.* 2010). Small, sparse samples of Turonian–Coniacian age are known from the Straight Cliffs Formation (Cifelli 1990a; Eaton 1995, 2006a; Cifelli and Gordon 1999), with the therians either largely indeterminate or unstudied. Eutriconodontans, which are diverse in the Cedar Mountain Formation, are not recorded again until the Santonian, while spalacotheriid symmetrodontans are present but rare. The fossil record from the Santonian is appreciably better, but sampling is still quite limited. A small but diverse fauna has been recovered from the Iron Springs Formation (Eaton 1999; Eaton *et al.* 2014), but the age of the unit is poorly constrained and could range from Cenomanian to early Campanian. Otherwise, knowledge of Santonian mammals from North America is currently limited to fossils from the John Henry Member of the Straight Cliffs Formation in southern Utah (Eaton 2006b, 2013) and the Milk River Formation in southern Alberta (R. C. Fox references, see below). Metatherian diversity is very high, with the appearance of pediomyoids and several "alphadontid" genera alongside more generalized forms, and eutherians are recorded for the first time since the Albian.
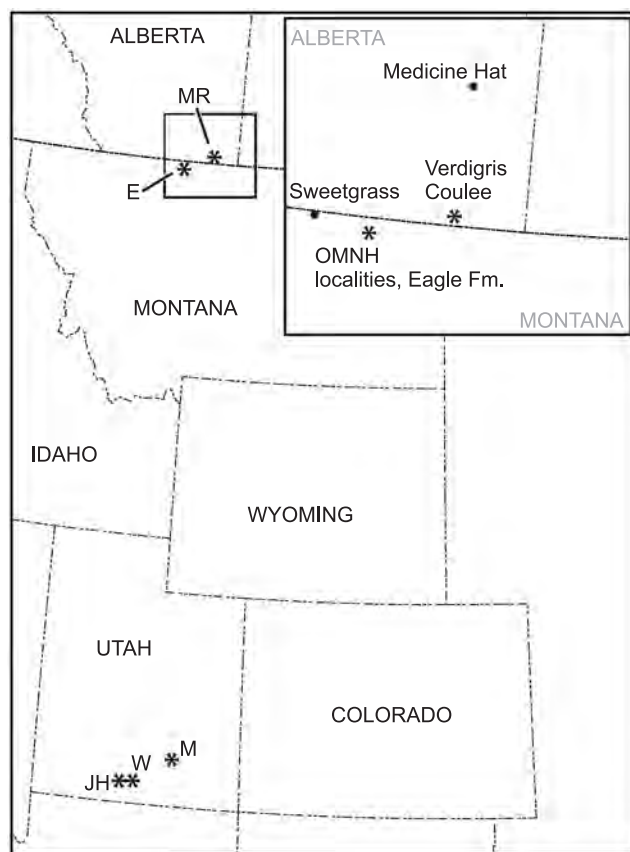
Fig. 1. Map of Aquilan North American Land Mammal Age localities (asterisks). Mammal localities from the John Henry Member of the Straight Cliffs Formation and Wahweap Formation are known on both the Paunsaugunt and Kaiparowits plateaus in southern Utah, and cannot be differentiated from one another at the scale of this map. Enlarged section shows Verdigris Coulee (Milk River Formation) and OMNH localities described in this paper (Eagle Formation). Abbreviations: E, Eagle Formation; JH, John Henry Member of Straight Cliffs Formation; M, Masuk Formation; MR, Milk River Formation; W, Wahweap Formation.

The mammalian fauna of the Milk River Formation, from a few localities in Verdigris Coulee, has been extensively studied by Richard C. Fox, resulting in a long series of publications (Fox 1968, 1969, 1970, 1971a, b, 1972a, b, 1976, 1980, 1982, 1984a, b, 1985, 1987; Montellano-Ballesteros et al. 2013; Montellano-Ballesteros and Fox 2015). This fauna records a number of notable first appearances, such as pediomyoids (*Aquiladelphis*), the stagodontid *Eodelphis*, and the eutherian *Paranyctoides*, as well as the last occurrence of eutriconodontans (*Alticonodon*). Because of these important differences with regard to older assemblages, the Milk River fauna was designated as the type for the Aquilan North American Land Mammal Age (NALMA) by Lillegraven and McKenna (1986). The Aquilan was expanded by Cifelli *et al.* (2004) to include a similar fauna from the early–middle Campanian Wahweap Formation and the faunule from a stratigraphically correlative unit, the Masuk Formation, both in southern Utah. While slightly older than the Milk River assemblage, the mammalian fauna from the upper part of the John Henry Member of the Straight Cliffs Formation is also broadly similar (Eaton and Cifelli 2013); for convenience of faunal comparisons, we provisionally refer it to the Aquilan (see the Discussion, below). Problems with the definition of the Aquilan, specifically with regard to the correlation of the Wahweap Formation, have been pointed out by several authors (Eaton 2013; Eaton and Cifelli 2013; Jinnah 2013); this issue will be explored below in the Discussion.

The Milk River Formation has a stratigraphic correlate exposed in central and northern Montana, the Eagle Formation (considered to be almost entirely Santonian in age, see Geologic Setting section, below). While the under- and overlying marine units contain invertebrate fossils and shark teeth, only palynomorphs have been recovered and studied from the Eagle Formation (Payenberg *et al.* 2002); no vertebrate fossils have been unambiguously described from the unit. Somewhat problematic dinosaur material, described by Marsh (1890) as the types of *Ornithomimus tenuis* and *O. grandis*, is possibly from the Eagle Formation. Marsh (1890, p. 85) states that these specimens were recovered from the same horizon but gives no locality details. In their thorough treatment of the fossils and geology in the Missouri Breaks region, Stanton and Hatcher (1905, p. 87) list the younger Judith River Formation as provenance for *O. tenuis* but claim unequivocally that the *O. grandis* material is from sandstones of the older Eagle Formation. Unfortunately, the type of *O. grandis* is lost (Gilmore 1920).

Field parties from the OMNH explored exposures of the Eagle Formation in the Sweet Grass Hills in northeastern Toole County, Montana in 2004 and 2005 (Fig. 1). Screen washing of small rock samples yielded abundant vertebrate fossils (see Methods and Conventions section, below), including fragmentary remains of osteichthyians, chondrichthyans, chelonians, lissamphibians, lacertilians, crocodilians, dinosaurs, and mammals. In addition to the symmetrodontan and therian fossils described in this paper, the OMNH collection from the Eagle Formation also includes relatively abundant and diverse multituberculate material, constituting nearly half of the informative mammalian specimens in the available sample. The multituberculates, which present their own unique challenges, are excluded from this paper and will be the focus of a subsequent study.

This paper is in tribute to the late Professor Zofia Kielan-Jaworowska, in recognition of her foundational work on mammals from the Cretaceous of central Asia. Of particular relevance to this present work are her discovery, description, and interpretation of wonderfully complete eutherian specimens from Campanian units in Mongolia (Kielan-Jaworowska 1969, 1975, 1977, 1978, 1984a–c). This series of publications placed the focus of early eutherian diversification squarely on the Asian landmass and provided vital points of morphological comparison for later studies of therian evolution and dispersal.

Institutional abbreviations. — AMNH, American Museum of Natural History, New York, New York, USA; MNA, Museum of Northern Arizona, Flagstaff, Arizona, USA; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; and UMNH, Utah Museum of Natural History, Salt Lake City, Utah, USA.

GEOLOGIC SETTING

The Upper Cretaceous Eagle Formation was deposited along the margin of the Western Interior Foreland Basin. The unit was first described as the Eagle Sandstone by Weed (1889), and later divided into three members by Bowen (1914; see Rice 1980; Meijer-Drees and Mhyr 1981 for summaries of early work on the unit). The unit is generally regarded as representing a progradational clastic wedge situated stratigraphically between two transgressive shale wedges (the Niobrara Formation below and the Claggett Formation above; Fig. 2). The Eagle Formation and the laterally equivalent Milk River Formation (see below) have been thoroughly studied due to their role as reservoirs of large amounts of biogenic gas (*e.g.*, Rice 1980; Ridgley 2000; Payenberg and Braman 2003). Thick, cliff-forming sandstones within the Eagle Formation (specifically the Virgelle Member) are responsible for the characteristic white bluffs of the Missouri Breaks region along the Missouri River in north-central Montana; the stratigraphic section is best exposed in this area and has received most attention. Farther north near the Canadian border, the Eagle Formation is exposed very locally along the flanks of a local uplift called the Sweet Grass Hills, a series of buttes (some of which are nearly 1000 m tall) in northern Toole and Liberty counties. These exposures yielded the fossils in this study.

The Eagle Formation sits conformably on the Telegraph Creek Formation, a sequence of dark, sandy shales that is thought to represent the transition from the open marine deposition of the Niobrara Formation to the shoreface and fluvial environments recorded by the Eagle Formation (Rice 1980; Payenberg and Braman 2003). The Eagle Formation is divided into three lithostratigraphic members (Fig. 2), the lowest of which is the Virgelle Member (the transition from the Telegraph Creek Formation is defined by the absence of shale beds). This predominately sandstone unit is generally massive, resistant, and cliff-forming, weathering at its top into small hoodoos. The lower portion preserves hummocky and swaley cross-stratification, which suggests storm-dominated deposition along the shoreface (Leckie and Cheel 1986; Meyer *et al.* 1998); upper portions of the member are more tabular. The overlying Deadhorse Coulee Member is entirely non-marine in origin, containing alternating mudstones, siltstones, and sandstones with occasional thin coal

Epoch	Stage		SOUTH-CENTRAL ALBERTA	NORTH-CENTRAL MONTANA	SOUTHERN UTAH
UPPER CRETACEOUS	CAMPANIAN		PAKOWKI FORMATION	CLAGGET FORMATION	WAHWEAP FORMATION
		80.7 Ma —	Ardmore bentonite	Ardmore bentonite	
		81.2 Ma —	HIATUS (MILK RIVER FORMATION)	UPPER EAGLE MEMBER (EAGLE FORMATION)	DRIP TANK MEMBER (STRAIGHT CLIFFS FORMATION)
	SANTONIAN	83.5 Ma —	DEADHORSE COULEE MEMBER	DEADHORSE COULEE MEMBER	JOHN HENRY MEMBER
			VIRGELLE MEMBER	VIRGELLE MEMBER	
		84.5 Ma —	TELEGRAPH CREEK MEMBER	TELEGRAPH CREEK MEMBER	
			NIOBRARA FORMATION	NIOBRARA FORMATION	

Fig. 2. Chronostratigraphic column correlating rock units of Santonian–Campanian age in south-central Alberta, north-central Montana, and southern Utah. Modified from Payenberg *et al.* (2003, fig. 3).

seams (fluvial channels and crevasse splays, as well as coastal plain deposits related to a prograding deltaic system). Exposures are often banded in color. The Deadhorse Coulee Member is separated from the Upper Eagle Member by a minor transgressive event, marked by a sudden appearance of mud-rich sandstones with a marine influence (Payenberg and Braman 2003). The presence of flaser bedding and invertebrate ichno-fossils suggests a protected tidal environment, perhaps a bay or lagoon. The Upper Eagle Member thins northward through Montana and is not present in a studied section of the laterally equivalent Milk River Formation (see below) in Writing-On-Stone Provincial Park (WOSPP), southern Alberta (Payenberg *et al.* 2002). The contact between the Eagle Formation and the overlying Claggett Formation is unconformable and distinctly marked by a dark chert pebble bed, termed the Eagle Shoulder.

Age estimates for the Eagle Formation have varied with respect to the Santonian–Campanian boundary, with different data sources collected at different latitudes yielding alternate placements of the unit. However, refinements of the age of the boundary itself have driven some of this instability. For the sake of clarity, only the most recent work, by Brahman (2001) and Payenberg *et al.* (2002), will be summarized here (discussion of previous work can be found in these two papers). The lower age limit for the Eagle Formation is based on the assignment of the Telegraph Creek Formation near Shelby in far northern Montana to the *Desmoscaphites bassleri* ammonite zone (Cobban 1955). Obradovich (1993) dated the base of this zone at 84.5 Mya. U-Pb and ^{40}Ar-^{39}Ar dates from the Ardmore bentonite near the base of the Claggett-Pakowki transgression consistently date this event to ~81 Mya, throughout the latitudinal range of the unit from southern Alberta south to Wyoming (Hicks *et al.* 1995; Payenberg *et al.* 2002); this establishes an upper age limit to the sequence.

Leahy and Lerbekmo (1995) identified the 34n–33r reversal in the Deadhorse Coulee Member in southern Alberta; this paleomagnetic event is placed just below the Santonian–Campanian boundary by Montgomery *et al.* (1998). The boundary itself is defined biostratigraphically (last occurrence of the crinoid *Marsupites testudinanus*, Hancock and Gale 1996), and has been dated to 83.5 Mya (Obradovich 1993). It is therefore likely, based on current data, that all or nearly all of the Eagle Formation is late Santonian in age and was deposited between 84.5–83.5 Mya. However, this applies only to the unit where it occurs in northern and north-central Montana. In the Elk Basin in southern Montana/northern Wyoming, Hicks *et al.* (1995) placed the entire Eagle Formation within chron 33r and dated a bentonite in the Upper Eagle Member at 81.14 ± 0.51 Mya, only slightly older than the Claggett transgression. The Eagle Formation appears to be time transgressive, with the southern-most portions of the unit being almost entirely Campanian in age.

Vertebrate fossils were recovered from four closely-spaced localities (within a few hundred meters lat-erally and no more than ten vertical meters), two of which yielded mammals and will be the focus of this paper (OMNH V1409 and V1412; specific coordinates are on file at the OMNH and are available to qualified investigators upon request). The exposures are within the Sweet Grass Hills in northeastern Toole County, Montana and consist of horizontal but laterally variable lenses of mudstones, sandstones, siltstones, and some very thin coal beds. No clear stratigraphic boundaries within the section were observed, and the tops and flanks of the exposures are grass-covered, hampering lateral correlation with any other exposures. The most productive microvertebrate locality (OMNH V1409) occurs in a fine, dull white sandstone containing dispersed invertebrate shell fragments, though an occasional complete but unarticulated pelecypod valve or gastropod steinkern is present. This sandstone sits on a structureless gray green mudstone, fines upward into a gray sandy mudstone, and is capped by another structureless gray green mudstone. Immediately lateral to this is a well indurated, approximately 0.8 m sandstone lens. OMNH V1412 occurs in a slumped, heavily weathered block of drab varicolored mudstone in shades of tan, green, and gray. This mudstone contains dispersed pebble- to small cobble-sized sideritic nodules. Exact stratigraphic context is impossible to de-termine, but it appears that the block slumped from lower in the section than V1409. The OMNH localities derive from vertically limited (10–15 m) exposures of the Eagle Formation; lithology throughout this section is characteristic of Deadhorse Coulee Member. While placement within the Upper Eagle Member cannot be entirely ruled out, this member is dominantly marine and thins northward, being absent at WOSPP; it is unknown if the Upper Member is present in the study area in northern-most Montana. The OMNH localities are only ~20 km southeast of WOSPP and preserve terrestrial and freshwater vertebrates, lending strong support to their stratigraphic placement within the Deadhorse Coulee Member.

CORRELATION WITH THE MILK RIVER FORMATION

The Eagle and Milk River formations are lithologically very similar and are divided laterally by noth-ing more than the international border. The Milk River Formation has been extensively studied in south-ern Alberta in and around WOSPP (Meijer-Drees and Mhyr 1981; McCrory and Walker 1986; Cheel and Leckie 1990; Payenberg *et al.* 2002; Meyer and Krause 2006). In Alberta, the Telegraph Creek Formation is included as the lowermost member of the Milk River Formation, with the Virgelle and Deadhorse Coulee members equivalent in status to their counterparts in the Eagle Formation (Fig. 2). Similarities in palyno-flora between the Virgelle and Deadhorse Coulee members of the Milk River Formation in WOSPP and the same members of the Eagle Formation in north-central Montana (near the Missouri River) suggest that these units are time-equivalent in these areas (Payenberg *et al.* 2002). An equivalent to the Upper Eagle Member is absent from exposures of the Milk River Formation in WOSPP, but the Deadhorse Coulee Member is capped by the same chert pebble bed which marks the top of the Eagle Formation in Montana. A hiatus of some 2.5 Ma is interpreted between the end of Milk River deposition and the Pakowki marine transgression (equivalent to the Claggett Formation), based on the presence of the 34n–33r reversal in the upper Deadhorse Coulee Member (Leahy and Lerbekmo 1995) and radiometric dates from the Ardmore bentonite in the Pakowki Formation (Hicks *et al.* 1995); this, presumably, was when the Upper Eagle Member was depos-ited in central and southern Montana (Payenberg *et al.* 2002). East of WOSPP and further basin-ward, the Alderson Member of the marine Lea Park Formation is likely time-equivalent with the Upper Eagle Member (Ridgley 2000). As summarized above, additional data from ammonites and magnetostratigraphy (Hicks *et al.* 1995) suggest that the entire Eagle Formation in southern Montana and Wyoming is lower Campanian in age and likely younger than exposures to the north, including most or all of the Milk River Formation. A complex picture thus emerges for the dynamic western shoreline of the Western Interior Seaway during the Santonian–Campanian.

The OMNH localities in the Eagle Formation are some 150 km away from the nearest studied section of the unit (along the Missouri Breaks in north-central Montana), making them difficult to place, both stratigraphically and chronologically, within the time transgressive latitudinal variation identified in the Eagle Formation. Considering the relative proximity of the OMNH localities to exposures of the Milk River Formation, the best correlation is likely with the Deadhorse Coulee Member in southern Alberta. As will be discussed below, the mammalian fauna overlaps broadly with that known from the Milk River Formation. It is on this basis that we tentatively assign a latest Santonian age to the OMNH localities in the Eagle Formation.

METHODS AND CONVENTIONS

Over the course of two field seasons (2004 and 2005), the OMNH processed 1100–1400 kg of sediment from OMNH V1409 and V1412 through underwater screen washing, following standard microvertebrate recovery techniques (Cifelli *et al.* 1996). Approximately 170 mammalian specimens from these localities have been catalogued to date. Scanning electron micrographs of specimens (polyurethane resin casts) were obtained at the OMNH using a Denton Vacuum Desk II (gold/palladium) sputter coater and a LEO 1450VP SEM. Tooth measurements (all in millimeters) were taken with a Reflex Microscope (see MacLarnon 1989, Consultantnet Ltd, 94 High Street, Linton, Cambridge, CB21 4JT, UK), as defined by Lillegraven and McKenna (1986) and Lillegraven and Bieber (1986): AP, mesiodistal length of tooth, in approximate anatomical orientation (including the clingulid for symmetrodontan lower molars); ANW, anterior (mesial) width (trigonid width on lower molars; distance from edge of stylar shelf, buccal to paracone, to line going through protocone, parallel to line defined by apices of paracone and metacone on uppers); POW, posterior (distal) width (talonid width on lower molars; distance from distal stylar shelf [metastylar corner] to line going through protocone, parallel to line defined by apices of paracone and metacone on uppers). Measurements are given in Table 1 (specimens omitted from Table 1 were too incomplete to be measured). Specimens for which tooth position cannot be determined are denoted with "X" (*e.g.*, MX or mx). Tooth terminology and conventions follow Kielan-Jaworowska *et al.* (2004).

SYSTEMATIC PALEONTOLOGY

Superlegion **Trechnotheria** McKenna, 1975

Family **Spalacotheriidae** Marsh, 1887

Genus *Spalacotheridium* Cifelli, 1990a

Spalacotheridium mckennai Cifelli, 1990a

(Fig. 3A)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66376, left m5.

Description. — OMNH 66376 is a very small spalacotheriid lower molar (Table 1). It is moderately worn and nearly complete, missing the mesiolingual corner of the cingulid and the tip of the paraconid. The protoconid is the tallest cusp, and though somewhat abraded it was only ~50% taller than the metaconid. The preserved base of the paraconid suggests that it was likely subequal in height to the metaconid; this is supported by the roughly equal height of the notches in the protocristid and paracristid. The paraconid and metaconid are positioned close to one another but are slightly divergent, forming a trigonid angle of 35°. The cingulid is complete buccally, with the lingual portion highest between the roots and dipping farthest distally to the swollen but low heel.

Comments. — Subequal height of the paraconid and metaconid (or, as a proxy, the height of the notches in the protocristid and paracristid) indicates referral of this specimen to *Spalacotheridium*. Its small size is most consistent with *S. mckennai* from the slightly older Smoky Hollow Member of the Straight Cliffs Formation (Turonian, southern Utah). The only well-preserved specimens of this species that have been previously described (MNA V5792, Cifelli 1990a, fig. 1; MNA V6046 and V6756, Cifelli and Gordon 1999, fig. 6) are somewhat smaller still. The best-preserved of these, MNA V5792 and V6046, have a less acute trigonid angle and a lingual cingulid that is relatively horizontal instead of distally sloping as in OMNH 66376. However, these differences are likely attributable to tooth position, with the Eagle Formation specimen representing a more distal molar (see Cifelli and Madsen 1999, fig. 6). In addition to a smaller species from the older Cedar Mountain Formation (*S. noblei*, Cifelli and Madsen 1999), isolated lower molars of *Spalacotheridium* are known from the upper Santonian John Henry Member of the Straight Cliffs Formation (Eaton 2006b, 2013). While these specimens are larger still than OMNH 66376, they agree well in morphol-

Table 1. Dental measurements (mm) of mammals from the Eagle Formation (upper Santonian), Montana, USA. Specimens for which no complete standard measurements could be obtained are omitted.

Taxon	Tooth	ID (OMNH)	AP	ANW	POW
Spalacotheridium mckennai	m5	66376	0.73	0.93	–
Symmetrodontoides canadensis	p2	66373	1.55	0.45	–
	p4	66370	1.96	0.85	–
	m2	66371	1.06	1.21	–
	m5	66372	0.69	1.48	–
Varalphadon wahweapensis	M2	66379	1.79	1.74	1.87
	M3	66357	1.92	2.10	2.23
	M3	66358	1.99	–	–
Varalphadon sp.	dp3	66367	1.46	0.65	0.66
	m1	66362	1.70	0.86	0.86
	m2	66361	1.68	0.89	0.98
	m3	66388	1.92	1.15	1.13
Alphadon halleyi	M3	66382	–	–	2.25
	m2 or 3	66387	2.02	1.15	1.16
Albertatherium primus	M1	66378	2.15	–	–
	M2	66377	2.25	–	–
	m2 or 3	66380	2.14	1.24	1.20
Aquiladelphis incus	M3	66351	5.64	5.69	5.92
Aquiladelphis minor	m2	66353	3.83	2.63	2.20
Leptalestes sp.	mx	66366	–	–	0.65
Metatheria indet.	dp3 or m1	66341	1.38	0.64	0.73
Tribosphenida indet.	upper molariform	64165	2.67	2.94	2.56

ogy with material referred to the genus. Improved samples will be needed to determine if more than one species of *Spalacotheridium* is present in the Turonian–Santonian interval.

Genus ***Symmetrodontoides*** Fox, 1976

Symmetrodontoides canadensis Fox, 1976

(Fig. 3B–E)

Locality and horizon: All OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66373, right p2; OMNH 66370, right p4; OMNH 66371 right m2; 66372 left m5.

Description. — Two lower premolars from the Eagle Formation are here referred to a single spalacotheriid taxon. OMNH 66370 closely resembles UALVP 12086 from the Milk River Formation, which Fox (1976, fig. 4) identified as an m1 of *Symmetrodontoides canadensis* (we follow Cifelli 1999b in regarding this specimen as a p4). OMNH 66370 (Fig. 3C) differs only in having a slightly broader cingulid at the mesial extent of the crown, and a slightly taller distal heel cusp; the tooth is well preserved except for some minor abrasion to the buccal cingulid and tip of the protoconid, and wear along the main distal crest. OMNH 66373 (Fig. 3B) matches the expected size and morphology of a premolar one or two positions mesial to OMNH 66370, and we provisionally identify this specimen as a p2 of *S. canadensis* based on the patterns for spalacotheriid premolars proposed by Cifelli (1999a). The specimen is mesiodistally elongate and is missing the mesial-most part of the crown, so the presence or size of a paraconid is unknown. The protoconid is positioned mesial to the presumed mid-point of the crown, and is slightly lower as compared to the p4 protoconid. Its mesial slope is steep, with the distal slope broadly worn and bearing a low metaconid and an additional small cusp at the terminus of the main crest. The distal heel is similarly developed as on the p4, though it is positioned directly above the root instead of projecting distally. A narrow cingulid encircles the entire preserved portion of the crown.

OMNH 66371 (Fig. 3D), identified here as a complete but rather worn right m2, is identical to the second preserved tooth in the holotype of *Symmetrodontoides canadensis* (UALVP 8588; Fox 1972b, 1976). It has a trigonid angle of 35°. We follow Cifelli and Madsen (1999), who interpreted UALVP 8588 as preserving the m1–m3 (instead of m3–m5) based on comparisons with abundant spalacotheriid material from the Cedar Mountain Formation of Utah. Finally, OMNH 66372 (Fig. 3E) resembles an isolated molar identified by Fox
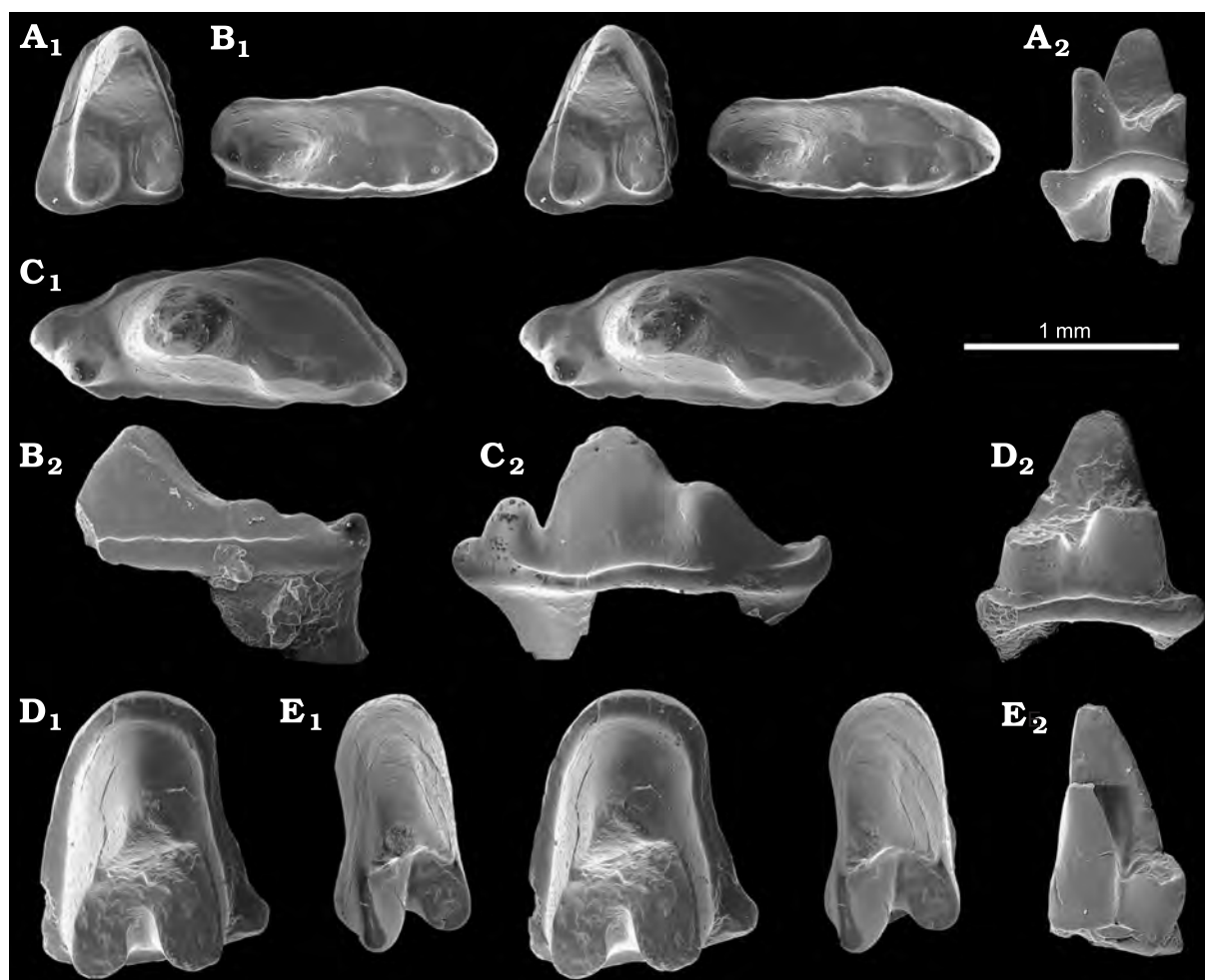
Fig. 3. Spalacotheriid symmetrodontans from the Eagle Formation (all OMNH locality V1409, Upper Cretaceous, Santonian, Montana). **A**. *Spalacotheridium mckennai*, OMNH 66376, left m5 in occlusal (A$_1$, stereopair) and lingual (A$_2$) views. **B–E**. *Symmetrodontoides canadensis*. **B**. OMNH 66373, right p2 in occlusal (B$_1$, stereopair) and lingual (B$_2$) views. **C**. OMNH 66370, right p4 in occlusal (C$_1$, stereopair) and lingual (C$_2$) views. **D**. OMNH 66371, right m2 in occlusal (D$_1$, stereopair) and lingual (D$_2$) views. **E**. OMNH 66372, left m5 in occlusal (E$_1$, stereopair) and lingual (E$_2$) views.

(1976, fig. 5, UALVP 12087) as the m6. The base of the crown is broken on the OMNH specimen, such that the cingulid and heel are missing, and the tip of the paraconid is damaged. The tooth is tall yet strongly mesiodistally compressed (trigonid angle 31°), and was likely only slightly narrower than the m2. The paraconid appears to have been considerably lower than the metaconid, which is slightly recurved and somewhat heavier in comparison to UALVP 12087. Due to damage and incomplete knowledge of the molar series of *Symmetrodontoides*, it is difficult to determine with certainty which position OMNH 66372 represents. Its morphology is consistent, however, with the antepenultimate molar in reference to spalacotheriids from the Cedar Mountain Formation and we tentatively identify it as an m5.

Comments. — Symmetrodontans are distinctive but rather rare components of the Eagle fauna, comprising roughly 4% of the catalogued mammalian specimens. By comparison, this group accounts for nearly a third of mammalian species, and nearly 40% of specimens identified to species level, in the Albian–Cenomanian Mussentuchit local fauna in the Cedar Mountain Formation (Cifelli and Madsen 1999; Cifelli *et al.* 2016 this volume).

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Subclass **Tribosphenida** McKenna, 1975

Infraclass **Metatheria** Huxley, 1880

Family "**Alphadontidae**" Marshall, Case, *et* Woodburne, 1990

Genus *Varalphadon* Johanson, 1996

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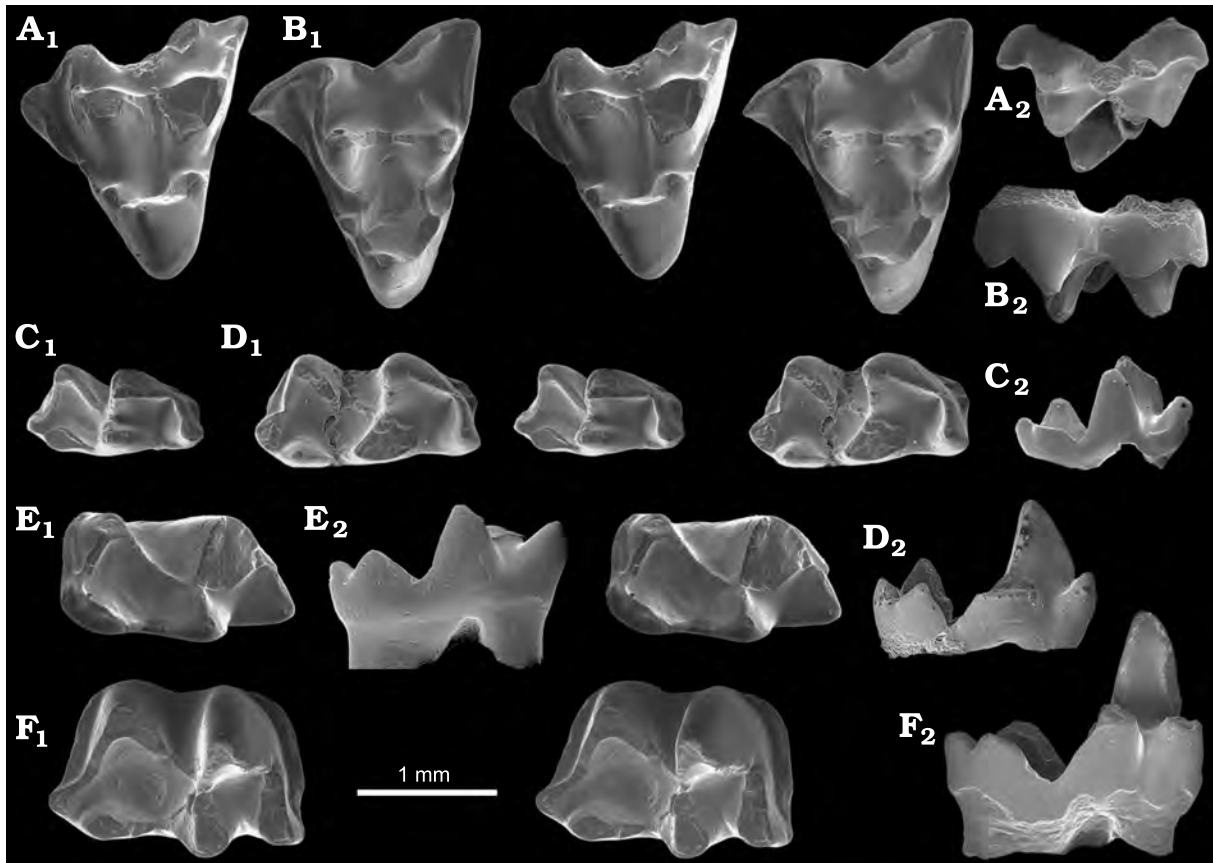
Fig. 4. The "alphadontid" marsupialiforms *Varalphadon wahweapensis* and *Varalphadon* sp. from the Eagle Formation (Upper Cretaceous, Santonian, Montana). **A–B**. *Varalphadon wahweapensis* (all OMNH locality V1409). **A**. OMNH 66379, left M2 in occlusal (A_1, stereopair) and buccal (A_2) views. **B**. OMNH 66357, left M3 in occlusal (B_1, stereopair) and buccal (B_2) views. **C–F**. *Varalphadon* sp. **C**. OMNH 66367 (OMNH locality V1409), left dp3 in occlusal (C_1, stereopair) and lingual (C_2) views. **D**. OMNH 66362 (OMNH locality V1409), left m1 in occlusal (D_1, stereopair) and lingual (D_2) views. **E**. OMNH 66361 (OMNH locality V1409), left m2 in occlusal (E_1, stereopair) and lingual (E_2) views. **F**. OMNH 66388 (OMNH locality V1412), left m3 in occlusal (F_1, stereopair) and lingual (F_2) views.

Varalphadon wahweapensis (Cifelli, 1990b)

(Fig. 4A, B)

Locality and horizon: All OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66379, left M2; OMNH 66357, left M3; OMNH 66358, left M3 missing protoconal region (not illustrated).

Description. — Two upper molars from the Eagle Formation are referred to *Varalphadon wahweapensis*. OMNH 66379 (Fig. 4A) is a slightly damaged left M2, missing most of the metacone and bearing abrasion to the tips of the paracone and stylar cusps. The metacone has a broader base than the paracone, but the relative height of the cusps is impossible to determine. While not connected at their bases, the two cusps are not widely spaced. The centrocrista is straight. The protocone is large but uninflated and unexpanded, with the lingual half of the crown somewhat narrow. The conules are well developed, bear very weak internal cristae, and are positioned close to the protocone; they flank a deep trigon basin. The preprotocrista continues past the paraconule to connect to the parastyle, while the postprotocrista does not extend buccally past the metacone. The preparacrista is short, notched, and travels to a large stylocone situated very close to the paracone. The postmetacrista is relatively short and oblique; it does not bear a substantial notch, and terminates at a low metastyle. The parastyle is about half the height of the stylocone and is connected to it by a weak crest. Stylar cusps are present at the C and D positions, but both are damaged. Cusp C is situated at the center of the shallow ectoflexus and, judging from what is left of its base, it was low and roughly conical. Cusp D is larger and more elongate, aligned with the ectocingulum and positioned directly buccal to the metacone.

OMNH 66357 (Fig. 4B) is a well-preserved left M3, agreeing very closely with other material in the OMNH collection referred to *Varalphadon wahweapensis*. The metacone is broader than the paracone but is subequal in height. The protoconal region is wider transversely than the M2, with conules farther spaced from the protocone and bearing stronger internal cristae. The stylocone is better separated buccally from the paracone, but the parastylar lobe is still narrower than the metastylar lobe and the ectoflexus is shallow. The postmetacrista is longer and oriented in a more directly buccal fashion. A tiny cuspule is present just mesial to the center of the ectoflexus, but a developed stylar cusp C is absent.

Comments. — These two specimens closely resemble material from the coeval John Henry Member of the Straight Cliffs Formation and younger Wahweap and Kaiparowits formations (Cifelli 1990b, c; Eaton 2013). Upper molars of *Varalphadon wahweapensis* are differentiated from those of *V. creber* in relative narrowness of the parastylar lobe; this is most apparent on M3 (Johanson 1996). The referred upper molars here show variation in development of stylar cusp C, a particularly labile character among specimens referred to this genus.

Varalphadon sp.
(Fig. 4C–F)

Locality and horizon: OMNH V1409 and V1412 (only OMNH 66388), Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66367, left dp3; OMNH 66362, left m1; OMNH 66361, left m2; OMNH 66388, left m3.

Description. — OMNH 66367 (Fig. 4C) is small and low crowned, with a widely open trigonid and low, procumbent paraconid—all features typical of metatherian deciduous lower premolars (*e.g.*, Clemens 1966; Cifelli and Muizon 1998). The tip of the protoconid is broken, but this cusp was heavier but only slightly taller than the metaconid. The paraconid is widely spaced from the metaconid but positioned directly mesial to it (on a line passing through the entoconid and metaconid). Cusp f is developed as an oblique shelf, while only a faint vertical keel is present in the position of cusp e along the mesial edge of the paraconid. The talonid is wider than the trigonid. The hypoconid is the largest talonid cusp; the entoconid is somewhat broad and strongly twinned with the hypoconulid. The cristid obliqua meets the trigonid below the protocristid notch, and there is a strong buccal postcingulid.

OMNH 66362 (Fig. 4D) is larger with a more acute trigonid, but otherwise shares many similarities with the dp3. The paraconid is low and procumbent; the metaconid is broken but was clearly much taller, and this cusp pinches distally into a sharp crest descending to meet the entocristid at a notch. The talonid is subequal to slightly wider than the trigonid, and shows the same morphology as the dp3 except that the entoconid is somewhat less elongate and more conical. The relatively low-crowned trigonid coupled with a wide talonid suggest this is a first molar.

OMNH 66361 (Fig. 4E) agrees with the other two lower molars in general morphology except that it is slightly larger, with a larger paraconid (though still lower than the metaconid). The protoconid is broken at its base, but the tooth is otherwise complete. The metaconid is relatively heavy. The talonid matches the other specimens in morphology, and is slightly wider than the trigonid. The base of the talonid is lower than the base of the trigonid in buccal view, suggesting that this tooth is from the middle of the molar series, probably m2.

OMNH 66388 (Fig. 4F) is slightly larger than OMNH 66361 and differs in morphology, consistent with a tooth from one position farther distal. The trigonid cusps form a more acute angle, and the talonid is slightly narrower in comparison to the trigonid. Otherwise, this specimen agrees well with the others assigned to *Varalphadon*: the paraconid is lower than the metaconid, and the entoconid is broad.

Comments. — As highlighted recently by Eaton (2013), there is a paucity of diagnostic lower molar characters for many generally primitive "alphadontid"-grade taxa; in her revision of the group, Johanson (1996) focused primarily on upper molar morphology. There are currently no described lower molars for *Apistodon*, known from the Milk River and Straight Cliffs formations (Fox 1971a; Davis 2007; Eaton 2013) and expected to occur (though not yet recognized) in the Eagle Formation. *Apistodon* does not differ tremendously from *Varalphadon* in upper molar morphology and should be expected to possess lower molars which are also very similar and perhaps difficult to distinguish with certainty. It is possible that future discoveries of more complete material and larger sampling will necessitate reevaluation of lower molars currently assigned to *Varalphadon* and similar taxa.

Genus *Alphadon* Simpson, 1927

Alphadon halleyi Sahni, 1972

(Fig. 5A, B)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66382, left M3 missing mesiobuccal corner; OMNH 66387, left m2 or m3.

Description. — OMNH 66382 (Fig. 5A) is identified as M3 based on the width of the distal stylar shelf relative to the lingual portion of the crown and the buccal orientation of the postmetacrista. The parastylar lobe is missing. The paracone and metacone are rounded, subequal in height, and well separated at their bases. The protocone is large and slightly inflated; the conules are accordingly well developed with strong internal cristae. Stylar cusps C and D are both moderately developed, with D slightly larger than C. The ectoflexus appears to have been rather shallow, with cusp C positioned distal to its midpoint. The postprotocrista does not extend buccally past the metacone.

OMNH 66387 (Fig. 5B) is likely from the middle of the lower molar series, as suggested by the relative heights of the bases of the trigonid and talonid in buccal view. It compares very well with specimens assigned to *Alphadon halleyi* from the Judith River Formation (particularly UCMP 131267, Montellano 1992). The tooth is well worn along the crests, with the hypoconid particularly worn and probably damaged. The paraconid is slightly lower than the metaconid, somewhat procumbent, and positioned slightly buccal to the metaconid—features typical of *Alphadon* lower molars. The talonid is slightly wider than the trigonid. Other aspects of its morphology are typical, and do not warrant full description.

Comments. — The upper molar from the Eagle Formation (OMNH 66382) agrees well with species of *Alphadon* (as opposed to *Varalphadon*) in having well-separated paracone and metacone and more robust protoconal region, while the lower molar has a relatively wider talonid. Referral to *Albertatherium* is unlikely, as stylar cusp C is small and positioned distal to the center of a shallow ectoflexus; the lower molar is smaller than specimens referred to *Albertatherium*, with weaker crests and a relatively taller protoconid. A lower molar from the John Henry Member (Santonian) of the Straight Cliffs Formation, described by Eaton (2006b), was left in open nomenclature but closely allied to *Alphadon halleyi*. Otherwise, this species is distributed broadly during the Judithian, from the Dinosaur Park (Fox 1979a), Judith River (Sahni 1972; Montellano 1992), Kaiparowits (Cifelli 1990b), and Aguja (Cifelli 1994) formations. Both Eagle Formation specimens are within the size range of molars referred to *A. halleyi*, and are smaller than molars referred to *A. sahnii* (see Montellano 1988; Montellano 1992; Cifelli 1994).

Genus *Albertatherium* Fox, 1971a

Albertatherium primus Fox, 1971a

(Fig. 5C, D)

Locality and horizon: All OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66378, right M1 missing protoconal region; OMNH 66377, left M2 missing protoconal region; OMNH 66391, fragmentary left M4.

Description. — OMNH 66378 is heavily worn and broken, but differs from OMNH 66377 only in morphology expected of a mesial molar (parastyle lingual in position and in line with the paracone and metacone, and a slightly more oblique postmetacrista). It is accordingly not illustrated here. OMNH 66377 (Fig. 5C) is missing the lingual portion of the crown, including the protocone and paraconule. It is identified as M2 based on the slightly narrower parastylar lobe as compared to the metastylar lobe (nearly equal in width on M3). The paracone and metacone are subequal in height with the metacone slightly broader. Crests are all well developed; the postmetacrista is long and mainly buccal in orientation, but not particularly tall nor notched. The preparacrista bows mesially before doubling back toward the apex of the very large stylocone (the preparacrista runs toward the parastyle in some specimens referred to *Albertatherium*, see Fox 1971a; Johanson 1994). A sharp, slightly notched crest connects the apices of the stylocone and parastyle, the latter of which bears a strong mesial keel which would likely have overlapped the preceding molar. Stylar cusps C and D are also large; cusp C is conical and positioned at or just distal to the center of a deep, somewhat wide ectoflexus. Cusp D is not connected to cusp C, though it has several short crests descending from
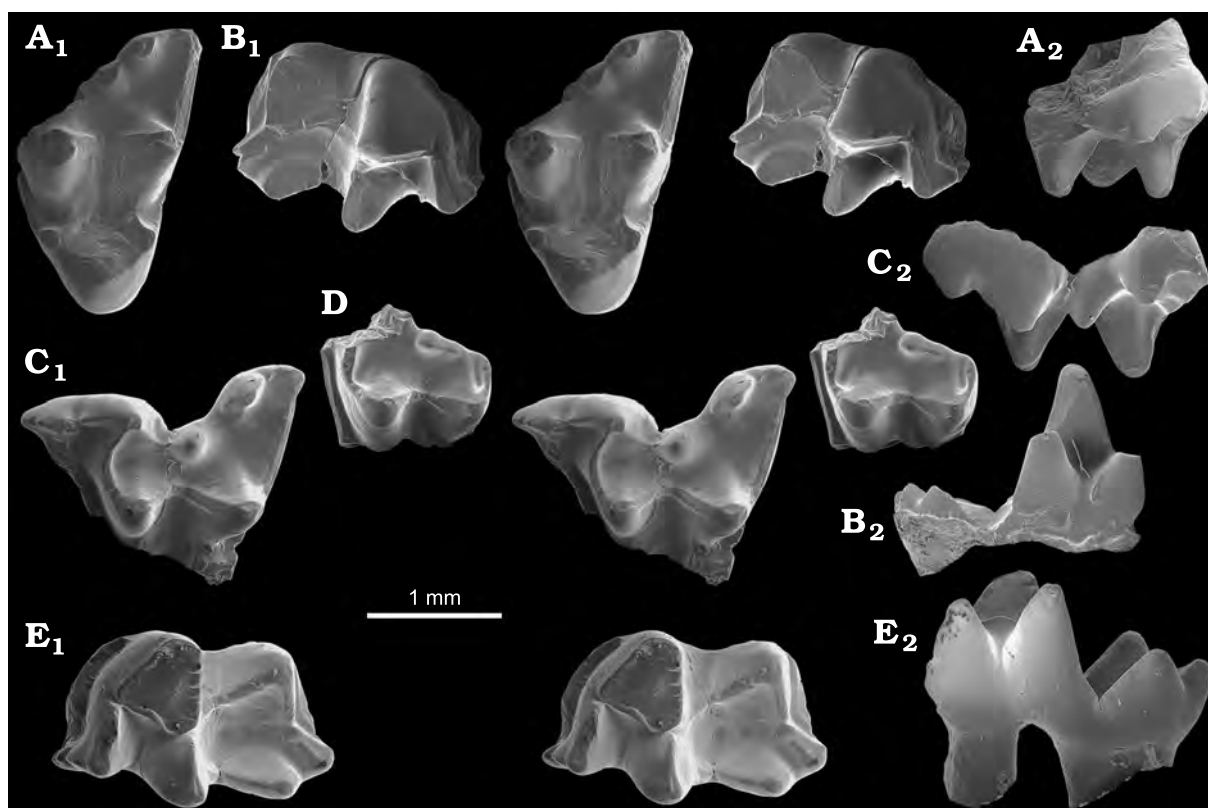
Fig. 5. The "alphadontid" marsupialiforms *Alphadon halleyi*, *Albertatherium primus* and *Albertatherium* sp. from the Eagle Formation (all OMNH locality V1409, Upper Cretaceous, Santonian, Montana). **A**, **B**. *Alphadon halleyi*. **A**. OMNH 66382, left M3 in occlusal (A_1, stereopair) and buccal (A_2) views. **B**. OMNH 66387, left m2 or m3 in occlusal (B_1, stereopair) and lingual (**B**2) views. **C**, **D**. *Albertatherium primus*. **C**. OMNH 66377, left M2 in occlusal (C_1, stereopair) and buccal (C_2) views. **D**. OMNH 66391, left M4 in occlusal (stereopair) view. **E**. *Albertatherium* sp., OMNH 66380, right m2 or m3 in occlusal (E_1, stereopair) and lingual (E_2) views.

its apex. Part of the metaconule is preserved, and internal conular cristae were present. The postprotocrista does not extend buccally past the metacone.

OMNH 66391 (Fig. 5D) has the reduced metacone and metastylar lobe typical of ultimate molars. The parastylar lobe and lingual half of the crown are missing. The paracone agrees well in size and shape with OMNH 66377, and the preserved part of the tooth is morphologically appropriate for referral to the same taxon. The preparacrista is strong and notched, and stylar cusp C is large and centrally positioned. Though short, the postmetacrista is also well developed.

Comments. — The spellings of the species names for *Albertatherium* were incorrectly emended by Kielan-Jaworowska *et al.* (2004) to *A. primum* and *A. secundum*. As the original species names were derived from Latinized nouns, it is not required that they agree with the gender of the generic name (ICZN 1999); therefore, we retain the original spellings here.

Albertatherium sp.
(Fig. 5E)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66380, right m2 or m3.

Description. — OMNH 66380 is a moderately worn lower molar, well preserved except for breakage of the protoconid. The cusps and crests are rather robust, and it is of appropriate size for referral to *Albertatherium*. The paraconid and metaconid are erect and of similar size at their bases, with the paraconid slightly shorter and positioned slightly buccal. The paracristid is quite strong and bears a well-developed notch. The protocristid is also notched. The mesial keel on the paraconid is very sharp and cuspidate along its height. The talonid is subequal in width to the trigonid. The cusps are all well developed, with the hypo-

conulid recumbent and the smallest of the three. A notch is present at the base of each crest connecting the cusps, including the entocristid and cristid obliqua, which rises to meet the protocristid notch. This lower molar is probably from the middle of the series.

Comments. — Johanson (1994) named a second species of *Albertatherium* from the Milk River Formation, *A. secundus*, on the basis of two upper molars which differed from those of the type species only in lacking stylar cusp C. The variability of this cusp among other "didelphid"-like taxa raises caution as to its taxonomic utility when employed alone, but perhaps a future larger sample will bolster diagnostic support of two species of *Albertatherium*. Johanson (1994) proposed no diagnostic characters for lower molars to separate these two species, and simply referred all lower molars from Verdigris Coulee to *A. primus*. We take a more conservative approach and leave the lower molar from the Eagle Formation in open nomenclature.

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Superfamily **Pediomyoidea** Simpson, 1927

Family **Aquiladelphidae** Davis, 2007

Genus *Aquiladelphis* Fox, 1971a

Aquiladelphis incus Fox, 1971a

(Fig. 6A)

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Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66351, left M3.

Description. — OMNH 66351 is a very large (Table 1), distinctive upper molar unquestionably belonging to *Aquiladelphis incus*, originally described from the Milk River Formation. The parastylar lobe is nearly as wide as the metastylar lobe (though the entire stylar shelf is narrow, a feature common to pediomyids and their relatives, Davis 2007), and the parastyle is buccal to the paracone; these features suggest that this specimen is an M3. The crown has heavy, somewhat low cusps with a very broad trigon basin and strong, cuspidate crests. The paracone and metacone are widely separated, with the paracone being the taller of the two. The preparacrista is weak, notched, and runs to a relatively low, broad stylocone positioned very close to the paracone. A series of cuspules trails distally along a crest from the apex of the stylocone. The ectocingulum is strong and cuspidate along the entire buccal margin of the crown. The dominant feature of the stylar shelf is the massive cusp C, positioned distal to the center of the very shallow ectoflexus. A number of crests descend from the apex of this pyramidal cusp, one of which reaches the base of the centrocrista. The abraded base of a small cusp corresponding to cusp D is present on the distal flank of cusp C. The postmetacrista is low. Crenulated cingula flank both sides of the low, broad protocone. The conules are blunt and bear weak internal cristae, one feature in which this specimen differs from others referred to this taxon. The postprotocrista extends buccally past the metacone, but does not reach the metastylar area.

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Aquiladelphis minor Fox, 1971a

(Fig. 6B, C)

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Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66352, left MX preserving only mesiobuccal corner; OMNH 66353, right m2.

Description. — OMNH 66352 (Fig. 6B) is a worn and fragmentary mesiobuccal corner of an upper molar. It agrees well in general morphology with OMNH 66351 except for its much smaller size, which is appropriate for *Aquiladelphis minor*. The paracone is fairly low and robust. The stylocone is small and the parastylar lobe quite narrow, and what remains of the ectocingulum is cuspidate.

OMNH 66353 (Fig. 6C) is a worn but complete lower molar. It is fairly low crowned with robust cusps and crests; this, together with its size and the buccal attachment of the cristid obliqua to the trigonid, indicates referral to *Aquiladelphis* (the paraconid is lower than the metaconid, which precludes stagodontid affinity). The specimen is very similar to UALVP 5534 from the Milk River Formation (see Davis 2007, fig. 22B), and likely represents the same locus (m2).
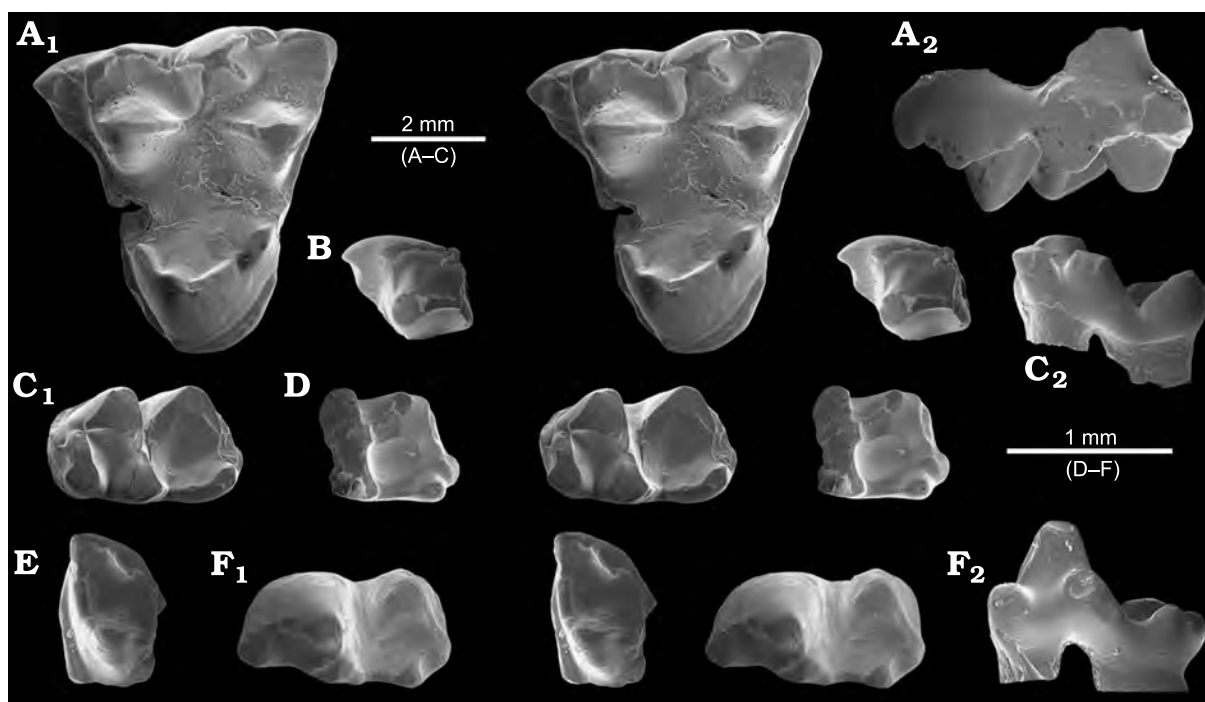
Fig. 6. The pediomyoid marsupialiforms *Aquiladelphis* and *Leptalestes*, and basal metatherians from the Eagle Formation (all OMNH locality V1409, Upper Cretaceous, Santonian, Montana). **A**. *Aquiladelphis incus*, OMNH 66351, left M3 in occlusal (A_1, stereopair) and buccal (A_2) views. **B–C**. *Aquiladelphis minor*. **B**. OMNH 66352, left MX in occlusal (stereopair) view. **C**. OMNH 66353, right m2 in occlusal (C_1, stereopair) and lingual (C_2) views. **D**. *Leptalestes* sp., OMNH 66366, right mx in occlusal (stereopair) view. **E**. *Iqualadelphis lactea*, OMNH 66347, Right MX in occlusal (stereopair) view. **F**. Metatheria indet., OMNH 66341, right dp3 or m1 in occlusal (F_1, stereopair) and lingual (F_2) views.

Comments. — Molars of *Aquiladelphis* are highly distinctive and readily identifiable. This taxon is somewhat broadly distributed, with a probable additional Aquilan occurrence in the John Henry Member of the Straight Cliffs Formation (unidentified pediomyids in Eaton *et al.* 1999, fig. 3C, D), as well as records in younger units (Judithian Fruitland Formation, Rigby and Wolberg 1987; and "Edmontonian" Williams Fork Formation, Diem 1999). A similar species (*A. laurae*) was described from a Campanian locality in Cedar Canyon, southwestern Utah, possibly in the Wahweap Formation or an equivalent unit (Eaton 2006a).

Family **Pediomyidae** Simpson, 1927
Leptalestes sp. Davis, 2007
(Fig. 6D)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66366, right mx preserving talonid only.

Description. — OMNH 66366 is a very small, fragmentary, and abraded lower molar missing all of the trigonid except the bases of the protoconid and metaconid. However, enough is preserved to permit brief description and comparisons. The talonid is subequal in width to the trigonid; the hypoconid is leveled by wear, but in distal view the base of this cusp is substantially lower than the lingual base of the talonid. The entoconid is quite tall and conical, and strongly twinned with the hypoconulid. The cristid obliqua is short and, based on its orientation, appears likely to have met the trigonid wall at a point buccal to the protocristid notch.

Comments. — This specimen, though poorly preserved, compares quite well with small pediomyids from younger rock units. Coupled with its very small size and delicate construction, the strong twinning of the talonid cusps, tall entoconid, and general buccal sloping of the talonid are all shared by the Judithian *Leptalestes prokrejcii* (Fox 1979b). While the preserved morphology of the specimen is a very close match, specific referral is left open due to the limited available material.

Family incertae sedis
Iqualadelphis lactea Fox, 1987
(Fig. 6E)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66347, right MX preserving only distobuccal corner.

Description. — OMNH 66347 is an upper molar fragment preserving only the distobuccal corner of the crown. The metacone is slender and angular, with a strong postmetacrista that is oriented buccally. A small but well-defined and elongate cusp D is present on the stylar shelf, and the postprotocrista extends buccally almost to the edge of the crown. In these regards (as well as size), the specimen is very similar to molars referred to *Iqualadelphis lactea* from the Milk River Formation (see Johanson 1993).

Infraclass **Metatheria** indet.
(Fig. 6F)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material.—OMNH 66341 right dp3 or m1.

Description.—OMNH 66341 is a small metatherian lower molariform representing a taxon not yet clearly known by other materials. Trigonid structure suggests a molar from the front of the series or, possibly, a deciduous premolar. The paraconid is low, procumbent, and positioned near the midline of the crown, making the trigonid quite open lingually. The metaconid is damaged but appears to have been low with a gentle distal slope towards the talonid, which is wider than the trigonid. The molar cusps are generally low and somewhat inflated. There is no clear development of a precingulid. A distinct neck is present at the distal root-crown junction, possible evidence that this tooth may have been in the process of root resorption and subsequent shedding of the crown. It is similar in size but quite different in morphology from the dp3 referred here to *Varalphadon*. The specimen is smaller than but otherwise very similar to UMNH VP 6793 from the Wahweap Formation (Eaton 2013, fig. 15.13B), tentatively referred to *Iugomortiferum*, a metatherian genus of uncertain affinities otherwise known from the Wahweap Formation (Cifelli 1990c). A larger sample is needed before a confident referral of this specimen can be made.

Infraclass **Eutheria** Gill, 1872
Incertae sedis
Paranyctoides sp. Fox, 1979c
(Fig. 7A)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66346, right MX preserving only protoconal region.

Description. — OMNH 66346 is the lingual half of an upper molar that agrees in size and preserved morphology with *Paranyctoides*, known from various Late Cretaceous occurrences, including the Milk River and Oldman formations (Fox 1979c, 1984a). The protocone is angular and leans mesially. Though the metaconule is missing it is clear that the paraconule was positioned higher on the crown. Internal conular cristae and the pre- and postprotocristae are very strong and sharp. Broad cingula flank both sides of the protocone at its base. The trigon basin is narrow and deep.

Comments. — *Paranyctoides* is also known from the early Campanian Wahweap Formation and several other units (Cifelli 1990d ; Kielan-Jaworowska et al. 2004). Older records from the Turonian–Coniacian of Asia have been referred to this genus (see review in Averianov and Archibald 2013), but the validity of Asiatic *Paranyctoides* has recently been questioned (Montellano-Ballesteros *et al.* 2013). Eutherians are rare components of the Eagle fauna, with only two specimens that can be referred with confidence: a single specimen of *Paranyctoides* and an indeterminate upper molar fragment described below. It is likely that further sampling will yield additional material — *Paranyctoides*, for example, is known by many more specimens in the comparatively much better sampled Milk River Formation (Fox 1984a; Montellano-Ballesteros *et al.* 2013).
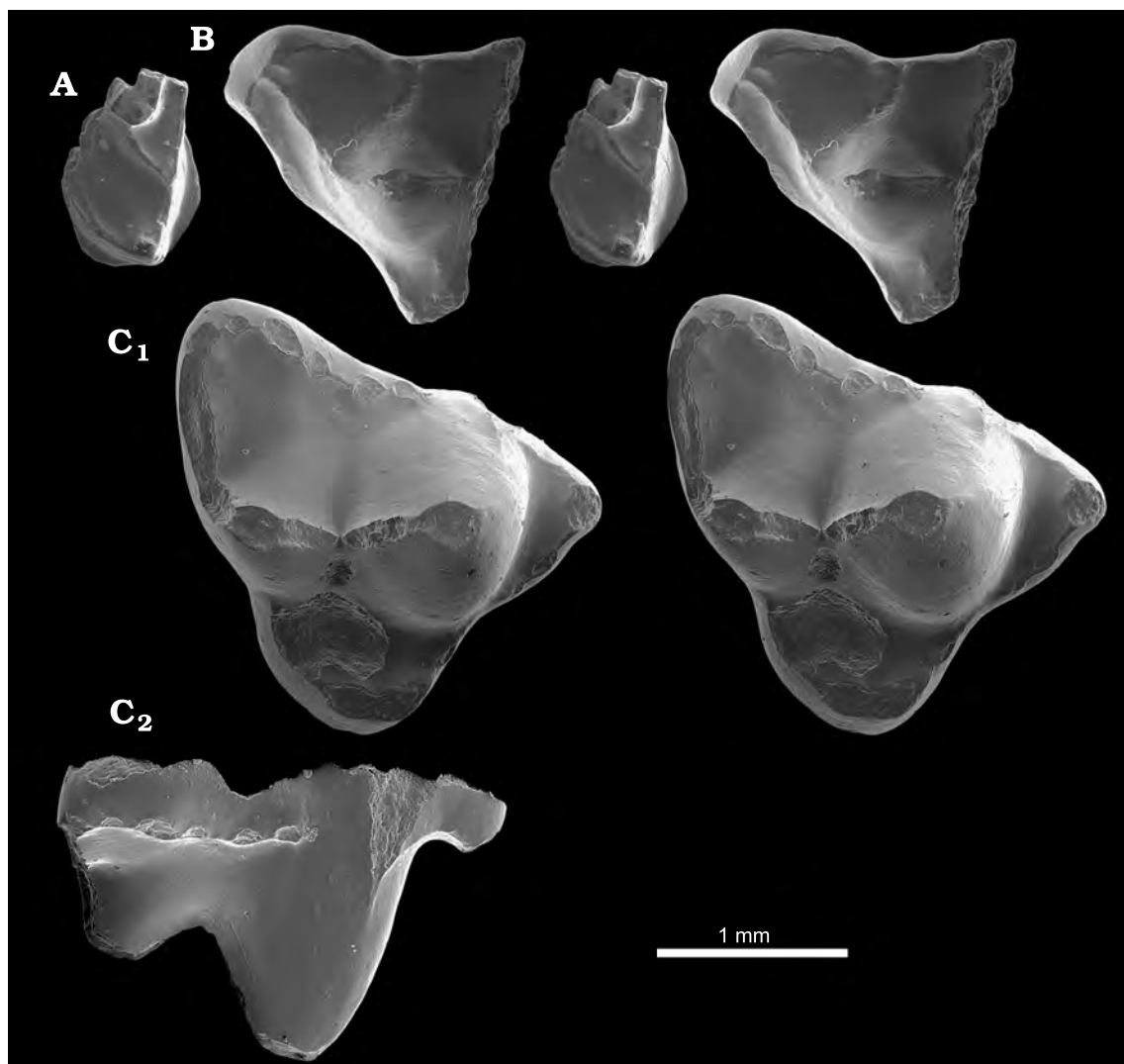
Fig. 7. Eutherians and Tribosphenida indet. from the Eagle Formation (Upper Cretaceous, Santonian, Montana). **A**. *Paranyctoides* sp., OMNH 66346 (OMNH locality V1409), right MX in occlusal (stereopair) view. **B**. Eutheria indet., OMNH 66344 (OMNH locality V1409), left MX in occlusal (stereopair) view. **C**. Tribosphenida indet., OMNH 64165 (OMNH locality V1412), right upper molariform in occlusal (C_1, stereopair) and buccal (C_2) views.

Infraclass **Eutheria** indet.
(Fig. 7B)

Locality and horizon: OMNH V1409, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 66344, left MX preserving only mesiobuccal corner.

Description. — OMNH 66344 is an upper molar fragment preserving only the mesiobuccal corner of the tooth. This specimen is identified as eutherian based on favorable comparisons with taxa known by relatively complete material (in particular, *Aspanlestes*, see Archibald and Averianov 2012, fig. 7). The paracone is robust and rounded, with a weak preparacrista oriented mesiobuccally. The preparacrista terminates just mesial to the apex of the parastyle, which is positioned far buccal and mesial to the paracone. The stylocone is absent or is represented by one or two small cuspules along the ectocingulum buccal to the paracone. A preparastyle is lingual to and in close proximity with the parastyle, and while the mesial cingulum in this region is broad, the preprotocrista is discontinuous at the level of the paracone. Nothing is preserved of the lingual portion of the tooth. The parastylar lobe is narrow but an ectoflexus was present and the stylar shelf appears to be widening distally at the broken margin of the crown, suggesting that this is not an ultimate molar.

Comments. — The preserved morphology of OMNH 66344 compares favorably to zhelestids, with its rounded paracone, crenulations along its ectocingulum, and a narrow parastylar lobe, although not quite as narrow as seen in *Aspanlestes* and *Parazhelestes* (Archibald and Averianov 2012). Some specimens referred to these taxa show a similar interruption in the preprotocrista. The buccal separation between the paracone and parastyle coupled with the interpreted width of the distal stylar shelf are most consistent with M2. Unfortunately, the limited portion of the crown preserved precludes taxonomic referral and further comparisons.

Subclass **Tribosphenida** indet.
(Fig. 7C)

Locality and horizon: OMNH V1412, Deadhorse Coulee Member of the Eagle Formation (Santonian, Upper Cretaceous), Toole County, Montana, USA.

Referred material. — OMNH 64165, right upper molariform.

Description. — OMNH 64165 is a complete upper molariform tooth with peculiar morphology. The swollen paracone is the dominant feature on the crown; its conical base occupies much of the occlusal surface. The metacone is closely appressed to the paracone and less than half its height. It is connected to the paracone by a well-worn, straight centrocrista. The postmetacrista is long, very well developed and is heavily worn; the enamel at the base of the metacone is pinched, suggesting the possible presence of a notch along the postmetacrista. The crest is oriented buccally and forms a 90° angle with the centrocrista. The only trace of a preparacrista is a faint mesiobuccal crest that blends with an abraded portion of the ectocingulum; this crest does not clearly reach the apex of the paracone. A stylocone is absent. The parastyle is low and positioned on a broad flange well separated from the paracone. A straight line can be formed through the apices of the parastyle, paracone, and metacone. The tooth has a nearly flat buccal margin with no development of an ectoflexus, and while stylar cusps are not clearly developed, a series of abraded cuspules are present along the ectoflexus, the largest of which is in the position of stylar cusp D. The protoconal region is low, somewhat flat, and small. Much of the enamel is missing from this part of the tooth, but the protocone appears to be poorly developed and somewhat mesiodistally long. Conules are not obvious; the area of the metaconule is damaged, and a very tiny cuspule is present in the position of the paraconule. The trigon basin is developed as a shallow, horizontal trough. The postprotocrista terminates at the lingual base of the metacone without wrapping distally; the preprotocrista is interrupted briefly near the lingual base of the paracone but continues to the parastyle. Wear facets are developed in the embrasure formed by the centrocrista and along the postmetacrista, but no facets are visible on the mesial face of the paracone or flanking the protocone.

Comments. — The unusual morphology exhibited by this tooth suggests a number of interesting possible affinities, none of which is completely convincing. Broadly similar fossils from the Cedar Mountain Formation (Cenomanian, Utah, USA) are described elsewhere in this volume (Cifelli *et al.* 2016 this volume), and we offer complementary comments here. OMNH 64165 invites comparison with deciduous upper premolars of metatherians. However, a stylocone is commonly present on dP3 of metatherians, and features of the protoconal region (such as conules and the pre- and postprotocristae) would be expected to be better developed (see Clemens 1966). The DP3 is unknown for *Aquiladelphis*, which is represented by two species in this assemblage. As in OMNH 64165, the stylocone of *Aquiladelphis* is reduced and the parastylar lobe is narrow to absent in this and related pediomyoid taxa (Davis 2007), but the lingual half of the tooth is very broad and the postcingulum is well developed. If OMNH 64165 were a DP3 of *Aquiladelphis*, these features should be present (albeit in reduced form). Additionally, the postmetacrista on this specimen is oriented directly buccally, while this crest is oblique in known Cretaceous metatherian DP3s.

Some features of OMNH 64165 can be interpreted as plesiomorphic for tribosphenidan molars in general: the relative proportions of the paracone and metacone and the very small protocone are reminiscent of the aegialodontid *Kielantherium* (Lopatin and Averianov 2006). Similarly, the Eagle specimen is a close match for some specimens referred by Fox (1980) to cf. *Picopsis* sp. from the Milk River Formation. *Picopsis pattersoni* was originally proposed as a basal tribosphenidan most closely allied with aegialodontids (including *Kielantherium*). The holotype of *P. pattersoni* is damaged, but it most likely instead represents a metatherian deciduous upper premolar: the metacone is well separated from the paracone and is not much smaller, the postmetacrista is oriented obliquely, and a large stylar cusp is present in the C or D position (Fox 1980, fig. 1; specimen better illustrated in Scott and Gardner 2013, fig. 3A,B). Though poorly preserved, the

material informally referred by Fox (1980) to cf. *Picopsis* sp. appears to depart from a typical metatherian DP3 and likely does not represent the same taxon as the holotype of *P. pattersoni*. The same can be said of OMNH 64165, yet the affinities of these specimens are still unclear.

A second primitive-grade tribosphenidan was recently described from the same locality that yielded *Picopsis* in the Milk River Formation, *Tirotherium aptum* Montellano-Ballesteros *et* Fox, 2015. Some features of the upper molars compare well with OMNH 64165, such as the inflated paracone, absence of a stylocone, and well-developed, buccally-oriented postmetacrista (on some specimens). However, the protocone and conules of *Tirotherium* are strong and rounded, with sharp internal cristae, flanking a deep trigon basin. The postprotocrista extends buccally to the level of the metacone. In these regards, *Tirotherium* is more derived than *Picopsis* (sensu lato) and the Eagle specimen or, more likely, *Tirotherium* more closely resembles a metatherian DP3. Further discussion of this taxon is beyond the scope of this paper, but see Cifelli *et al.* (2016 this volume) for more thorough comments on *Picopsis*-like taxa.

The loss of the stylocone and mesial stylar shelf on OMNH 64165 can also be regarded as derived features relative to the primitive therian condition. The strong emphasis on postvallum shearing and structural neglect of the protocone are characteristic of advanced deltatheroidans, among these in particular the Lancian *Nanocuris* (Fox *et al.* 2007; Wilson and Riedel 2010; Rougier *et al.* 2015). OMNH 64165 is superficially very similar to AMNH 59451, identified as ?*Nanocuris* sp. (Wilson and Riedel 2010, fig. 4). The Eagle specimen is about a third smaller. The protocone is better developed and transversely wider in *Nanocuris*, but is still quite small and (like OMNH 64165) lacks conules. The paracone and metacone have similar relative proportions, and in both specimens the postprotocrista lacks buccal extension, the mesial stylar shelf is narrow to absent, and the preparacrista is very poorly developed. The Eagle specimen is comparatively narrower transversely, and the complete absence of the stylocone and extreme swelling of the paracone are inconsistent with known deltatheroidans. The enlarged paracone lacking a stylocone and the poorly developed protoconal region are, however, characteristic of some semi-molariform eutherian premolars. The same upper molar referred to ?*Nanocuris* sp. by Wilson and Riedel (2010) was originally described by Clemens (1973, p. 71), with discussion of possible identity as a DP3 of an unknown cimolestid. While OMNH 64165 does bear some superficial similarities to known Paleocene cimolestids (*e.g.*, Williamson *et al.* 2011), the length and orientation of the postmetacrista and narrow protocone do not compare favorably. Further comparison must await additional specimens representing other tooth positions of this enigmatic mammal from the Eagle Formation.

DISCUSSION

The discovery of fossil mammals in the Eagle Formation is significant not only in that it brings to light unrecognized, highly productive paleontological potential in a rock unit within the United States Western Interior, but because it also contributes data to improve our understanding of an important interval in the evolution of modern mammalian faunas in North America. Knowledge of mammal evolution on this continent during the first ~60 Ma of the Cretaceous (Berriasian–Santonian) is generally poor, punctuated by a few well-sampled assemblages that rarely form an overlapping or continuous record (see the following and references within: Kielan-Jaworowska *et al.* 2004; Davis and Cifelli 2011; Eaton and Cifelli 2013; Cifelli *et al.* 2014; Cifelli and Davis 2015; Cifelli *et al.* 2016 this volume). Consequently, there are no widely-recognized NALMAs for faunas older than Aquilan (Cifelli *et al.* 2004). It is not until the Santonian–Campanian that sampling and taxonomic resolution are sufficient to permit the recognition of a broad biostratigraphic framework for correlating local faunas. The Aquilan NALMA was originally defined on the basis of the fauna from the Milk River Formation (Lillegraven and McKenna 1986), and later expanded to include assemblages from the Wahweap and Masuk formations (Cifelli *et al.* 2004). Characteristic first occurrences are the neoplagiaulacid multituberculate *Mesodma*, the stagodontid *Eodelphis*, and the eutherian *Paranyctoides*. The first pediomyoids also appear, including the large and distinctive *Aquiladelphis*.

It should be no surprise that the known components of the mammalian fauna from the Eagle Formation are broadly similar to that of the contemporary and geographically proximal Milk River Formation (Table 2). Of the taxa described here, three are absent from Verdigris Coulee: *Alphadon halleyi* (several isolated lower molars from the Milk River Formation were initially assigned to *Alphadon*, but later intimated to

Table 2. Mammal taxa (excluding multituberculates and some taxa left in open nomenclature) from units currently assigned to the Aquilan North American Land Mammal Age (NALMA), and occurrences in older (Turonian–Coniacian) and younger (Judithian NALMA) assemblages. Inclusion of the upper John Henry Member of the Straight Cliffs Formation in the Aquilan is best regarded as provisional. Abbreviations: E, Eagle Formation; J, Judithian (includes Judith River, Dinosaur Park, and Kaiparowits formations); JH, John Henry Member of Straight Cliffs Formation; MR, Milk River Formation; SH, Smoky Hollow Member of Straight Cliffs Formation; W, Wahweap Formation. Compiled from Kielan-Jaworowska *et al.* (2004) and Eaton and Cifelli (2013).

| | | Aquilan | | | | | |
		SH	E	MR	JH	W	J
Eutriconodonta	*Alticonodon lindoei*			×			
	Alticonodon sp.				cf.		
"Symmetrodonta"	*Spalacotheridium mckennai*	×	×				
	Spalacotheridium sp.				×		
	Symmetrodontoides canadensis		×	×			
	Symmetrodontoides foxi					×	
	Symmetrodontoides oligodontos	×			cf.		
	Symmetrodontoides sp.				×		
Tribosphenida indet.	*Potamotelses aquilensis*			×			
	Potamotelses sp.				×		
	Zygiocuspis goldingi					×	
	Picopsis pattersoni			×			
	Picopsis sp.			×	×		
	Tirotherium aptum			×			
Metatheria indet.	*Iugomortiferum thoringtoni*					×	
	Iqualadelphis lactea		×	×			
	Apistodon exiguus			×	cf.	cf.	
"Alphadontidae"	*Albertatherium primus*		×	×			
	Albertatherium secundus			×			
	Alphadon halleyi		×		cf.		×
	Alphadon sp.	×		×			×
	Varalphadon creber			×		cf.	
	Varalphadon crebreforme					×	
	Varalphadon wahweapensis		×	×		×	×
	Varalphadon sp.		×		×	cf.	
	Turgidodon russelli					cf.	×
	Turgidodon sp.					×	×
Pediomyoidea	*Aquiladelphis incus*		×	×			
	Aquiladelphis minor		×	×			×
	Leptalestes sp.		×		×		×
Stagodontidae	*Eodelphis* sp.			×	×		×
Eutheria	*Paranyctoides maleficus*			×			×
	Paranyctoides sp.		×			×	×

belong to either *Turgidodon praesagus* or a different genus, Fox 1979a), the pediomyid *Leptalestes*, and *Spalacotheridium mckennai*. The occurrence of *Spalacotheridium* is interesting in that this spalacotheriid genus is otherwise only known from southern Utah, including older assemblages in the Smoky Hollow Member of the Straight Cliffs Formation (Turonian) and the Cedar Mountain Formation (Albian–Cenomanian). The absence from the Eagle assemblage of certain other Aquilan taxa (*e.g.*, the distinctive euriconodontan *Alticonodon*, the basal tribosphenidan *Potamotelses*, the basal metatherian *Apistodon*, and the stagodontid *Eodelphis*) could be attributed to the small sample so far attained from the unit.

The fauna from the upper part of the John Henry Member of the Straight Cliffs Formation is similar in age to the Eagle assemblage (Eaton 2006b, 2013), but current taxonomic resolution does not allow close comparison. The two units share many genera (including the geologically oldest record of the pediomyid *Leptalestes*, otherwise known from the Judithian–Lancian), but no taxa identified to the species level are in common. Some key taxa are shared between the John Henry and Milk River Formation, such as *Alticonodon*, *Potamotelses*, and *Apistodon*, so it is likely that additional collections (especially of more complete material)

will permit formal inclusion of the John Henry assemblage into the Aquilan; for present purposes, we do so only provisionally.

The somewhat younger Wahweap Formation (and its lateral correlate, the Masuk Formation) has been included in the Aquilan based on taxa shared with the Milk River Formation, notably the multituberculates *Cimexomys antiquus* (though the Wahweap taxon is only conferred), *Cimolodon similis* and *C. electus*, the spalacotheriid *Symmetrodontoides*, and the marsupialiform *Varalphadon*. However, the presence of several other multituberculate taxa and the marsupialiform *Turgidodon* hint at closer ties with younger, Judithian assemblages (see Eaton and Cifelli 2013, table 14.1). The age of the Wahweap Formation has recently been adjusted based on a radiometric date from low in the unit (Jinnah *et al.* 2009); the Wahweap occupies a slice of time some ~3 Ma younger than the Milk River Formation, yet still several million years older than most Judithian assemblages (Jinnah 2013). Perhaps, as suggested by Eaton and Cifelli (2013), the Wahweap fauna should be housed in a separate biostratigraphic zone for the early–middle Campanian.

Whether the differences between the Milk River fauna in southern Alberta and those from southern Utah are related to slight differences in age or are due to differences in latitude or paleoenvironment remain open questions. Still, several trends emerge regarding patterns of mammal diversity during the Santonian–Campanian. Symmetrodontans make their final appearance during this interval, but they were reasonably diverse. At the same time, eutherians are beginning to diversify after a hiatus of ~25 Ma since their first (Albian) appearance on the continent (Cifelli and Davis 2015). The presence of *Paranyctoides* and an indeterminate zhelestid-like taxon (OMNH 66344, Eagle Formation) hint at the possibility of migration playing a role in seeding some of this diversity, as these groups are present in older rocks in central Asia (Archibald and Averianov 2005). Pediomyoid marsupialiforms also make their first appearance during the Aquilan. Though direct competition between extinct groups is difficult to evaluate, the demise of symmetrodontans may be related to the diversification of latest Cretaceous therian lineages (see also Grossnickle and Polly 2013). While zhelestids have broad, rather generalized molars, the Judithian records the appearance of therians with much more insectivorous or sectorial teeth, such as *Gypsonictops* and *Cimolestes*. Moreover, many pediomyid taxa are quite small (*e.g.*, *Leptalestes*) and likely occupied the same dietary niche as most symmetrodontans.

Finally, the first appearances of *Eodelphis* and *Aquiladelphis* are noteworthy in that these taxa are large and possess molars with heavy cusps and crests. These are not the first Cretaceous records of therians with such a modified dentition: the stagodontid *Pariadens* is known from the Cenomanian Cedar Mountain and Dakota formations (Cifelli and Eaton 1987; Cifelli 2004), and while poorly known, *Argaliatherium* from the Albian Cloverly Formation clearly has similar specializations (Cifelli and Davis 2015). However, the presence of this morphotype in the Aquilan suggests increased utilization of a dietary niche among marsupialiforms during the Late Cretaceous. Increased sampling and better taxonomic resolution, especially from promising but poorly explored units such as the Eagle Formation, is ultimately needed to further address questions of ecological specialization and the timing of events such as diversification or dispersal. The biostratigraphic definitions linking the geographically broad but discontinuous mammalian record are in need of refinement, and additional fossils will shed light on the major transitions evident among Cretaceous mammal faunas in North America.

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A NEW ZALAMBDALESTID (EUTHERIA) FROM THE LATE CRETACEOUS OF MONGOLIA AND ITS IMPLICATIONS FOR THE ORIGIN OF GLIRES

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Barunlestes butleri Kielan-Jaworowska, 1975 from the Late Cretaceous of Mongolia was erected as a second genus of Zalambdalestidae, a specialized family of Asiatic Cretaceous eutherian mammals. Since the beginning, the peculiarities of one specimen (MgM-I/135), which could not be attributed to individual variation, led to questioning not only its generic but even family status. Among the differences the most notable are: more enlarged lower incisor (i1), which reaches the end of the tooth row, enamel cover on the i1 only ventral, deeper mandible body, the ultimate lower premolar with more strongly developed trigonid having large metaconid, a well-shaped high paraconid, and the metaconid transversely aligned with the protoconid. Thus, this specimen is herein assigned to *Zofialestes longidens* gen. et sp. n. It is definitely a zalambdalestid, although the most derived of all genera currently known. On the other hand, a combination of morphological characters shared also with some basal Glires suggests paraphyletic status of Zalambdalestidae and their plausibly ancestral position to the entire Euarchontoglires clade.

Key words: Crown placentals, Anagalida, Zalambdalestidae, *Barunlestes*, Mongolia, Late Cretaceous.

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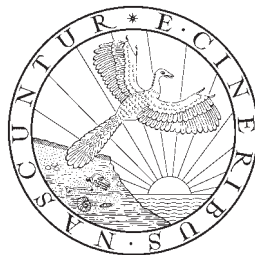
INTRODUCTION

Zalambdalestidae constitute a family of specialized Eutheria restricted to the Late Cretaceous of Asia (Kielan-Jaworowska *et al.* 2004). The nominal genus *Zalambdalestes* was originally described by Gregory and Simpson (1926) on the basis of three specimens. Kielan-Jaworowska (1975) recognized a second monotypic genus *Barunlestes* and included it into Zalambdalestidae. Apart from the fragmentary holotype skull with both mandibles in association (cataloged under ZPAL MgM-I/77), the preliminary description of the material mentioned three damaged skulls and two isolated mandibles, not figured in that paper. Kielan-Jaworowska and Trofimov (1980) provided a detailed account of the cranial morphology of *Barunlestes butleri* together with all specimen numbers and descriptions. Specifically, under ZPAL MgM-I/135 they listed: "incomplete lower jaw with alveoli for P_1–P_2 and P_3–M_3", figured in Jaworowska and Trofimov (1980: pl. 7: 2a–c). They noted that the specimen shows the best-preserved molars among *Barunlestes* specimens, but otherwise the teeth do not differ from those of *Zalambdalestes* (Kielan-Jaworowska and Trofimov 1980, p. 178). The first to formally recognize the morphological incompatibility of this specimen with other mandibles of *Barunlestes* were Li and Ting (1985). They proposed that MgM-I/135 represents a new genus and may be related to Paleocene eurymylids (Mammalia, Glires) on the basis of a greatly enlarged lower incisor and mesiodistally compressed lower molar trigonids. Subsequently, Li *et al.* (1987) included this single individual into a new family named "MgMidae" assigned to the order Mimotonida and hypothesized it as the most basal clade of Glires (Li *et al.* 1987, p. 105, fig. 2). McKenna (1994, p. 57) almost certainly referred to that specimen when commenting on "outer U-shaped band of single-layered enamel" on i1 of *Barunlestes* (but see Wible 2004, p. 30). Finally, Fostowicz-Frelik and Kielan-Jaworowska (2002) accepted that MgM-I/135 belongs to a new genus but did not name it, while pointing to the invalid status of "MgMidae" by virtue of being indicative only.

Currently Zalambdalestidae include five genera: *Alymlestes* Averianov *et* Nessov, 1995, *Barunlestes* Kielan-Jaworowska, 1975, *Kulbeckia* Nessov, 1993, *Zalambdalestes* Gregory *et* Simpson, 1926, and *Zhangolestes* Zan *et al.*, 2006; all are monospecific (but see Wible *et al.* 2004 for *Zalambdalestes*). While *Zalambdalestes* is among the most completely known Late Cretaceous mammals from the standpoint of cranial and postcranial morphology (*e.g.*, Kielan-Jaworowska 1978, 1984; Wible *et al.* 2004), *Alymlestes* is represented only by the crown of left m1 (Averianov and Nessov 1995).

In the present paper I reexamine the specimen MgM-I/135 and formally recognize it as a representative of a new genus and species within Zalambdalestidae. Further, some anatomical characters in *Barunlestes* are clarified; thirdly, I discuss the issue of zalambdalestid paraphyly and their suggested affinities with Glires, a crown clade of placental mammals.

Institutional abbreviations. — AMNH, American Museum of Natural History, New York, NY, USA; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

MATERIAL AND METHODS

Initially, the specimens ZPAL MgM-I/135, *Barunlestes butleri* (ZPAL MgM-I/90), and *Zalambdalestes lechei* ZPAL MgM-I/43 were studied with DIMA Soft P41 (Feinfocus, Garbsen, Germany) central focus

X-ray system at 25 and 29 kV (exposure *ca.* 7 s for all) at the Museum für Naturkunde Berlin, Germany. MgM-I/135 was CT-scanned with Phoenix v|tome|x L 240 scanner (GE Measurement & Control Solutions) (voxel size 0.020 mm, voltage 120 kV at the AMNH), while the holotype specimen of *Barunlestes butleri* (ZPAL MgM-I/77) was studied with a micro-CT scanner Zeiss XRadia MicroXCT-200 (Laboratory of Microtomography, Institute of Paleobiology Polish Academy of Science); the images of this specimen are accessible as the SOM (Supplementary Online Material available at http://www.palaeontologia.pan.pl/SOM/pp67-Fostowicz-Frelik_SOM.mpg). The photographs were taken with a Leica microscope with photo-stacking software (at the Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw) and DinoLite PRO digital microscope. All measurements were taken with a Sylvac electronic caliper with the accuracy of 0.1 mm for mandible fragments and 0.01 mm for teeth.

The dental nomenclature follows Kielan-Jaworowska *et al.* (2004). Premolar counting is after Archibald and Averianov (2003), recently advocated by O'Leary *et al.* (2013). According to this convention five premolar loci in eutherians are consecutively marked as p/P1 through p/P5. On the other hand, Cifelli (2000) proposed to count the premolars consistently as p/P1 through p/P4 for the eutherians having four premolars, and in the genera displaying five premolars mark the teeth as p/P1–2, p/Px, and p/P3–4, where "p/Px" is the tooth of uncertain position. Although teeth counting consecutively from p/P1 through p/P5 is straightforward for basal eutherians (see Archibald and Averianov 2003; Zan *et al.* 2006), the matter gets complicated when referring to more derived eutherian taxa and dental homologies within large clades, *e.g.*, Glires, which have premolars traditionally numbered as p/P1 through p/P4. Mimotonids, eurymylids and lagomorphs of modern aspect lost the anterior premolars and retain only three upper and two lower premolars (marked usually as P2, p/P3, and p/P4). It is obvious that in basal Glires the ultimate premolar was never lost and the two retained lower premolars should be actually marked as p4 and p5 *sensu* O'Leary *et al.* (2013); however, the traditional counting method for this group allows us to avoid potential confusion, especially when discussing homologies with extant placentals. The lower and upper dental loci are indicated by lowercase and uppercase letters, respectively.

I recognize Anagalida Szalay *et* McKenna, 1971 (*sensu* McKenna and Bell 1997) in a restricted sense; that is, to the exclusion of Macroscelidea Butler, 1956. The Linnean classification provided below follows Kielan-Jaworowska *et al.* (2004). This paper and nomenclatural acts contained herein have been registered in ZooBank, the Official Register of the International Commission on Zoological Nomenclature (ICZN) and can be accessed at http://zoobank.org using LSID identifiers.

SYSTEMATIC PALEONTOLOGY

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Infraclass **Eutheria** Gill, 1872 (*sensu* Huxley, 1880)

Magnorder **Epitheria** McKenna, 1975

Grandorder **Anagalida** Szalay *et* McKenna, 1971

Family **Zalambdalestidae** Simpson *et* Gregory, 1926

Genus *Zofialestes* gen. n.

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Type species: *Zofialestes longidens* sp. n., monotypic.

Etymology: *Zofia-*, after the given name of the late Professor Kielan-Jaworowska, my demanding but always generous-to-teach mentor; and *-lestes* from Greek: robber or thief, a common suffix for small mammals of suggested predatory behavior.

Distribution. — As for the type and only species.

Diagnosis. — As for the type and only species.

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Zofialestes longidens sp. n.

(Figs 1, 2)

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Barunlestes butleri: Kielan-Jaworowska and Trofimov 1980, pp. 169, 177, 178, pl. 7: 2 [in part].
Barunlestes butleri: Martin 2004: pp. 411, 417, 418, 421, fig. 2B [in part].
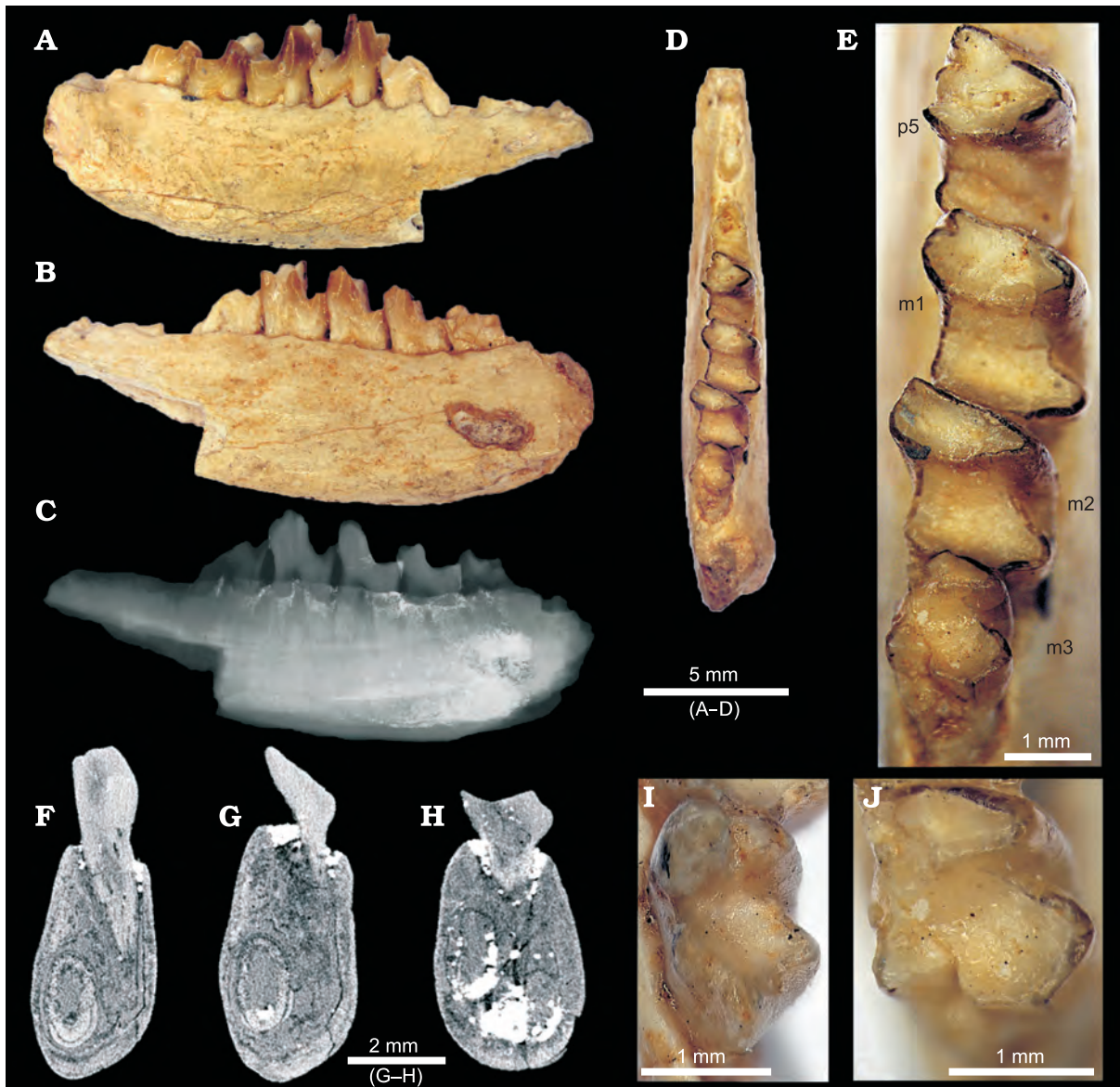
Fig. 1. *Zofialestes longidens* gen. et sp. n., right mandible (ZPAL MgM-I/135) with p4–m3 and roots of p1 and c; Baruungoyot Formation, Nemegt, Eastern Sayr (**A–H, J**); and *Barunlestes butleri* holotype (ZPAL MgM-I/77) (**I**). **A**. Buccal view. **B**. Lingual view. **C**. An X-ray image. **D**. Occlusal view of the whole mandible fragment. **E**. Occlusal view of p5–m3. **F**. Cross-section of the mandible at the level of p4/p5 transition (note the thick enamel layer). **G**. Cross-section at the level of m1. **H**. Cross-section at the level of distal m2 (note the lack of a distinct enamel layer at the distal end of the incisor). **I**. Structure of m3 in *Barunlestes butleri*. **J**. Structure of m3 in *Zofialestes longidens* gen. et sp. n.

Holotype: ZPAL MgM-I/135, fragmentary right mandible body with partially preserved lower incisor i1, root portions of c and p1, and p3–m3 *in situ*.

Etymology: From Latin "*longus*", long and "*dens*" tooth; refers to a notably elongated lower incisor.

Type locality and horizon: Nemegt, Eastern Sayr, Nemegt Basin, Gobi Desert, Mongolia; Baruungoyot Formation, Late Cretaceous (?late Campanian) (see Gradziński *et al*. 1977, fig. 4).

Diagnosis. — Differs from *Barunlestes*, *Kulbeckia*, *Zalambdalestes*, and *Zhangolestes* in more enlarged lower incisor (i1), which reaches the end of the tooth row, in being slightly larger with a deeper mandible body, and in lacking hypoconulids on p5–m2. From *Kulbeckia*, *Zhangolestes*, and *Zalambdalestes* it differs in having only three premolars. *Zofialestes* differs from all four aforementioned genera in having enamel covering only the ventral half of i1, in a more molarized ultimate lower premolar that has a stronger developed trigonid with a large metaconid, well-shaped high paraconid, and metaconid aligned with protoconid. Further, it differs from *Barunlestes* in having two mental foramina on the lateral surface of the dentary, larger and wider m3 (with wider talonid) and from *Kulbeckia* in having a one-rooted canine.
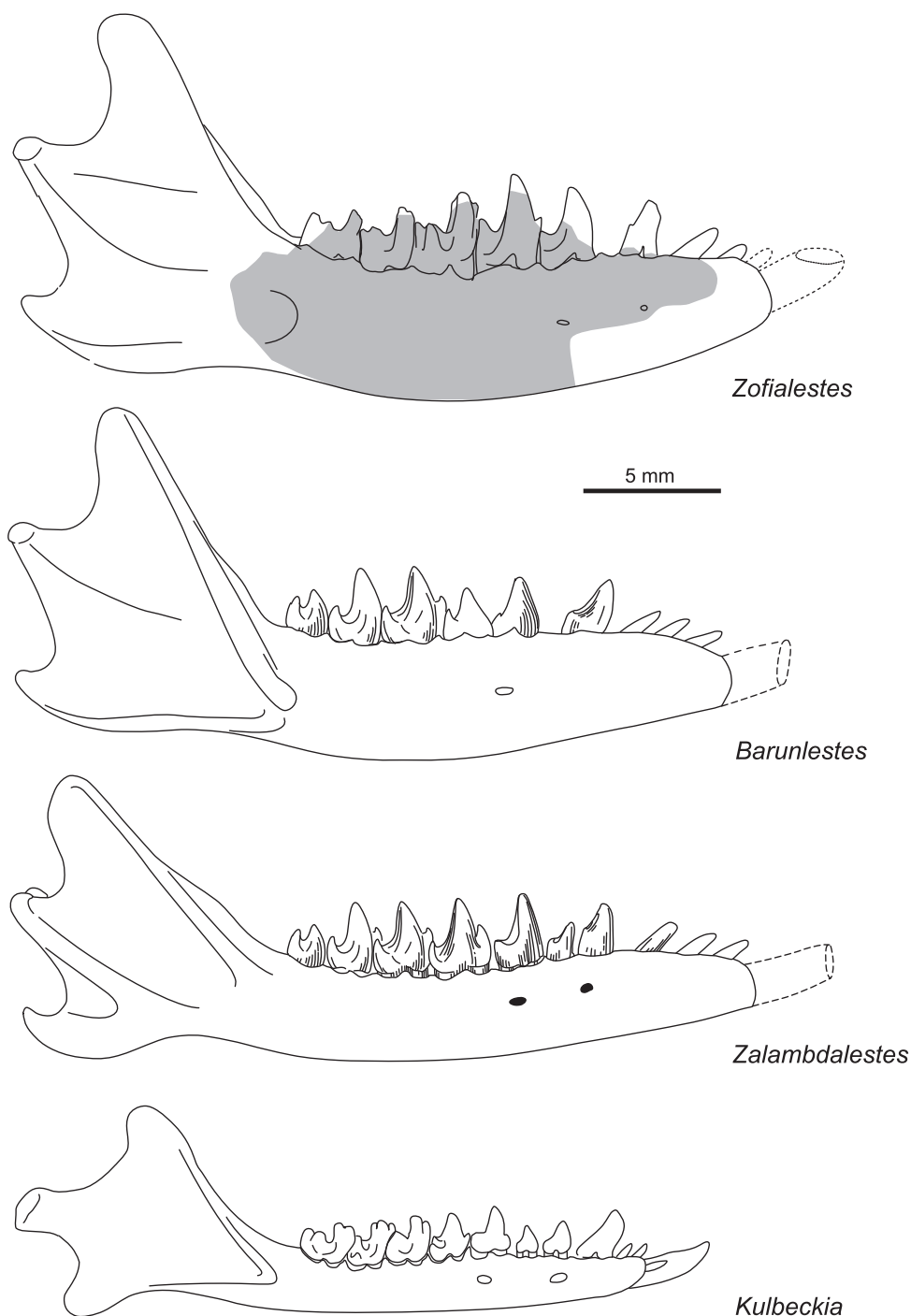
Fig. 2. Reconstructions of the right lower jaw in Zalambdalestidae. *Barunlestes butleri* and *Zalambdalestes lechei* redrawn from Kielan-Jaworowska (1975), *Kulbeckia kulbecke* redrawn from Archibald and Averianov (2003).

Comparative description. — The present external appearance of the specimen MgM-I/135 differs from that shown in Kielan-Jaworowska and Trofimov (1980, pl. 7: fig. 2) by the absence of the ventral part of the mandible body in the premolar portion, which was removed in order to study the incisor cross-section (by the late M.C. McKenna, AMNH).

The mandible is slightly more massive and relatively higher (Fig. 2; see Table 1) than in other zalambdalestids, including *Barunlestes*, which was previously cited as the species with the highest mandible body among zalambdalestids (Kielan-Jaworowska and Trofimov 1980). The molars are slightly wider than those of *Barunlestes* and *Zalambdalestes*, although the strong wear of most *Barunlestes* and *Zalambdalestes* specimens housed at the ZPAL collection makes the metrical comparisons not very informative. The ven-
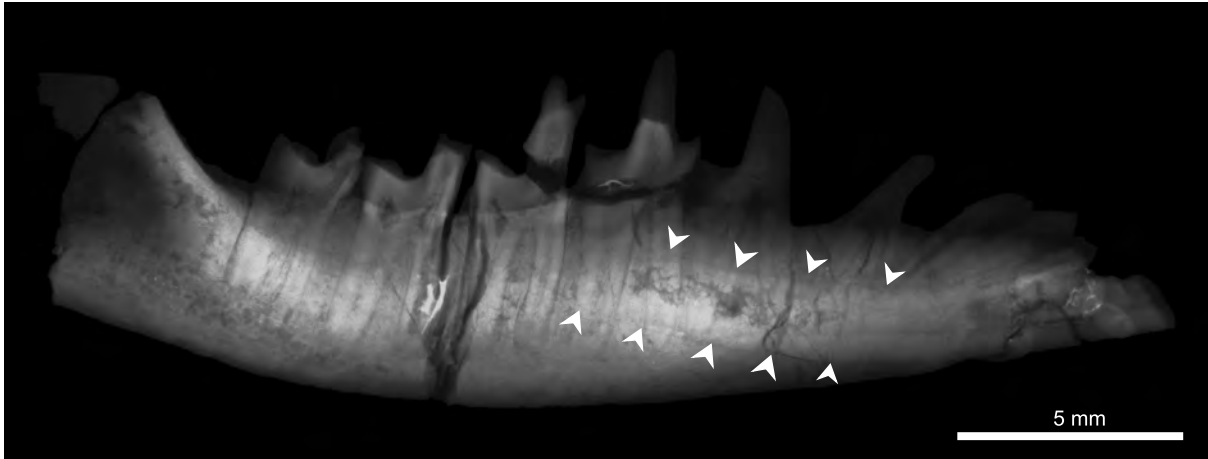
Fig. 3. X-ray image of the right mandible of *Zalambdalestes lechei* (ZPAL MgM-I/43) from Bayn Dzak locality, showing position and course of the i1 (white arrowheads).

tral margin of the mandible body is gently convex and is deeper than in *Barunlestes* (Fig. 2). In *Zofialestes* the curvature of the ventral margin of the mandibular body reaches its maximum under p4, and visibly decreases distally starting from the talonid of m1. The molar portion of the mandibular body is somewhat swollen and much thicker linguobuccally than in *Barunlestes* and other Zalambdalestidae, which have more delicate and slender mandibles (Figs 2, 3). Two mental foramina appear below p1 and p3, respectively, the same as in *Kulbeckia* and *Zalambdalestes* (in *Zhangolestes* the posterior mental foramen is visible under a p3 [p4 of Zan *et al.* 2006] alveolus). The masseteric tubercle is round and quite large, although it does not protrude as sharply as in *Barunlestes* (ZPAL MgM-I/104) but is rather blunt. It occurs below the distal part of the m3 talonid, slightly more anteriorly than in *Barunlestes*, where it occurs distal to the tooth row.

The tooth row is generally straight, with teeth erect (apart from m3, which is slightly slanted anteriorly), thus the occlusal surface of the entire tooth row is level.

The most characteristic feature of *Zofialestes* is a greatly elongated i1, which extends along the entire lower tooth row (at the lingual side of the roots, Fig. 1F–H) and ends at the distal margin of the m3 talonid (Fig. 1C), much farther distally than in *Kulbeckia* (see Archibald and Averianov 2003), *Zalambdalestes* (Fig. 3), and *Barunlestes* (see SOM); where it ends either under the ultimate premolar or the first molar (Fostowicz-Frelik and Kielan-Jaworowska 2002). Compared to *Zalambdalestes*, i1 of *Zofialestes* does not rise dorsally at its distal end (as in *Zalambdalestes*, Fig. 3), but is subparallel to the convex ventral margin of the mandible (Fig. 1C). The i1 of *Zofialestes* is massive, compressed buccolingually (oval in cross-section, with gently rounded ventral and dorsal sides) and open-rooted as in other zalambdalestids (see Fostowicz-Frelik and Kielan-Jaworowska 2002; Archibald and Averianov 2003; Zan *et al.* 2006). The enamel layer does not cover all the circumference of the tooth but is mostly restricted to the ventrobuccal side of the tooth; it encroaches on the ventrolingual side but does not reach this side as dorsally as it reaches buccally (*ca.* half of the tooth height; Fig. 1F, G). Compared to *Kulbeckia* and *Zhangolestes* the enamel layer is more restricted ventrally, forming, in cross-section, a U-shaped structure different from the C- or D-shaped band in *Kulbeckia* or *Zhangolestes*, respectively (Archibald and Averianov 2003; Zan *et al.* 2006). The enamel layer is thicker than in *Barunlestes* and *Zalambdalestes*, and its thickness is uniform along the circumference of the tooth; although the enamel layer gradually becomes thin distally, along the tooth length.

Table 1. Mandible parameters of chosen Zalambdalestidae taxa (measurements in mm). Abbreviations: MH, mandible height at p5; N, number of specimens; OR, observed range.

Species	m1–m3 L	MH	MH/m1–m3 ratio
Zofialestes longidens N = 1	5.8	5.2	0.89
Barunlestes butleri N = 8	5.9±0.42 OR 5.2–6.6	4.4±0.58 OR 3.2–5.0	0.75± 0.11 OR 0.58–0.87
Zalambdalestes lechei N = 2	6.4 OR 6.2–6.5	4.4	0.69 OR 0.68–0.70

The holotype of *Zofialestes longidens* has preserved the root portions of the canine and p1. Distal to p1 there is a small diastema marking the lack of p2 (absent also in *Barunlestes*), but present in *Zalambdalestes* and *Kulbeckia* (Kielan-Jaworowska and Trofimov 1980; Archibald and Averianov 2003). The canine was single-rooted and most probably was peg-like and semi-procumbent, similar to the condition in *Barunlestes* (Kielan-Jaworowska and Trofimov 1980). The gap between the canine and the root portion of p1 is narrower than in *Barunlestes* (about twice as narrow), the same applies to the diastema between p1 and p4 (p3 *sensu* Kielan-Jaworowska and Trofimov 1980). The p1 has two roots and their structure indicates that the tooth morphology may have been similar to that of *Barunlestes*, forming a sharp blade, slightly inclined anteriorly, and supported by a weaker anterior root and stronger distal one.

The p4 has a broken trigonid cusp, thus its structure cannot be fully ascertained. Nevertheless, judging from its remains, the tooth was structured as in other Zalambdalestidae, with a prominent spiky trigonid and a small heel-like talonid, sloping sharply in the lateral direction. However, the p4 of *Zofialestes* is slightly wider than in *Barunlestes* and *Zalambdalestes* and gives the impression of being more massive than in any of the other genera. The distolateral margin of the trigonid is sharp and adjoins the similar structure created by the distolateral margin of the talonid. Both edges meet laterally at the base of the crown, forming an acute angle, which is lacking in *Zalambdalestes* and more weakly expressed in *Barunlestes* (best visible in MgM-I/104). The talonid is a relatively small triangle-shaped groove, rapidly tapering laterally and inclined in that direction. The distal part of the talonid rises up and conforms to the trigonid of p5 (p4 *sensu* Kielan-Jaworowska and Trofimov 1980), as in *Barunlestes*. The distal margin of the talonid shows two nascent folds or cusps, which may or may not be homologous with the entoconid and hypoconulid. Such cusps are absent in *Zalambdalestes*, while in *Barunlestes* only the hypoconulid-like fold is displayed in the adult specimen MgM-I/104. The talonid of p4 in *Zofialestes* is slightly larger and better defined than in *Zalambdalestes*; on the other hand, while it is very similar to that of *Barunlestes*, it is also shorter (compressed mesiodistally) and wider, with its sharp lateral edge forming a small but distinct projection.

The p5 is the longest tooth in the lower tooth row (Table 2). Its occlusal surface almost equals that of m1, but the tooth seems more strongly built in lateral view. The occlusal surface is slightly crumbled and partly worn, but the general shape and location of all cusps can be recognized. The trigonid of p5 is larger and more robust than in *Zalambdalestes*. It has an outline close to a right triangle, formed by an eminent protoconid and well-developed paraconid and metaconid. The presence of a well distinguished and large paraconid differentiates *Zofialestes* from other zalambdalestids and suggests that p5 displays more advanced molarization. The p5 paraconids of *Zalambdalestes* and *Kulbeckia* are relatively small cusps located anteriorly and relatively low at the tooth crown (Kielan-Jaworowska 1975; Archibald and Averianov 2003). Kielan-Jaworowska and Trofimov (1980) stated that in *Barunlestes* p5 (p4 in their paper) lacks the anterior basal cusp (= paraconid) entirely (but see PIN 3142-701, *ibidem* pl. 4, 1b, d). Moreover, in a relatively young specimen, ZPAL MgM-I/72, a freshly erupted p5 displays a similar small basal anterior cusp. The p5 paraconid in *Zalambdalestes* and *Kulbeckia* is placed more centrally (almost in the parasagittal plane of the tooth) than in *Barunlestes* where it is slightly linguad. In *Zofialestes* the p5 paraconid has its base higher on the crown and is larger than in other zalambdalestids; it is also located much more lingually, almost aligned with the metaconid, which protrudes slightly more lingually (Fig. 1D, E). The p5 metaconid in *Zofialestes* was larger and much longer than in *Barunlestes* judging from its preserved lingual margin. The protoconid was most probably the largest and highest of the cusps (as in *Zalambdalestes* and *Barunlestes*). The talonid of p5 is less inclined laterally than in *Barunlestes* and *Zalambdalestes*, creating a slightly larger and more horizontal occlusal surface. Compared to *Barunlestes* the occlusal surface of the p5 talonid in *Zofialestes* is of similar size, but wider in relation to the trigonid, and more basined. Moreover, it has a distinct large entoconid, protruding lingually. The distal margin of the talonid is flat and lacks any traces of the hypoconulid.

The molars show moderate tooth wear but all dental structures are visible. The m1 is largest of the molars and has the greatest occlusal surface of all teeth in the row. The trigonid of m1 is somewhat triangular in outline with a small paraconid and larger metaconid at the lingual side, and a large protoconid. The metaconid is slightly higher than the protoconid at this stage of wear, as in *Zalambdalestes* (also in a less worn specimen ZPAL MgM-I/51). The well-defined paraconid differentiates *Zofialestes* from *Barunlestes*, in which this cusp is

Table 2. Dental measurements (in mm) of *Zofialestes longidens* holotype (ZPAL MgM-I/135). Abbreviations: L, tooth length; Wtal, talonid width; Wtri, trigonid width.

Tooth	L	Wtri	Wtal
p5	2.46	1.76	1.48
m1	2.43	1.95	1.93
m2	2.11	1.91	1.85
m3	–	1.49	1.50

very weakly developed (observed only in a young specimen, ZPAL MgM-I/72). The talonid of m1 is large and basined with a large hypoconid projecting buccally and a smaller entoconid. There is no trace of a hypoconulid on m1.

The m2 is smaller than m1, with the trigonid more compressed mesiodistally. The paraconid is more reduced than in m1 but it is still recognizable. The talonid is similar to that of m1 with a well-developed hypoconid, also slightly protruding buccally. The entoconid is slightly damaged and smaller than the hypoconid; no trace of the hypoconulid is observed.

The m3 differs somewhat in structure from m1–2. The medial side of the trigonid is damaged; thus, the exact shape of the paraconid and metaconid cannot be ascertained (Fig. 1E, J). I presume that both cusps were present as in *Zalambdalestes* because the lingual part of the tooth is relatively long, compared to *Barunlestes*, which has no paraconid on m3 (see ZPAL MgM-I/107; Fig. 1I). The talonid of m3 in *Zofialestes* is also partly damaged but the presence of a relatively large hypoconulid is certain, judging from the extended distal root portion (Fig. 1E), unlike in *Barunlestes* and *Zalambdalestes* where it tends to be spiky in younger specimens and small and insignificant in mature, more worn individuals. The hypoconid (Fig. 1J) is larger and more round than in *Barunlestes* and *Zalambdalestes*. However, the hypoconulid in *Zofialestes* was most probably shorter and more compressed anterodistally than in *Barunlestes* and *Zalambdalestes*.

DISCUSSION

According to Li *et al.* (1987, p. 104), the dubious status of MgM-I/135 as a zalambdalestid stems from the following characters shared with all Glires: "(3) I1/1 and I2/2 (permanent) lost, (4) dI2/2 retained, enlarged and ever-growing, with di2 extending back to below m2 or m3 (extrapolation from living rodents and lagomorphs; see Luckett, 1985), and (5) molar trigonids compressed." Of these characters only the last is valid, but it is a plesiomorphy for Glires, and is listed as typical of Zalambdalestidae (Kielan-Jaworowska *et al.* 2004).

The total count of the lower incisors is unknown in *Zofialestes longidens*; the other genera of Zalambdalestidae have retained three to four lower incisors, with the largest being identified as i1 (Kielan-Jaworowska 1975; Archibald and Averianov 2003; Zan *et al.* 2006); thus, I assume that *Zofialestes* did not differ significantly in this respect. However, the homologies of zalambdalestid incisors with the incisors of Lagomorpha are uncertain (Fostowicz-Frelik and Kielan-Jaworowska 2002); in particular it is unclear whether the enlarged and procumbent lower incisors in Zalambdalestidae are deciduous teeth and whether they represent the second pair of the incisors; in Lagomorpha the enlarged anteriormost incisors are identified as DI2/di2.

A variously procumbent and enlarged lower incisor is not unusual in Euarchonta, as it is known for Paleogene *Plesiadapis* and living *Daubentonia* (see Szalay and Delson 1979, figs 32 and 73, respectively); also some Anagalidae express definitely procumbent, although less enlarged incisors (*e.g.*, *Anagale*, Simpson 1931, fig. 2; *Qipania*, Hu 1993, fig. 6). In fact, the lower incisors of the earliest duplicidentate *Mimotona* are more bladelike than those of any lagomorphs (see Li and Ting 1993, figs 11.3, 11.4C, D) and they have the occlusal surfaces shaped very similar to those of plesiadapids, although in a more gentle way. Thus, the shape of the incisors is variable within Glires (and Euarchontoglires; see Meng *et al.* 2003, pp. 118–119, character 11, for more data on incisor morphology in Glires).

Another question is the extent of restricted enamel on the incisor; in *Zofialestes* the enamel layer covers only the ventral half of the tooth (Fig. 1F, G), which is suggestive of and parallels the enamel formation in lower incisors of Glires, including the basal representatives (see *e.g.*, *Tribosphenomys*, Meng and Wyss 2001, fig. 4A); while in *Barunlestes* and *Zalambdalestes* enamel covers also the lingual and most of the buccal side of the tooth, and in *Kulbeckia* and *Zhangolestes* it covers most of the incisor circumference and is only lacking on the lingual side of the tooth, creating in cross-section either a C- or D-shaped pattern of distribution (see Archibald *et al.* 2001, fig. 5B; Zan *et al.* 2006, fig. 4).

The available morphological evidence indicates that *Zofialestes longidens* should be included in Zalambdalestidae, and it is definitely not a member of Glires. However, inclusion in Zalambdalestidae does not necessarily preclude *Zofialestes* from belonging to the lineage which eventually gave rise to Glires or the Glires+Anagalidae clade, as previously suggested (Archibald *et al.* 2001, fig. 3b; Archibald and Averianov 2003; see also Meng 2004 for more discussion). Taking into account the enlarged i1 reaching the end of the

tooth row, the presence of only three premolars, a higher mandibular body and more advanced molarization of premolars and development of molar talonids, *Zofialestes* is undoubtedly the most derived of zalambdalestids. Further, *Zofialestes* shows some characters which may be interpreted as antecedent to Glires: a distinct paraconid on p5 (marked in Glires as "p4"), shifted lingually and present in a slightly reduced form in the permanent dentition of some basal Glires (*e.g.*, *Rhombomylus*, see Meng *et al*. 2003, figs 8D, E, 13, 14F, larger in Dp4 of eurymylids; *ibidem*, fig. 14A–C; Dashzeveg *et al*. 1987), slight enlargement of m3 in relation to m2 (a noticeable trend for increasing m3 size is known for eurymylids, mimotonids and rodents), and slight inclination of the m3 in the anterior direction as an incipient stage towards formation of a slightly concave occlusal surface of the entire tooth row (also typical of Glires). Additionally, the alignment of the metaconid and protoconid in ultimate premolar and molars is characteristic of some basal Glires (*e.g.*, *Rhombomylus*, Meng *et al*. 2003 and *Eurymylus*, Sych 1971). As for Glires these characters are mostly plesiomorphic; nevertheless they indicate overall evolutionary trends and may become synapomorphic for a more inclusive clade. The evolutionary morphology of Glires is well known to demonstrate a very high level of convergence and parallelism in dental and osteological characters (*e.g.*, Lazzari *et al*. 2008; Cox *et al*. 2012, fig. 2; Fostowicz-Frelik and Meng 2013), thus obscuring phylogenetic relationships by frequent homoplasies.

Phylogenetic analyses involving the three best-studied zalambdalestids (*Barunlestes*, *Kulbeckia*, and *Zalambdalestes*) returned this group as a monophyletic clade (Archibald *et al*. 2001, fig. 3a; Meng *et al*. 2003; Asher *et al*. 2005) close to Asioryctitheria. In the analysis of Archibald *et al*. (2001, fig. 3b) with the inclusion of the basal Glires taxa *Tribosphenomys* and *Mimotona*, Zalambdalestidae tend to be paraphyletic and group at the base of the clade joining them with Glires. However, this analysis did not include anagalids, Scandentia and Dermoptera, which may have placed Zalambdalestidae immediately outside the entire Euarchontoglires clade (see Meng *et al*. 2003; fig. 74 and Meng 2004 for a broader discussion). To evaluate the broad concept of Anagalida that would include also some Cretaceous placental taxa (see McKenna 1975) and thus, actually may extend crown placental mammals below the K-Pg boundary (unsupported by O'Leary *et al*. 2013), an increased coverage (both taxonomical and morphological) of Glires, Anagalidae and Pseudictopidae is needed for further phylogenetic analysis. In particular, the primitive state for characters should be meticulously analyzed and all characters scrutinized against homoplasies.

Concluding, the scarcity of material precludes a definitive placement of *Zofialestes* within the crown placentals. However, it currently appears to be the Cretaceous placental morphologically closest to Glires, to which it may be related.

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BIRD OR MANIRAPTORAN DINOSAUR?
A FEMUR FROM THE ALBIAN STRATA OF SPITSBERGEN

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The first known fossil vertebrate found in the Lower Cretaceous of Spitsbergen (Svalbard,
Arctic Norway) is presented and described. The specimen, a femur, was collected from the
Zillerberget member of the Carolinefjellet Formation at Schönrockfjellet in 1962 and was re-
cently re-discovered. The bone is referred to ?Avialae based on a combination of characters,
including extreme thinness of the cortex, a well-developed head, and the presence of a pa-
tellar sulcus. From biostratigraphic analysis, it is demonstrated that the bone comes from the
lower part of the middle Albian. This find is important because the Early Cretaceous fossil
record of Avialae remains poorly documented in most parts of the World and is non-existent
in Arctic strata. A general overview of the geology and stratigraphy of the Lower Cretaceous
in Spitsbergen is presented in order to provide context for the fossil occurrence, with a par-
ticular focus on the Aptian and Albian sedimentary system and with the first-ever report on
the entire stratigraphy on the east face of Schönrockfjellet.

Key words: Avialae, Albian, Spitsbergen, Carolinefjellet Formation, Cretaceous, Svalbard,
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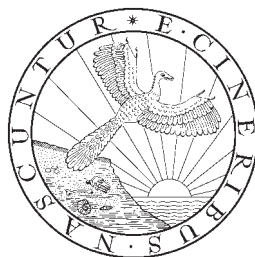
INTRODUCTION

Although tracks and footprints of medium- and large-sized ornithopod dinosaurs have been previously reported from the Lower Cretaceous in Svalbard (Lapparent 1962; Hurum *et al.* 2006, 2016; Midtkandal *et al.* 2007; Midtkandal and Nystuen 2009), no vertebrate fossils have hitherto been described. This paper reports the finding of the first known fossil vertebrate from the Lower Cretaceous in Svalbard. In order to provide a stratigraphic context, the paper also provides an overview of the Early Cretaceous palaeogeography, sedimentary environments and biostratigraphy of the Svalbard region. The specimen, an almost complete right femur, was originally found by Jenö Nagy in 1962 and was deposited in the Natural History Museum, Oslo, on a shelf of uncatalogued material. This dust-covered fossil was rediscovered by JHH in 2011. Nagy's detailed field notes made it possible to locate the fossil's exact stratigraphic position and locality (Fig. 1). In 2012, some of the authors (JHH, HAN, IM, and SO) revisited the Schönrockfjellet locality to see if any more vertebrate remains could be found. Although our team relocated Nagy's stratigraphic horizon, no additional bones were found on the hillside.

Although only a single element (Fig. 2), the first documented bone in the Lower Cretaceous of Svalbard is significant. At the time of deposition, the Svalbard Archipelago was situated between 63–66°N (Torsvik *et al.* 2012) and had a warm-temperate (mean annual temperature of 7–10°C) and humid climate supporting an ornithopod dinosaur population, deciduous conifers, ginkgo trees, and peat accumulations in the Barremian (Steel and Worsley 1984; Nemec 1992; Hurum *et al.* 2006, 2016; Harland *et al.* 2007). The sporadic occurrence of calcitic pseudomorphs (glendonites) and ice-rafted debris at several stratigraphic intervals within the Lower Cretaceous may suggest periods of cold (4–7°C) bottom-water conditions (De Lurio and Frakes 1999; Maher *et al.* 2004; Price and Nunn 2010; Price and Passey 2013)

Despite a great increase over the last 15 years in our knowledge of mid-Late Cretaceous non-avian and avialan theropods (including birds), the earliest stages of the Cretaceous still remain under-sampled (Brocklehurst *et al.* 2012; Mitchell and Makovicky 2014; Wang *et al.* 2015). However, recent fossil discoveries indicate that, by the Early Cretaceous, all of the currently recognised major lineages of birds had diversified (Wang *et al.* 2015). These lineages include the diverse enantiornithines, which did not survive after the end of the Cretaceous; and Ornithuromorpha, another widespread and phylogenetically diverse clade that includes the antecedents of all living birds (Wang *et al.* 2015). Any additions to the Early Cretaceous avialan fossil record are thus important, especially at extreme palaeolatitudes; with the exception of the famous Jehol Biota of western China, the bulk of the Early Cretaceous avialan fossil record is comprised of isolated and incomplete fossil remains (Brocklehurst *et al.* 2012).

This paper gives a detailed description and interpretation of the femur from Schönrockfjellet, and further argues for an avialan affinity of the fossil. The finding is also discussed in a broader context and is compared to global and other Arctic bird fossil discoveries. The fossil was collected from the Zillerberget member (Carolinefjellet Formation), which has only been briefly described and dated until this paper.

Institutional abbreviation. — PMO, Natural History Museum (formerly Paleontologisk Museum), University of Oslo, Oslo, Norway.

Fig 1. Map of Svalbard emended from original by Winfried Dallmann (unpublished), Norwegian Polar Institute.

GEOLOGICAL SETTING

The bulk of Mesozoic strata on Spitsbergen are exposed along the margins of the SSE–NNW trending Central Palaeogene Basin. In western Spitsbergen, the Mesozoic strata are tectonically steeply dipped, while in eastern Spitsbergen they are gently inclined (< 3°; Steel *et al.* 1985; Midtkandal and Nystuen 2009).

During the Early Cretaceous, Svalbard was a part of the epicontinental Boreal Basin, which has since been fragmented as a result of the opening of the Atlantic (Steel and Worsley 1984). Tectonics related to igneous activity and opening of the Canada Basin during the Hauterivian to Aptian (Grantz *et al.* 2011) caused regional thermo-tectonic uplift of the northern margin of the Barents Sea Shelf, including the Svalbard

Archipelago (Maher *et al.* 2004; Corfu *et al.* 2013; Polteau *et al.* 2016). The tilting and resultant subsequent erosion of the northern shelf displaced the shoreline southeastward during the Barremian (Steel and Worsley 1984; Gjelberg and Steel 1995; Maher 2001; Midtkandal and Nystuen 2009).

Svalbard's Lower Cretaceous strata and the coeval intrusive and extrusive Diabasodden Suite are exposed on Spitsbergen and Kong Karls Land (Fig. 3). Sediments consist mainly of mudstone, siltstone and sandstone with subordinate amounts of coal and conglomerates, forming a > 1500 m thick succession, mapped as the Upper Jurassic to Lower Cretaceous Adventdalen Group (Parker 1967; Mørk *et al.* 1999). In Spitsbergen, the Cretaceous part of the Adventdalen Group comprises, in ascending stratigraphic order, the Rurikfjellet, Helvetiafjellet and Carolinefjellet formations (Parker 1967; Nagy 1970; Dypvik *et al.* 1991). The fossil specimen described here belongs in the Carolinefjellet Formation.

Carolinefjellet Formation. — The study area is confined to Schönrockfjellet in Heer Land on the east coast of Spitsbergen, the largest island of the Svalbard Archipelago, Arctic Norway (Fig. 1), where the specimen, PMO 228.582, was found. The locality is on the east side of Schönrockfjellet about 500 m from the coastline (*i.e.*, Schönrockfjellet Profile 4 in Nagy 1970, pl. 12; *ca.* 5 m above a sand layer; *Hoplites*/*Grycia* horizon, level 23; 116 m above mean sea level).

The Carolinefjellet Formation was first investigated by Nathorst (1910) and Stolley (1912), who both focused primarily on marine fossils and provided only brief stratigraphic descriptions. More detailed stratigraphic work was conducted by Hagerman (1925), Różycki (1959), and later by Parker (1967), who suggested the formal and present unit name.

The Carolinefjellet Formation is up to 1000 m thick and records an open-marine, storm-dominated shelf succession. It comprises five members that are alternatingly sandstone-rich or shale-dominated: Dalkjegla, Innkjegla, Langstakken, Zillerberget, and Schönrockfjellet members (the latter two have informal member status) (Parker 1967; Nagy 1970). The shale-dominated units represent outer shelf environments, and the local occurrences of sideritic mudstone horizons, strata-bound concretions and micritic hardgrounds within these units indicate periods of sediment starvation. The sandstone-rich units form southward- to southeastward-thinning wedges that contain abundant hummocky cross-stratification and scattered coquinas representing storm-dominated, inner shelf conditions (Nagy 1970; Nøttvedt and Kreisa 1987). Low relief, coastal barrier/lagoon systems have also been suggested by Mutrux *et al.* (2008). A high abundance of volcanic detritus and plagioclase in the sandstones indicates that some material was derived from a volcanic terrain that formed in association with the High Arctic Large Igneous Province north and east of Svalbard (Maher 2001; Maher *et al.* 2004; Senger *et al.* 2014; Polteau *et al.* 2016).

An angular Palaeocene unconformity truncates the Carolinefjellet Formation, leaving no Upper Cretaceous strata preserved in Svalbard. The relief of this unconformity increases to the northwest due to northern uplift (Parker 1967; Nagy 1970; Major and Nagy 1972). Therefore, all five members of the Carolinefjellet Formation are completely preserved in the southeastern parts of Spitsbergen (Fig. 3). This contrasts with central Spitsbergen, where only the two lower members are preserved (Nagy 1970; Major and Nagy 1972).

The fossil was collected from within the second youngest unit, the Zillerberget member, which has only been briefly described to date. Uncertainties remain as to the extent and distribution of the uppermost two members of the Carolinefjellet Formation in eastern and southern Spitsbergen, hence their informal status. However, there is a general consensus that the Zillerberget member formed as outer shelf deposits, while the succeeding Schönrockfjellet member represents a lower shoreface environment (Nagy 1970; Grundvåg *et al.* 2015). Storm surges on the continental shelf seems the most likely process to have been the agent of placement of the bone and its juxtaposition along with the pelecypods in the Zillerberget member.

MATERIAL AND METHODS

Specimen PMO 228.582 was scanned using µ-Computer tomography (µ-CT) with a Nikon XT H 225 ST. Visualisation and digital modelling processing was completed utilising 3D Analysis Software, Avizo version 8.1 at the Natural History Museum, University of Oslo. Avizo allows for the exclusion of material in different densities, permitting the visualisation of PMO 228582 in all dimensions, including the side imbedded in matrix, thus yielding important anatomical information otherwise unavailable.

Based on the stratigraphic sections published by Nagy (1970) and Århus (1991), and more recent field-

work conducted in 2014 (by SAG), a composite stratigraphic description was constructed (Fig. 3). The log covers all the stratigraphic units present on Schönrockfjellet (*i.e.*, the Zillerbeget and Schönrockfjellet members). The log was measured bed-by-bed, and includes descriptions of rock type, grain size, sorting, sedimentary structures, body and trace fossils, and palaeocurrent directions (no data presented here).

Five samples were collected for palynological analysis during fieldwork in the summer of 2014. All samples were prepared at the Geological Survey of Denmark and Greenland by conventional techniques used for palynological preparation. Slides were prepared from both oxidized and unoxidized residues, and each has been scanned in order to identify key species for the Lower Cretaceous dinocyst zonation of Nøhr-Hansen (1993). Note that age estimates are based on preliminary analysis, where only presence/absence data have been collected; the results of a more detailed analysis will be published elsewhere.

RESULTS

BIOSTRATIGRAPHIC DATING OF PMO 228.582

Ammonite zonation. — Ammonites and dinoflagellate cysts are the two main age-diagnostic fossil groups in the Carolinefjellet Formation. In the lower part of this formation, which is not exposed in the studied section, ammonites indicate an early-to-late Aptian age for the Dalkjegla Member (Nagy 1970), whereas late Aptian ammonites (*e.g.*, *Tropaeum arcticum*) are present in the Innkjegla Member (Stolley 1912; Frebold and Stoll 1937; Owen 1988). Nagy (1970) produced a comprehensive study of the ammonites in the upper part of the Carolinefjellet Formation in southeastern Spitsbergen. According to this study, the uppermost part of the Innkjegla Member and the entire Langstakken Member are early Albian in age because of the presence of a fauna attributable to the *Otohoplites* Ammonite Zone, the later part of the *Douvilleiceras mammillatum* Superzone (*e.g.*, Owen 1996). Nagy (1970) also suggested that the youngest units of the formation, the Zillerberget and Schönrockfjellet members, are of middle Albian age based on an ammonite fauna dominated by *Hoplite*s and *Grycia*, and attributable to the *Hoplites dentatus* Ammonite Zone (*e.g.*, Owen 1996, 1999). In addition, Nagy (1970) reported on the sporadic occurrences of *Euhoplites*, *Dimorpholites* and *Gastroplites* in loose scree. These ammonites possibly belong to the *Euhoplites lautus* Ammonite Zone and suggest that some parts of the succession may also be of late middle Albian age (Owen 1999). Nagy (1970) did not report any age-diagnostic ammonites from the Schönrockfjellet member; a middle Albian age for this unit is based solely on the lack of late Albian ammonites.

Dinocyst zonation. — Using dinoflagellate cysts, Århus (1991) suggested a middle Albian age for both the Zillerberget and Schönrockfjellet members. This suggestion was based mainly on the recognition of *Litosphaeridium arundum*, *Pseudoceratium expolitum* and *Odontochitina singhii*. Although Århus (1991) did not establish any formal dinocyst zonation, he noted similarities with other taxa described from northern Europe and East Greenland. As a part of the present study, correlation between the taxa reported by Århus (1991) and the Lower Cretaceous dinocyst zonation from North-Eastern Greenland suggested by Nøhr-Hansen (1993) has been conducted. New supplementary evidence includes five samples analysed from the uppermost part of the Schönrockfjellet member, an interval which was not covered by Århus (1991). By putting together the data from Århus (1991; nine samples marked as red triangles in Fig. 3) with our new samples (five samples, marked as black triangles in Fig. 3), we are able to report coverage for the entire stratigraphic section exposed on the east face of Schönrockfjellet. Our preliminary results show that most of the studied section is of middle Albian age and belong to the *Rhombodella paucispina* Zone (IV) of Nøhr-Hansen (1993).

Århus' (1991) samples show a low abundance of dinoflagellate cysts in general and a low number of age-diagnostic dinoflagellate cysts in particular. The lowest sample (SCH 660 of Århus 1991) yielded no age-indicative taxa. The two higher samples (SCH 700 and 735 of Århus 1991) contained *Pseudoceratium polymorphum* (referred to as *Aptea polymorpha/Cyclonephelium compactum* Group by Århus 1991), which belongs to the Zone III Subzone 4 or possibly the lower part of Zone IV of Nøhr-Hansen (1993). This indicates a latest early to middle Albian age. The higher-located samples (SCH 795, 825, 935, 965, 995 of Århus 1991) contain *Chichaouadinium vestitum*, *P. polymorphum* (referred to as *A. polymorpha/C. compactum* Group by Århus 1991), *Litosphaeridium arundum* and *Odontochitina singhii*, and are attributed to the Zone IV of Nøhr-Hansen (1993), thus indicating a middle Albian age. Some samples (SCH 700, 855 and 895 of

Århus 1991) were more problematic to analyse and date because the dinocyst fauna was insufficiently diverse (Århus 1991, p. 211) and not many age-markers were observed or preserved.

In five new samples from the Schönrockfjellet member, the co-occurrence of *Chichaouadinium vestitum* and *Rhombodella paucispina* narrows the age to middle Albian (and Zone IV of Nøhr-Hansen 1993). The lower part of the member (sample position: two lower black triangles in Fig. 3) most probably represents the *Litosphaeridium arundum* Subzone 1. The common presence of *C. vestitum* in the uppermost part of the member (sample position: three upper black triangles in Fig. 3) suggests that this interval belongs to the *Chichaouadinium vestitum* Subzone 2.

Other age-diagnostic fossils. — The large pelecypod shell that protected PMO 228.582 is a pectinid, and probably belongs to the (sub) genus *Maclearnia* (Crickmay 1930; synonym = *Boreionectes* Zakharov 1965). The specimen is preserved as an internal mold and, as such, the shell which is necessary for species identification is missing. However, additional specimens, some preserved as external molds, were collected during field work in 2012 by some of the authors (JHH, HAN, SO, IM) from the same level. These are rather smooth and display growth lines. *Maclearnia* is common in the Tithonian to Aptian (Kelly 1984; Fürsich and Thomsen 2005); the reported stratigraphic ranges for this genus are in the Early Cretaceous of Europe and Canada, and in the Pliensbachian and Valanginian of Russia (Crickmay 1930; Zakharov 1965). The present findings at the Schönrockfjellet locality expand this genus' range up into the Albian; the youngest occurrences thus far reported.

Non-age diagnostic bivalves (including pectinids) and *Ditrupa* worm tubes are very common, whereas belemnites, gastropods, crinoid fragments and echinoderms (asteroids and ophiuroids) occur more rarely (*e.g.*, Nagy 1963, 1970; Grundvåg 2015).

In sum, the available biostratigraphic data indicate that the femur PMO 228.582 is of early–middle Albian age.

PALEONTOLOGICAL DESCRIPTION OF THE FEMUR

PMO 228.582 is a well-preserved but fragile femur, preserved in three dimensions in the proximal and partly in distal views (Fig. 2). The excellent preservation of this element is due to its placement under a large shell of a pelecypod (*Maclearnia* sp.); during compaction, this shell protected the fragile bone in a pressure shadow. The bone is 35 mm long and the cortex is 0.2 mm thick at midshaft, and even thinner in the femoral head. The fossil is preserved in a lens of ironstone containing a coquina of pelecypod bivalves and, close to the bone, a serpulid (*Ditrupa* sp.) and small gastropods can also be seen.

PMO 228.582 is preserved embedded in matrix, such that only the cranial aspect is visible (Fig. 2). The bone is gracile compared to small theropods (*e.g.*, Hwang *et al.* 2002), not markedly pinched in its midshaft, and is slightly arched craniocaudally. The shaft is partially collapsed and some parts of the cortex are missing, making it possible to observe the trabeculae, especially on the proximal end. The cortex is thin: the bone wall thickness (cortex) /diameter of midshaft ratio is $0.2/2.8 = 0.07$. The missing parts of the cortex mean that intermuscular lines cannot be seen on the cranial surface (Fig. 2).

The femoral head of PMO 228.582 is well-defined and spherical. It faces medially and is separated from the trochanter by a slender neck (Fig. 2). The capital region is not preserved. The femoral trochanter is low; a trochanteric shelf is present and this region does not project proximally above the femoral head. An expanded iliotrochanteric muscle attachment is present just distal to the missing cortex of the trochanter (Fig. 2).

The distal end of PMO 228.582 is well-preserved and a distinct patellar groove separates the lateral and medial condyles joining the intercondylar sulcus distally (without forming a distinct ridge) (Fig. 2). The medial condyle is larger than its lateral counterpart while the latter is more distally projected (Fig. 2) and the entire distal end is turned medially (Fig. 2). There are no lateral or medial epicondyles. On the lateral condyle a fossa for the *musculus tibialis cranialis* is seen; proximal to this condyle there is an impression for the *musculus iliofibularis* (Fig. 2).

A high-resolution CT analysis was conducted in order to visualise the caudal surface of PMO 228.582 embedded in matrix (Fig. 2). However, contrast between the bone and the matrix is poor; in micro-CT images the mid shaft is undetectable but the proximal and distal ends of this bone can clearly be seen. On the proximal end, the spherical femoral head and trochanters are visible (Fig. 2) along with a distinct groove separating the greater and posterior trochanters. The posterior trochanter is about one third the size of the greater trochanter and does not project as high.
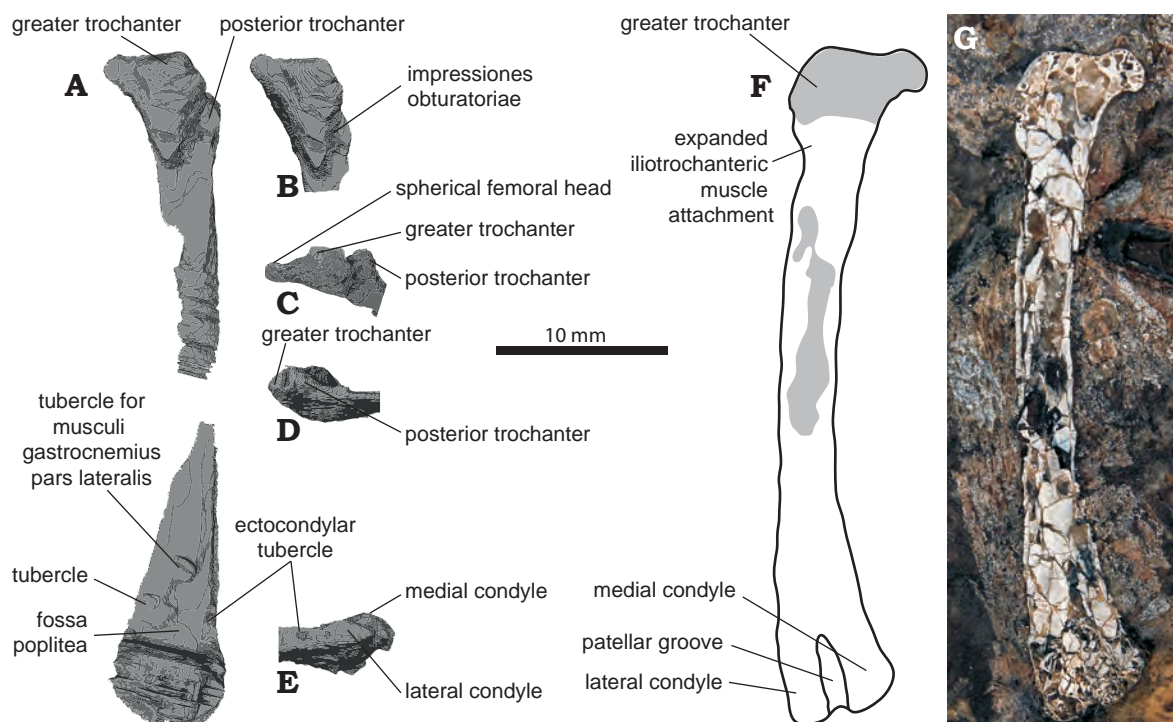
Fig. 2. Femur PMO 228.582 from Zillerberget member of the Carolinefjell Formation, Schönrockfjellet, Spitsbergen. **A**. Complete bone in caudal view, reconstructed from micro CT. **B**. femoral head in a slightly caudomedial view. **C**. Femoral head in proximal view. **D**. Femoral head in lateral view. **E**. Condyles in lateral view. **F**. Interpretive drawing of cranial aspect. Grey shading delineates where the cortex is missing. **G**. Cranial aspect of bone in matrix.

The two distal condyles of PMO 228.582 are partly crushed; the medial condyle is somewhat larger than the lateral (Fig. 2). Proximal to the condyles there are three tubercles; one is present on the medial side of the popliteal fossa; the second, on the lateral margin, is interpreted as the ectocondylar tubercle. A third, larger tubercle is placed more proximally to the latter and may be interpreted as the tubercle for the *musculus gastrocnemius pars lateralis*.

DISCUSSION

Limited taxonomically useful characters are preserved in the specimen described here, owing to the fact that recent phylogenetic studies of basal birds do not rely heavily on femora as sources for informative characters (*e.g.*, Wang *et al.* 2015) and these elements tend to preserve a mixture of basal and derived features. For example, the femoral popliteal fossa is not distally bounded by a complete transverse ridge and the ectocondylar tubercle and lateral condyle are separated by a deep notch (primitive characters). The femoral posterior trochanter is separated from the greater trochanter, as seen in some euenantiornithurine femora (Chiappe and Walker 2002), several theropods, *Archaeopteryx* Meyer, 1861 and Confuciusornithidae (Hutchinson 2001).

We tentatively place the femur in ?Avialae based on a combination of three of the characters described above: the presence of extremely thin-walled cortex, a well-developed femoral head, and a patellar sulcus. These three characters suggest that the femur belongs to an avialan but they are not autapomorphies exclusive to Avialae. Thin-walled bone occurs in pterosaurs, certain derived theropod dinosaurs and some mammals. Comparative data published by Currey and Alexander (1985) and Hutchinson (2001) show that the ratio is of cortical thickness to mid-shaft diameter is generally around 0.2 in non-avian theropods; pterosaurs down to half of that (0.1); in more basal archosaurs about 0.3 and in most birds less than 0.2. The described femur has a ratio of 0.07 which is low even for a bird, and somewhat lower than pterosaur long bones (Fastnacht 2005; Elgin and Hone 2013). *Confuciusornis* Hou *et al.*, 1995 is comparable, with a ratio of 0.09 (Hutchinson 2001, table 3).
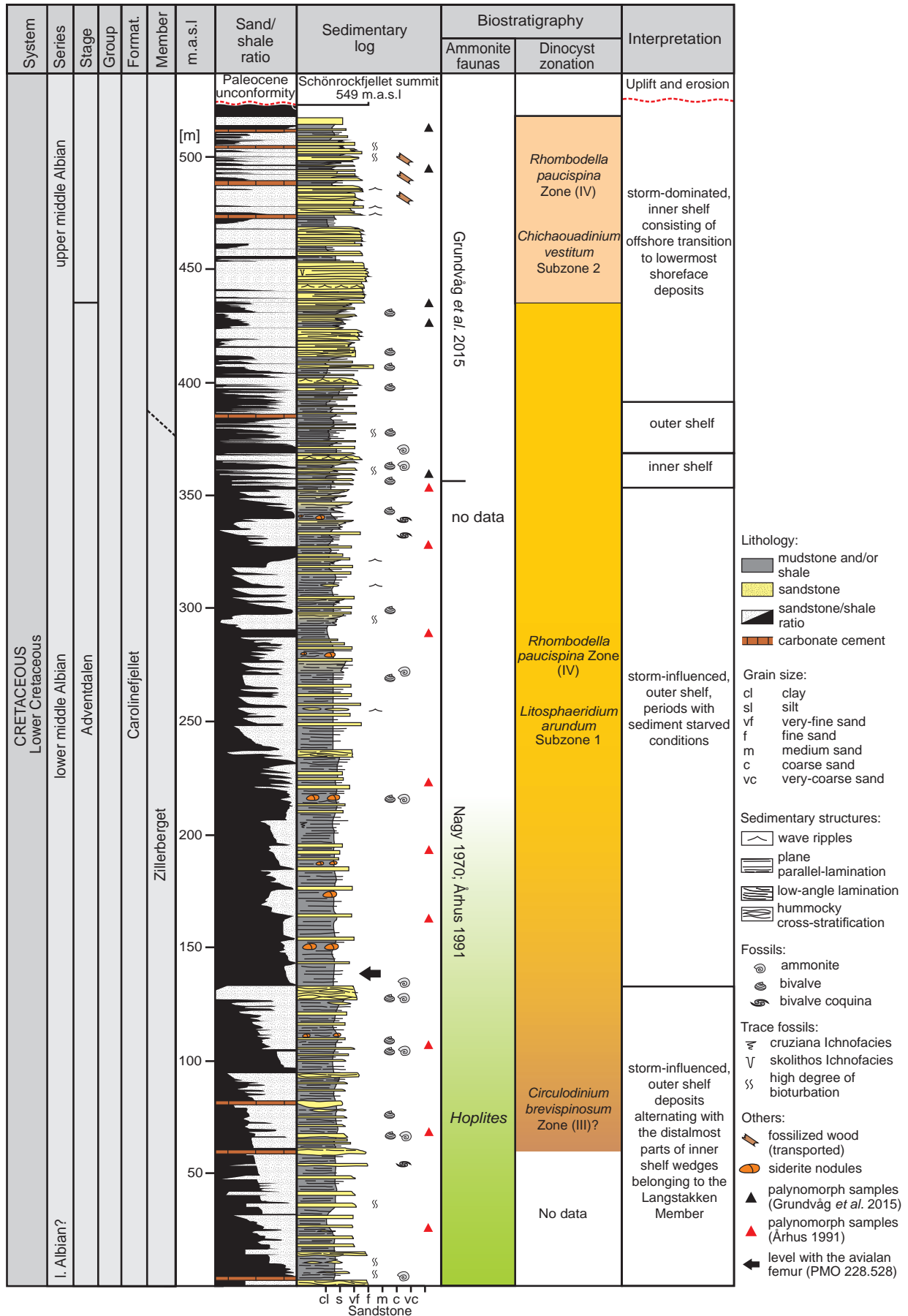
A well-developed femoral head and a patellar sulcus occur in mammals and some non-avian theropod dinosaurs. Even so, a patellar sulcus is suggested as an autapomorphy of Aves by Regnault *et al.* (2014) and further used as such by Wang *et al.* (2015). A well-developed femoral head projecting in an acute angle to the shaft is not present in pterosaurs (see *e.g.*, Witton 2013).

The condition of the trochanters is similar to that present in non-avian theropods, but also various birds. The inflated trochanteric area that extends lateral to the femoral shaft in cranial view is a character that is not present in most non-avian outgroups. In derived maniraptorans, the trochanteric crest is generally in line with the femoral shaft (Hutchinson 2001, figs. 3, 6, 8).

The bone is gracile and slightly arched craniocaudally, differing from hesperornithiforms (see *e.g.*, Zinoviev 2011, fig. 3) and pterosaurs (Witton 2013), in which the femur is straight; additionally, this element is more compact in hesperornithiforms. Hesperornithiforms represent the only avialan clade known from the Cretaceous of the Arctic at present and, excluding trace fossils, no prior occurrences antedate the Campanian (Rees and Lindgren 2005; Wilson *et al.* 2011). In basal avialans like *Confuciusornis sanctus* (see Martin *et al.* 1998, fig 2G) and *Sapeornis chaoyangensis* Zhou *et* Zhang, 2002 (see Zhou and Zhang 2003, fig. 9) the craniocaudal arch is more prominent than seen in PMO 228.582. In comparison to PMO 228.582, the small and similarly-aged theropod *Microraptor zhaoianus* Xu *et al.*, 2000 (Dromaeosauridae) has a femur twice the length (74 mm) and is a considerably more robust bone, with minimum midshaft diameter of 4–5 mm (Hwang *et al.* 2002, fig. 27), as does the femur of *Confuciusornis* (Martin *et al.* 1998, fig 2G).

The taxonomic position of PMO 228.582 is unclear, as few diagnostic characters are available. However, this specimen represents the first Cretaceous vertebrate fossil from Svalbard, demonstrating the possibility of future discoveries in the region. More avialan or theropod material from Svalbard is needed to fully resolve the phylogenetic position of PMO 228.582.

CONCLUSIONS

The ?avialan femur described herein is the only vertebrate fossil recovered to date from Cretaceous strata on Svalbard. It is also the oldest ?avialan found in the Arctic. While several ornithopod footprints have been described, PMO 228.582 is exceptional in its status as a fossil bone. This paper adds an important data point to the ongoing discussion regarding the true age of the Cretaceous strata on Svalbard and their corresponding units in the Barents Sea. It also highlights the potential for fragile non-marine vertebrate fossils to be discovered in a marine setting. The accompanying new biostratigraphic interpretation and the resolution it provides place important new constrains on the older Cretaceous strata in the region.

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← Fig. 3. Composite sedimentary log from Schönrockfjellet. Black arrow indicates the level where the fossil bird bone was found. Red (from Århus 1991) and black (from Grundvåg et al. 2015) triangles indicate stratigraphic positions of the shale samples used for biostratigraphic dating. Ammonites are sparse and belong to the *Hoplites* Ammonite Zone (Nagy 1970). The ammonite fauna and the dinoflagellate cysts together indicate that the investigated bone was deposited during the early middle Albian. Note that the lower part of the log (0–355 m) is based on data from Nagy (1970) and Århus (1991), whereas the upper part (355–520 m) is based on data from Grundvåg et al. (2015).

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CRURO-PEDAL STRUCTURE OF THE PAULCHOFFATIID *RUGOSODON EURASIATICUS* AND EVOLUTION OF THE MULTITUBERCULATE ANKLE

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Here we describe the osteological structures of the lower hind limb and foot of the Late Jurassic *Rugosodon eurasiaticus*, the earliest-known postcranial fossil of a multituberculate mammal. This fossil extends the key cruro-tarsal apomorphies, previously known from multituberculates of the Cretaceous and Paleogene, to the paulchoffatiid multituberculates of the Jurassic. Multituberculates as a group can now be diagnosed by derived features of the astragalus, the navicular, and the entocuneiform. These features are correlated with the mobility of the upper ankle joint and pedal digit I, indicating that early multituberculates acquired new locomotor functions of the limb and foot. However, the standing pedal posture of the basal multituberculates is plantigrade, typical of primitive mammaliaforms. The digitigrade posture appeared later in derived multituberculates of the Late Cretaceous and Paleogene, and was accompanied by several derived features of the calcaneus: elongation of the calcaneal tuber, development of the peroneal process and groove, and medio-lateral compression of the proximal part of calcaneus. These derived features enhanced locomotor function by increasing the in-lever of the Achilles muscles to lift the calcaneal heel off the substrate. The derived calcaneo-cuboidal features also facilitated a wider range of movement (including abduction) of the distal pedal elements. We concur that derived multituberculates may have had digitigrade pedal posture, although only facultatively. New fossils of the Jurassic *Rugosodon* and Early Cretaceous *Sinobaatar* have revealed fresh evidence that the astragalar features of the earliest paulchoffatiids are correlated with sophisticated cruro-tarsal rotation as in other multituberculates. *Rugosodon* provides the ancestral condition from which more diverse calcaneal features for more versatile functions evolved in geologically younger and more derived multituberculates.

Key words: Hind limb, tarsals, multituberculates, mammal evolution, Jurassic.

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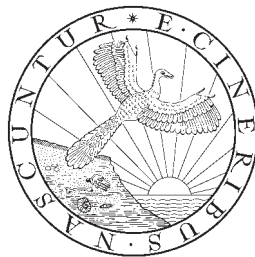
INTRODUCTION

Multituberculates are the most diverse mammals of the Mesozoic. They are not only speciose (Kielan-Jaworowska *et al.* 2004; Rose 2006; Luo 2007), but also show significant morphological disparity and variation in body size during the Late Cretaceous (Wilson *et al.* 2012). Multituberculates have a range of dental morphological features that indicate versatile feeding adaptation from animal-dominated omnivory to herbivory (Wilson *et al.* 2012). They also have very distinctive tarsal characteristics related to their locomotor functions (Simpson 1926; Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994; Szalay 1994; Yuan *et al.* 2013).

The paulchoffatiids represent the basal-most clade of multituberculates (Hahn 1969, 1993; Hahn and Hahn 1998, 2000; Kielan-Jaworowska *et al.* 2004). They are almost entirely Late Jurassic (Hahn and Hahn 1998; Kielan-Jaworowska *et al.* 2004), with one possible exception in the Early Cretaceous of North America (Cifelli *et al.* 2013). The morphological features of paulchoffatiids are informative about the ancestral condition of multituberculates, and are also useful for distinguishing multituberculates from other mammaliaforms. The type specimen of *Rugosodon* is the only skeletal fossil known, so far, from the family Paulchoffatiidae. It is also the earliest-known skeletal fossil of any multituberculate. Previously, the hind limb and tarsal features of *Rugosodon eurasiaticus* only received a brief description in a preliminary study (Yuan *et al.* 2013). Here we offer a detailed description of these features and explore their ramifications for the skeletal evolution of multituberculates as a whole.

Multituberculates of the Late Cretaceous and Paleogene have been long known for their derived hind limb and pedal features (Simpson and Elftman 1928; Kielan-Jaworowska 1979, 1989; Jenkins and Krause 1983). Some of the better-preserved postcranial skeletal fossils have been documented by detailed studies (Krause and Jenkins 1983; Kielan-Jaworowska and Qi 1990; Kielan-Jaworowska and Gambaryan 1994; Szalay 1994; Hurum and Kielan-Jaworowska 2008; Bolortsetseg 2008). Our present study of *Rugosodon* reveals that many derived hind limb and pedal features, hitherto known in the Cretaceous and Paleogene multituberculates, can now be traced to the basal-most paulchoffatiids of the Jurassic, and are therefore diagnostic of all multituberculates (inclusive of paulchoffatiids; Yuan *et al.* 2013).

Our comparative study can now also demonstrate that multituberculates show a range of disparity of their hind limb and pedal structures. These morphological differences can be attributable to diverse locomotor functions among different multituberculates, and suggest that different Mesozoic multituberculates may have developed preferences for different substrates. Their limbs and pedes show a significant ecomorphological diversity, as was already known from the functional morphology of their teeth.

FOSSIL MATERIAL

Holotype specimen. — The holotype of *Rugosodon eurasiaticus* (BMNH 1142) consists of the main slab (1142A) and the counter-slab (1142B) (Figs 1–5). The fossil was originally found at the Daxishan fossil site of the Jurassic Tiaojishan Formation, and was later acquired by Beijing Museum of Natural History. The site has been dated to between 158.5±1.6 ma and 161.0±1.44 ma (Liu *et al.* 2012). These dates for the site have been corroborated by an independent study (Wang *et al.* 2013).

The holotype slabs were preserved with two specimens of the small estheriid conchostracan *Qaidamestheria* (*sensu* Liao and Huang 2014). This is an index invertebrate fossil from the main fossiliferous layers of the Tiaojishan Formation. Shale and mudstone slabs of vertebrate fossils from the several quarries of the Daxishan site are typically preserved with a moderate abundance of *Qaidamestheria* specimens (Liao and Huang 2014; Huang 2015; Huang *et al.* 2015). The presence of the small conchostracan *Qaidamestheria* on the slabs of this mammal fossil helped to authenticate that the specimen is from the Daxishan site.

Taxonomy. — *Rugosodon eurasiaticus* (BMNH 1142) is assigned to the paulchoffatiid clade by its dental features. The lower molars of *R. eurasiaticus* are nearly identical to those of *Plesiochoffatia*, a paulchoffatiid multituberculate from the Late Jurassic Guimarota Mines of Portugal (Hahn and Hahn 1998, 1999, 2000). *Rugosodon* and *Plesiochoffatia* show strong similarities in the occlusal surfaces of both upper and lower molars: dense pits, ridges, grooves, and a highly corrugated middle valley, rimmed by crenulated tooth margins with coalesced cusps. The lower molars are also similar in having a tall and trenchant anterolingual cusp, and in overall oblong shape of the occlusal basin (Yuan *et al.* 2013, figs S3, S4). The M2 is similar to M2s assigned to *Plesiochoffatia* and the upper molars of other paulchoffatiids in having a crenulated antero-buccal ridge or shelf (Hahn 1969, 1993; Hahn and Hahn 2000). M2 of *Rugosodon* and paulchoffatiids from the Late Jurassic of Portugal are also similar in that the middle valley is posteriorly closed by a cusp or ridge (Hahn and Hahn 1998; see also Yuan *et al.* 2013, figs S3, S4). *Rugosodon* can be distinguished from most non-paulchoffatiid multituberculates in having these derived features (Yuan *et al.* 2013).

Of all paulchoffatiid multituberculates, *Rugosodon* is most similar to *Plesiochoffatia* but it is 150% to 200% larger than *Plesiochoffatia* by the size of lower m1. Also its occlusal surfaces are more densely ornamented than those of *Plesiochoffatia* (Yuan *et al.* 2013).

Orientation of fossil structure on slabs. — Because the same bones and their impressions and mold outlines are preserved on both the main slab (1142A) and the counter-slab (1142B), it is necessary to establish the right versus the left sides of the skeleton, for descriptive purposes. We designate, *a priori,* the right side versus the left side of the skeleton, as seen on the main slab (BMNH 1142A) (Figs 1, 2, 4). The right vs. left sides of the skeletal structures (or the impressions thereof) on the counter-slab (BMNH1142B; Figs 3, 5) are determined according to the left-right orientation on BMNH1142A.

CRURAL MORPHOLOGY

The proximal part of the tibia possesses an anterior tibial tuberosity, a medial tuberosity, and a large, hook-like lateral process (Figs 5, 6). The latter process is also known as proximolateral process (Kielan-Jaworowska and Gambaryan 1994). This is homologous to the "lateral condyle" of extant therian mammals (*sensu* Evans 1995). The proximal end of the tibia is asymmetrical because the lateral process is much larger and longer than the medial tuberosity (Fig. 6). A low anterior tibial crest extends from a prominent anterior tibial tuberosity, distally for about 1/3 of the tibial length (Figs 5, 6). The flat surface lateral of the anterior tibial crest is interpreted to be the area of origination for M. tibialis anterior (*sensu* Kielan-Jaworowska and Gambaryan 1994). This is similar to the tibialis anterior fossa of extant small placentals (Neveu and Gasc 2002). The shaft of the tibia is relatively straight (Figs 5, 6), and is not bowed medially as seen in the Late Cretaceous *Chulsanbaatar*, *Nemegtbaatar*, and *Catopsbaatar* (Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008).

The distal extremity of the tibia is distinctly longer than the distal extremity of the fibula (Figs 5, 6). It shows a distinctive suture between the epiphysis and the diaphysis (shaft). The distal end of the tibial epiphysis has a medial malleolus, called the medial tibial condyle (*sensu* Krause and Jenkins 1983). Although the
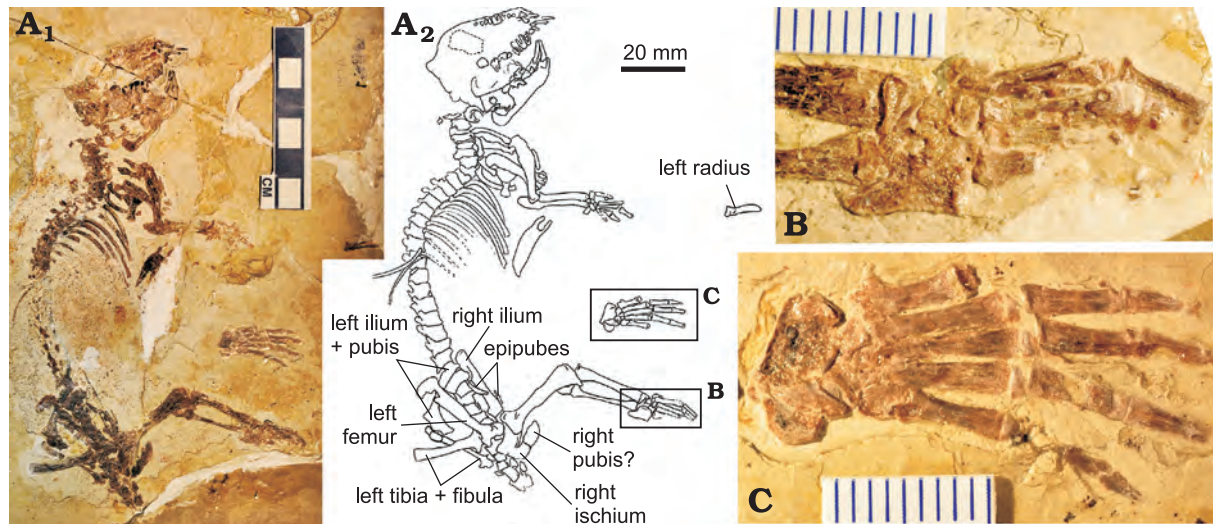
Fig. 1. The paulchoffatiid *Rugosodon eurasiaticus* Yuan *et al.*, 2013 (BMNH1142A), Daxishan Site, Tiaojishan Formation, Upper Jurassic, Liaoning Province, China. Pedal structure preserved on the main slab of the type specimen. **A**. Skeleton and the location of the right and left pedes, photo (A₁) and explanatory drawing (A₂). **B**. Right pes in dorsal view. **C**. Left pes on main slab in dorsal view.

distal part of the tibia is not fully exposed in distal view due to its intact association with the astragalus, the medial tibial condyle can be seen in the anterior view of the tibia (Figs 4, 6). In anterior view, the profile of the distal tibia is similar to those of *Ptilodus* and *Eucosmodon* (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994); thus we interpret *Rugosodon* as having the medial and lateral articulating condyles on the tibia, for the corresponding structures on the astragalus (Figs 6, 7), as in the Paleocene multituberculates *Ptilodus* and *Eucosmodon*.

A large and plate-like parafibula is present, and abuts the proximal end of the fibula (Figs 5, 6), but it is not fused with the fibula, thus differing from those of monotremes (Lessertisseur and Saban 1967; Gambaryan *et al.* 2002), or as seen in the spalacotherioid *Akidolestes* (Li and Luo 2006; Chen and Luo 2013). The overall features of the parafibula and the proximal fibula are similar in *Sinobaatar* (NGMC3000).

The unfused parafibula of *Rugosodon* (Figs 5, 6) is shared by all other multituberculates in which the relevant anatomy is preserved (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994; Hu and Wang 2002; Bolortsetseg 2008). The condition in *Rugosodon* suggests that a separate parafibula is a plesiomorphy of all multituberculates including paulchoffatiids. The bone, however, is much larger in *Rugosodon* than in *Kryptobaatar* and *Chulsanbaatar* (Kielan-Jaworowska and Gambaryan 1994) and *Sinobaatar* (Wang *et al.* 2003; personal observation).

Implications of the parafibula for functional comparison with other mammals will be discussed below in the "Functional Morphology" section of this paper.

The fibula has a straight shaft (diaphysis; Figs 5, 6), not bowed as those of several Cretaceous multituberculates (Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008). The fibular head is bilaterally compressed and fan-shaped. It is significantly wider than the shaft. *Rugosodon* lacks the hook-like posterior projection from the proximal end of the fibula, as seen in several Cretaceous multituberculates.

The distal fibula has a clear suture between the diaphysis and the epiphysis (Fig. 4). The articulating surface is relatively flat to slightly convex (Figs 4, 6). By our assessment, it does not show a distinctive, pointed lateral malleolus, as in *Kryptobaatar* (Kielan-Jaworowska and Gambaryan 1994, fig. 2), *Ptilodus* (Krause and Jenkins 1983), and *Eucosmodon* (Szalay 1993). As preserved, the distal end of the fibula clearly contacted the calcaneus (Fig. 6), in addition to the astragalo-fibular contact. However, the fibula of *Rugosodon* does not show a dividing crest that separates the astragalo-fibular facet from the calcaneo-fibular facets (Figs 4, 6). Together, the distal end of the fibula and the distal extremity of the tibia form a curved contact with the astragalus and the calcaneus (Fig. 6D), as characterized for *Nemegtbaatar*, *Chulsanbaatar* and *Catopsbaatar* (Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008; Bolortsetseg 2008), *Ptilodus* (Krause and Jenkins 1983), and other multituberculates (Szalay 1993). In all essential respects, *Sinobaatar* is similar to *Rugosodon* in these features.
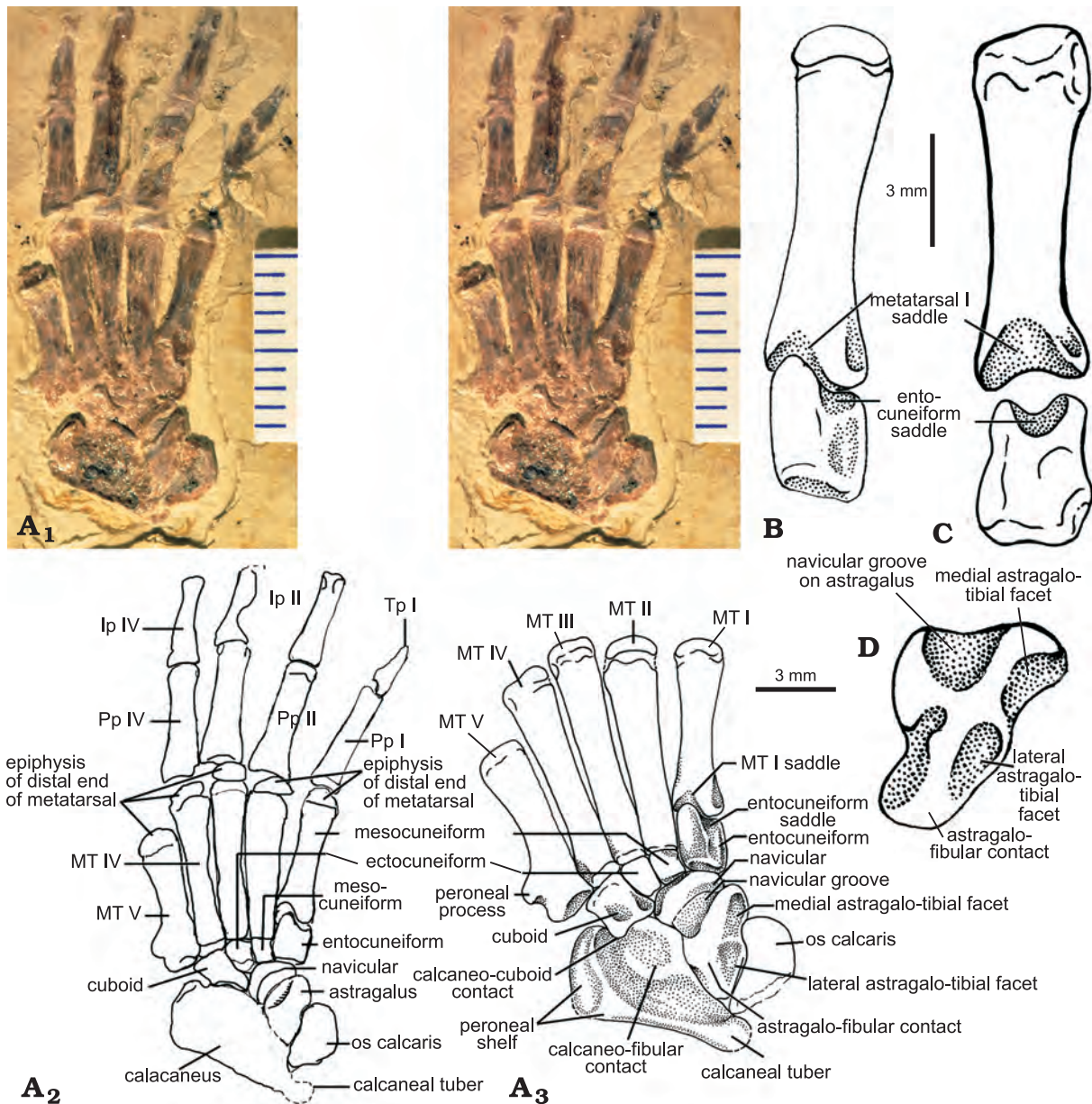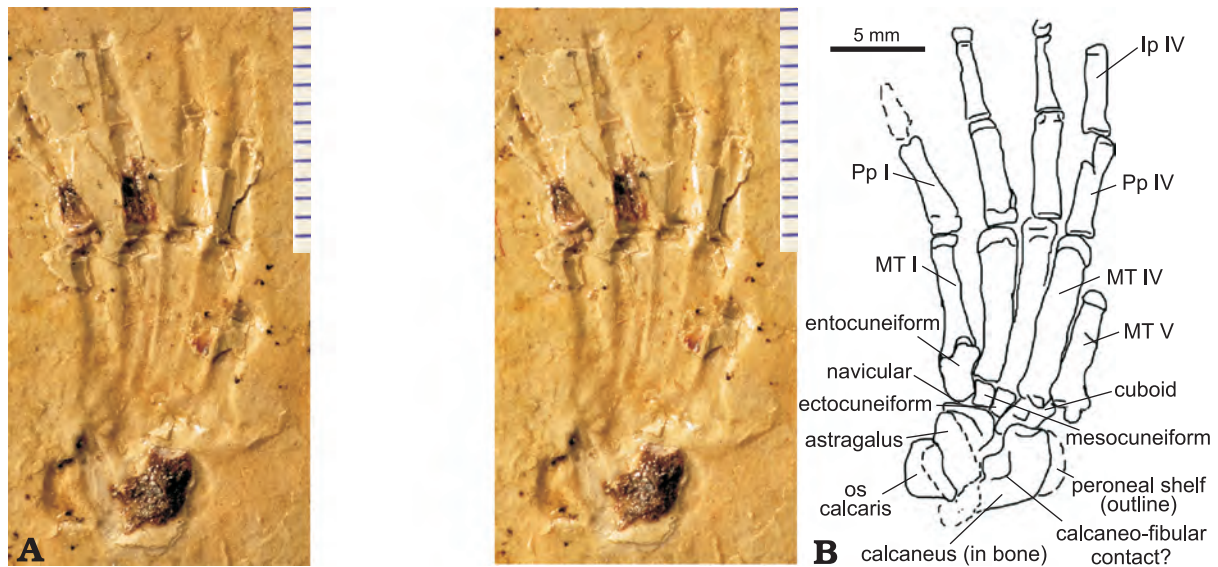
Fig. 2. Foot and tarsal elements of *Rugosodon eurasiaticus* Yuan *et al.*, 2013 (**A**, **B**; BMNH1142A, Daxishan Site, Tiaojishan Formation, Upper Jurassic, Liaoning Province, China) and *Eucosmodon* sp. (**C**, **D**; AMNH 16325, locality near Kimbetoh, Nacimiento Formation, early Paleocene, New Mexico, USA). **A**. Left pes in dorsal view, stereo photographs (A₁) and explanatory drawing (A₂); proximal and intermediate phalanges of digit V are missing. Details of tarsals and metatarsals in dorsal view (A₃); the navicular is ajar from the astragalus; the astragalus is slightly displaced relative to the calcaneus (in Yuan *et al.* 2013: fig. 2, this illustration was incorrectly identified as "ventral view"). **B**. Articulated entocuneiform and MT I in oblique dorsal view. **C**. Entocuneiform in medial view and metatarsal in dorsal view, showing the reciprocal saddle-shaped joint on the distal end of entocuneiform and the proximal end of MT I. **D**. Astragalus in dorsal view (or tilted dorsal view). Abbreviations: Ip, intermediate phalanx; MT, metatarsal; Pp, proximal phalanx; Tp, terminal phalanx.

TARSAL MORPHOLOGY

The calcaneus is the largest of all tarsal bones of *Rugosodon* (Figs 1–6). The peroneal shelf has a rectangular outline and is mediolaterally broad (Fig. 8). It lacks the distinctive peroneal process (or peroneal tuber of some authors) separated by a peroneal groove (*sensu* Kielan-Jaworowska and Gambaryan 1994; Szalay 1994). The calcaneal body is dorsoventrally compressed and wide mediolaterally between the sustentacular area on the medial side and the lateral (peroneal) border (Fig. 8E). The calcaneal tuber is short, being less

Fig. 3. *Rugosodon eurasiaticus* Yuan *et al.*, 2013 (BMNH1142B), Daxishan Site, Tiaojishan Formation, Upper Jurassic, Liao-ning Province, China; left pes preserved in outlines and impressions in dorsal view on the counter slab. **S**tereo photographs (**A**), explanatory drawing (**B**). Proximal and intermediate phalanges of digit V are missing. Abbreviations: Ip, intermediate phalanx; MT, metatarsal; Pp, proximal phalanx.

than 20% of the total length of the calcaneus, and it is pointed (Figs 4–6). The cuboid facet is on the medio-distal corner of the calcaneus. Although its surface is not fully exposed, we infer from its exposed dorsal margin that, overall, the cuboidal facet is concave. The astragalar facet on the calcaneus is convex (Figs 4, 6) , as seen in other multituberculates (Krause and Jenkins 1983; Szalay 1994). However, the sustentacular area of the calcaneus is not exposed. As preserved in the intact ankle (Figs 4, 6), the calcaneo-fibular contact appears to be extensive but the tibia has no possibility to contact the calcaneus (Figs 4, 6, 9), as interpreted for several Paleogene multituberculates (Krause and Jenkins 1983; Szalay 1993).

The astragalus is exposed in dorsal view on the left pes (Fig. 2) and in dorso-medial view on the right (Fig. 4). The bone is ajar from the calcaneus in the right pes in such a way that the flexed surface (under side) of the right astragalus is partially visible (Figs 4, 6B). This reveals the calcaneo-astragalar contact to some extent. The curvature and the shape of the calcaneo-astragalar contact (Fig. 6B) are similar to those of the isolated calcaneus and astragalus of other multituberculates (Jenkins and Krause 1983; Krause and Jenkins, 1983; Szalay 1993, 1994; Kielan-Jaworowska and Gambaryan 1994; Hurum *et al.* 2008). The calcaneo-astra-galar facet appears to be separate from the sustentacular facet in the right astragalus, as in other mammals. However, the dividing sulcus is not well preserved; the part of the sulcus where the astragalar foramen would be located in an intact astragalus (Hurum and Kielan-Jaworowska 2008; Bolortsetseg 2008) is not exposed, so our interpretation of these two facets is tentative.

The proximal (posterior) part is narrower than the distal (anterior) end. The dorsal aspect of the astrag-alus has extensive contact with the fibula. On the medial (proximal) surface the astragalus has two shallow depressions, which we interpret to be the medial astragalo-tibial facet and the lateral astragalo-tibial facet (*sensu* Jenkins and Krause 1983), respectively for articulation with the medial tibial condyle and the lateral tibial condyle (Figs 2B, C, 6C). These shallow facets are not distinctively demarcated from each other, sim-ilar to the condition of several Late Cretaceous multituberculates as noted in some previous studies (Szalay 1993, p. 121; Hurum and Kielan-Jaworowska 2008; Bolortsetseg 2008) but different from the distinctive crest of the two facets as seen in *Eucosmodon* (Krause and Jenkins 1983; Szalay 1994).

The navicular facet on the distal aspect of the astragalus is a curved groove. It is concave in dorso-ven-tral plane and also slightly curved from the medial side to the lateral side. Overall, the astragalo-navicular contact is somewhat like a saddle (Figs 2, 7). This morphology is similar to the astragalo-navicular joint well described for other multituberculates (Krause and Jenkins 1983; Szalay 1994; Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008; Bolortsetseg 2008).

We identify the os calcaris bone for supporting the extratarsal spur in the left foot of the main slab (BMNH1142A; Fig. 2). The bone has a crescent shape. As preserved, it is attached to the posterior aspect of the astragalus. A similar association of the os calcaris and the astragalus has been documented for several
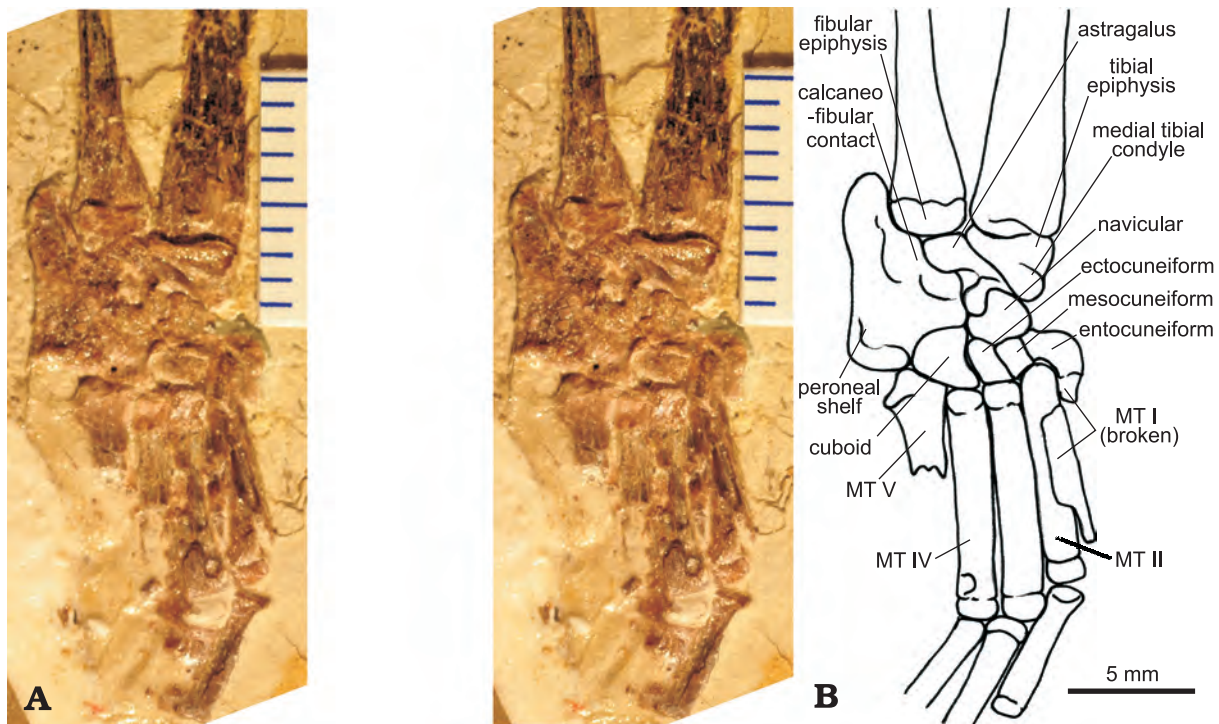
Fig. 4. *Rugosodon eurasiaticus* Yuan *et al.*, 2013 (BMNH1142A; Daxishan Site, Tiaojishan Formation, Upper Jurassic, Liaoning Province, China); right lower leg and pes preserved on the main slab in dorsal view. **A**. Stereo photographs. **B**. Explanatory drawing. The right pes is mostly preserved in bones on BMNH1142A, and its corresponding impression and mold outlines are on BMNH1142B. MT, metatarsal.

Late Cretaceous multituberculates, including *Kryptobaatar dashzevegi* (ZPALMgM-I/41) and *Catopsbaatar catopsaloides* (PM120/107) (Hurum *et al.* 2006, p. 5, fig. 5; Hurum and Kielan-Jaworowska 2008). A less likely possibility is that this bony piece would belong to a disarticulated tibial epiphysis of the left hind limb of the specimen. This can be ruled out because the preserved left tibia has at least a part of its epiphysis in situ and still attached to the diaphysis of the tibia. The identification of the os calcaris in multituberculates and other extinct mammaliaforms is ultimately based on a similar association of the os calcaris and the astragalus in extant monotremes (Hurum *et al.* 2006; Ji *et al.* 2006; Kielan-Jaworowska and Hurum 2006; Zhou *et al.* 2013; Luo *et al.* 2015). Because the os calcaris is embedded in the soft-tissues of the ankle region but not directly articulated with the astragalus in extant monotremes, its close proximity to the astragalus is the only way to identify this structure (Hurum *et al.* 2006).

The cuboid has a square-like outline in dorsal view and is antero-medial (disto-medial) to the calcaneus in *Rugosodon* (Fig. 2). The bone fits, obliquely, into the concave proximo-medial margin of the calcaneus. It is medial to the imaginary proximo-distal (long) axis of the calcaneus. In the proximo-distal orientation of the calcaneus and the cuboid, this facet faces antero-medially (Fig. 6C). The facet appears to be oriented vertically for the dorso-ventral orientation. This orientation of the cuboid-calcaneus and the dorsal extent of the cuboidal facet on the calcaneus, as documented here for *Rugosodon*, is plesiomorphic for multituberculates (Fig. 9).

The navicular has a triangular outline in dorsal view (Figs 2, 4). The navicular is slightly ajar from the astragalus on the left pes (Fig. 2) but appears to be intact and articulated with the astragalus on the right pes (Fig. 4). We interpret that the proximal part of the navicular contacts the saddle-shaped navicular facet of the astragalus (Fig. 2: an-groove), as shown by previous studies for other multituberculates (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008) (Fig. 7). The ectocuneiform and the mesocuneiform show oblong outlines in dorsal view (Figs 4, 6). They are small and only half the size of the cuboid and the entocuneiform. The entocuneiform is twice as long proximo-distally as the ectocuneiform and the mesocuneiform in *Rugosodon* (Figs 2–4), and it is a bilaterally compressed bone, as well illustrated for other multituberculates (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994; Szalay 1994). The entocuneiform of the left pes on the main slab (BMNH1142A) clearly shows the saddle-shaped joint to the metatarsal I. Its distal end is concave dorsoventrally and slightly convex mediolaterally. This articulating surface fits the saddle-shaped proximal end of metatarsal I.
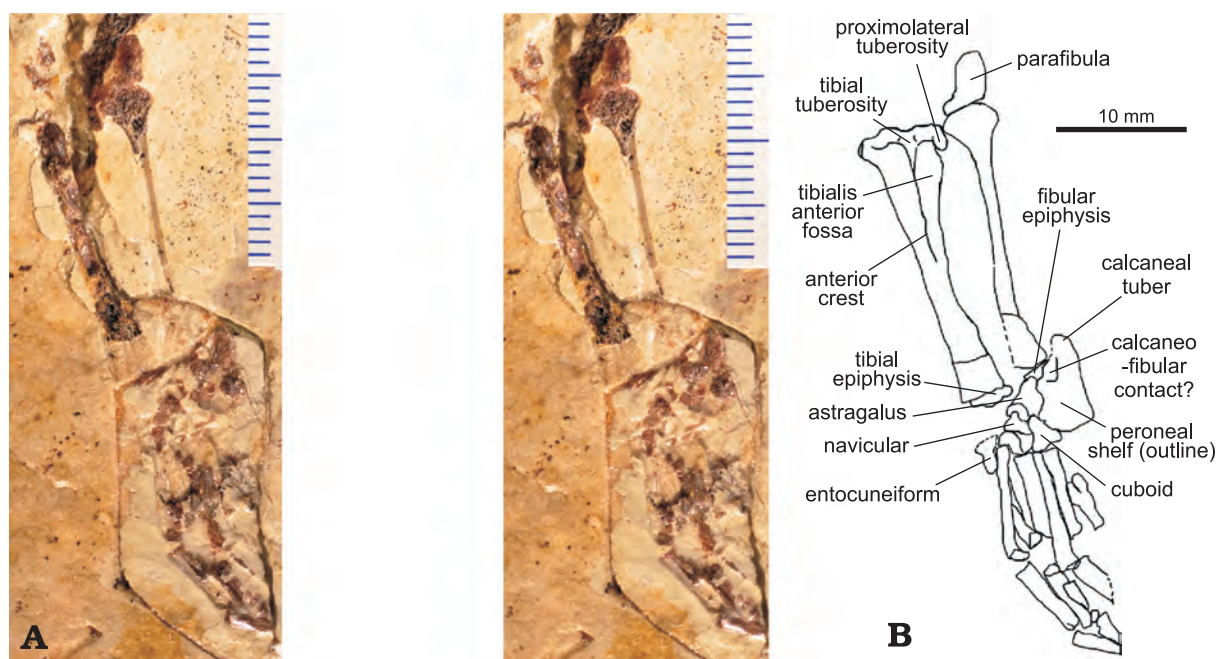
Fig. 5. *Rugosodon eurasiaticus* Yuan *et al.*, 2013 (BMNH1142B), Daxishan Site, Tiaojishan Formation, Upper Jurassic, Liaoning Province, China; right crus and pes preserved on the counter slab, mostly in impression and mold outlines (mostly in dorsal view). **S**tereo photographs (**A**), explanatory drawing (**B**).

METATARSALS AND PHALANGES

Metatarsal (MT) I is wider in the proximal end than the distal, and its proximal end has a saddle joint that is mediolaterally concave and dorso-ventral convex (Figs 2, 7). The shape of this contact surface reciprocates the saddle shaped joint of the entocuneiform, and is thus called here "reciprocal saddle joint." This is a unique and diagnostic feature of all multituberculates (Krause and Jenkins 1983; Szalay 1993, 1994; Kielan-Jaworowska and Gambaryan 1994; Yuan *et al.* 2013).

MT II–IV are bilaterally compressed in the proximal ends, which are slightly narrower than the distal ends. MT II–IV are also tightly packed together near their proximal ends. MT V is about 80% of the length of MT II–IV. It is the shortest of all metatarsals, but is also the widest in its proximal end among all metatarsals. A peroneal process (*sensu* Bolortsetseg 2008) or the proximolateral tubercle of MT V is present in both pedes (Figs 2, 3, 6). All metatarsals show distinctive distal epiphyseal sutures between the epiphyses and the diaphyses, but there are no epiphyseal sutures in the proximal ends of any metatarsals. The articulating surface of the distal epiphysis is uniformly convex and almost dome-shaped for digits I–IV. Although the epiphysis of MT V is slightly obscured by a fracture, we interpret that it, too, is dome-shaped, as in the other metatarsals.

Absence of the proximal epiphyseal growth plate of MT II–IV is a uniform feature of extant therian mammals (Reno *et al.* 2006, 2007). We add that this is also the case for MT II–IV of multituberculates. However, in MT I of extant therians, it is the proximal end of the bone that has an epiphyseal suture and a growth plate in the sub-adult stages. By contrast, in *Rugosodon*, an epiphysis and a distinctive epiphyseal suture are preserved on its distal end on the intact MT I on the left pes (Figs 2, 3). In this regard, *Rugosodon* is distinctive from extant therians, in that the single epiphysis is on the opposite end of MT I. According to our observation, MT I of *Sinobaatar* also has a distal epiphyseal suture. A distal epiphyseal suture is also visible in the published photo of MT I belonging to *Kryptobaatar* and *Catopsbaatar* (Hurum and Kielan-Jaworowska 2008). Thus multituberculates, as a group, are different from extant therians in the distal location of the epiphysis on MT I.

Proximal phalanges of pedal digit rays I–IV are generalized; the proximal phalanx for digit V is missing on both feet. Their proximal ends are preserved well enough to show a slight lip along the dorsal rim of the concave proximal end. The proximal ends are slightly wider and thicker than the distal ends. The distal end of this phalangeal segment shows an epiphyseal suture on at least proximal phalanges of digits II–IV. The distal articulating surface of the epiphysis is transversely cylindrical.
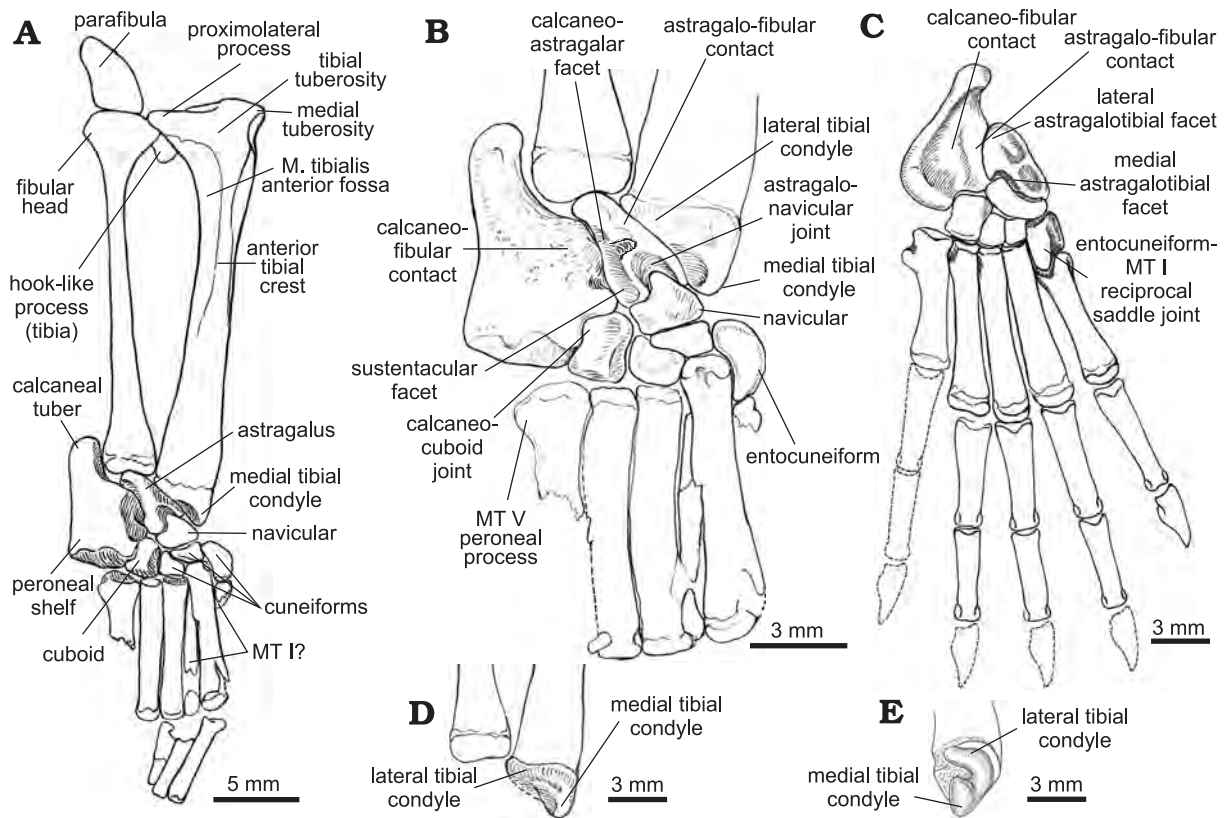
Fig. 6. *Rugosodon eurasiaticus* (**A–D**), Daxishan Site, Tiaojishan Formation, Upper Jurassic, Liaoning Province, China; composite reconstruction of cruro-pedal structure and *Eucosmodon* sp. (**E**), distal tibia (AMNH 16325), locality near Kimbetoh, Nacimiento Formation, early Paleocene, New Mexico, USA. **A**. Reconstruction of the right cruro-pedal features from camera lucida drawings, tibia in anterior view, proximal part of fibula rendered in lateral view. **B**. Details of preserved tarsals and metatarsals (based on right side of BMNH1142A), most bones seen in dorsal view. **C**. Reconstruction of the right pes in dorsal view. **D**. Reconstruction of distal tibia and fibula, right side in anterior view. **E**. Tibia in distal view (redrawn from photos of Krause and Jenkins 1983 and Kielan-Jaworowska and Gambaryan 1994). MT, metatarsal.

The intermediate phalanges are preserved on digital rays II–IV. Each of these is slightly wider (thicker) on the proximal end than the distal end. The proximal end is flat to slightly concave without epiphyseal suture on digits II–IV. But the distal epiphyseal suture is visible in at least two proximal phalanges. On the intermediate phalanx of digit IV, the distal surface of the epiphysis has a grooved contact surface for the terminal phalanx.

The terminal phalanx is only preserved on digit I. It is transversely wide and has a dorsal lip over its proximal articular surface. It clearly lacks a high and arch-like dorsal profile and is not bilaterally compressed. Functional inference on the proportions of the metatarsals and phalanges will be discussed below.

FUNCTIONAL MORPHOLOGY OF JOINTS

Hip and knee joints. — The socket of the acetabulum lacks a continuous dorsal margin in that the articular facets of the ilium and ischium in the acetabulum are not dorsally continuous in *Rugosodon*. The same is true of well-preserved pelves belonging to several other multituberculates. This would have permitted the femur to rotate dorsally, such that the femur could be held in a strongly abducted orientation (Simpson and Elftman 1928; Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994).

Based on osteological characteristics of the femur, tibia, and parafibula, we interpret the knee of *Rugosodon* as asymmetrical. Although the femur is flattened in slab preservation, the size and shape differences of its two distal condyles are still distinctive. The lateral condyle of the femur is much wider and slightly lower than the medial condyle. The condyle and its ectepicondylar prominence are markedly more pointed than the medial condyle and the entepicondyle (not illustrated). The extensor aspect of the distal
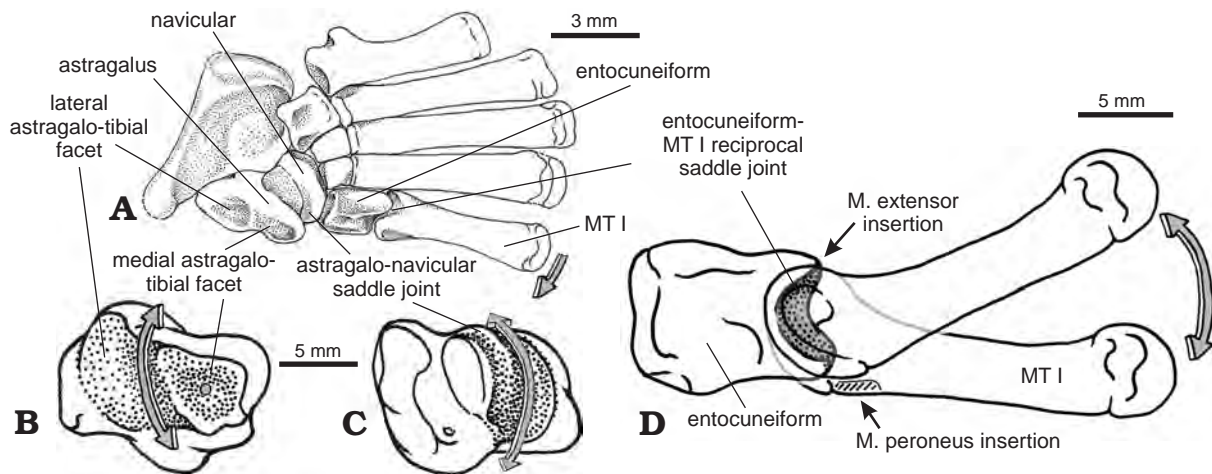
Fig. 7. *Rugosodon eurasiaticus* (**A**), Daxishan Site, Tiaojishan Formation, Upper Jurassic, Liaoning Province, China, cruro-tarsal joint functions (modified from Yuan *et al.* 2013), compared to the cimolodontan *Eucosmodon* sp. (**B–D**), site near Kimbetoh, Nacimiento Formation, early Paleocene, New Mexico, USA. **A**. Pes in dorsal view, showing abduction-adduction of digit I (arrow) on the reciprocal saddle joint of the entocuneiform and MT I. **B**. Astragalus in dorsal view, showing pivotal rotation (gray dot) of the astragalus relative to the tibia, which represents the contact of the medial condyle of distal tibia to the medial astragalo-tibial facet of the astragalus. The arrow shows the lateral condyle of the distal tibia, which glides along the lateral astragalo-tibial facet. **C**. Astragalus in ventral view showing the grooved and saddle-shaped astragalo-navicular joint; the arrow indicates movement of the navicular relative to the astragalus. **D**. Dorsiflexion and plantarflexion of MT I at the reciprocal saddle joint. Phylogenetic topology is based on the Adam's consensus tree in Yuan *et al.* (2013). MT, metatarsal.

femur of *Rugosodon*, as exposed in the right femur on the main slab of the fossil (BMNH1142A), is similar to that illustrated for other multituberculates. Krause and Jenkins (1983) noted that, in *Ptilodus*, both condyles are largely confined to the flexor side of the femur and do not extend around to be continuous with the patellar groove on the extensor side of the distal femur. They suggest that this is consistent with a crouched stationary posture of the knee. Kielan-Jaworowska and Gambaryan (1994, figs 51–53) postulated, similarly, a flexed knee posture for Late Cretaceous multituberculates.

The tibia of *Rugosodon* is noticeably asymmetrical mediolaterally, on its proximal end. This is similar to extant *Ornithorhynchus*, in which the proximal tibia is asymmetrical. With this pattern of tibial distal condyles, the knee joint is obligately flexed, related to the sprawling posture of the hind limb (Gambaryan *et al.* 2002; Li and Luo 2006, fig. 4).

The presence of a large parafibula is also consistent with a crouched posture of the knee. In monotremes (Gambaryan *et al.* 2002; Li and Luo 2006), the knee can only flex in sprawling posture because the parafibula projects dorsally behind the lateral femoral condyle. This would exclude the possibility for the knee to bend if the femur and the crus had been aligned parasagittally. In other words, the femur and the crus had to be sprawling in a crouched posture, given the large size and the location of the parafibula. Similar to *Rugosodon*, another Mesozoic mammal, the spalacotheriid *Akidolestes*, has also been interpreted as having a habitually flexed knee, as constrained by the hypertrophied parafibular process of the fibula (Li and Luo 2006, fig. 4; 2013, fig. 20).

For *Rugosodon* and *Sinobaatar*, the sprawling hind limb is consistent with evidence of taphonomic preservation. As noted by Kielan-Jaworowska and Hurum (2006), the Mesozoic mammals interpreted to have sprawling hind limb by osteological characters also tend to show a sprawling posture in typically passive preservation in lacustrine rock slabs. Mammaliaform skeletons that were determined to have crouched posture by osteological characters (Gambaryan and Kielan Jaworowska 1997) are also predominantly preserved in dorso-ventral compression of the skeleton, with sprawling fore and hind limbs. This differs from the limbs of crown therian mammals, which, if passively preserved in rock slabs, tend to be preserved on their lateral flanks (Kielan-Jaworowska and Hurum 2006). The lateral flank preservation is more consistent with their presumptive parasagittal limb postures. So far, the skeleton of *Rugosodon* and several skeletal specimens of *Sinobaatar* (*e.g.*, the holotype of *S. lingyuanensis*, IVPP V12517; see Hu and Wang 2002) found in lacustrine shales are preserved also in dorso-ventral compression with sprawling posture. In sum, the osteological interpretation of an abducted femur and a flexed knee of *Rugosodon* here is consistent with ancillary, but supportive evidence of its taphonomic preservation on shale slabs.
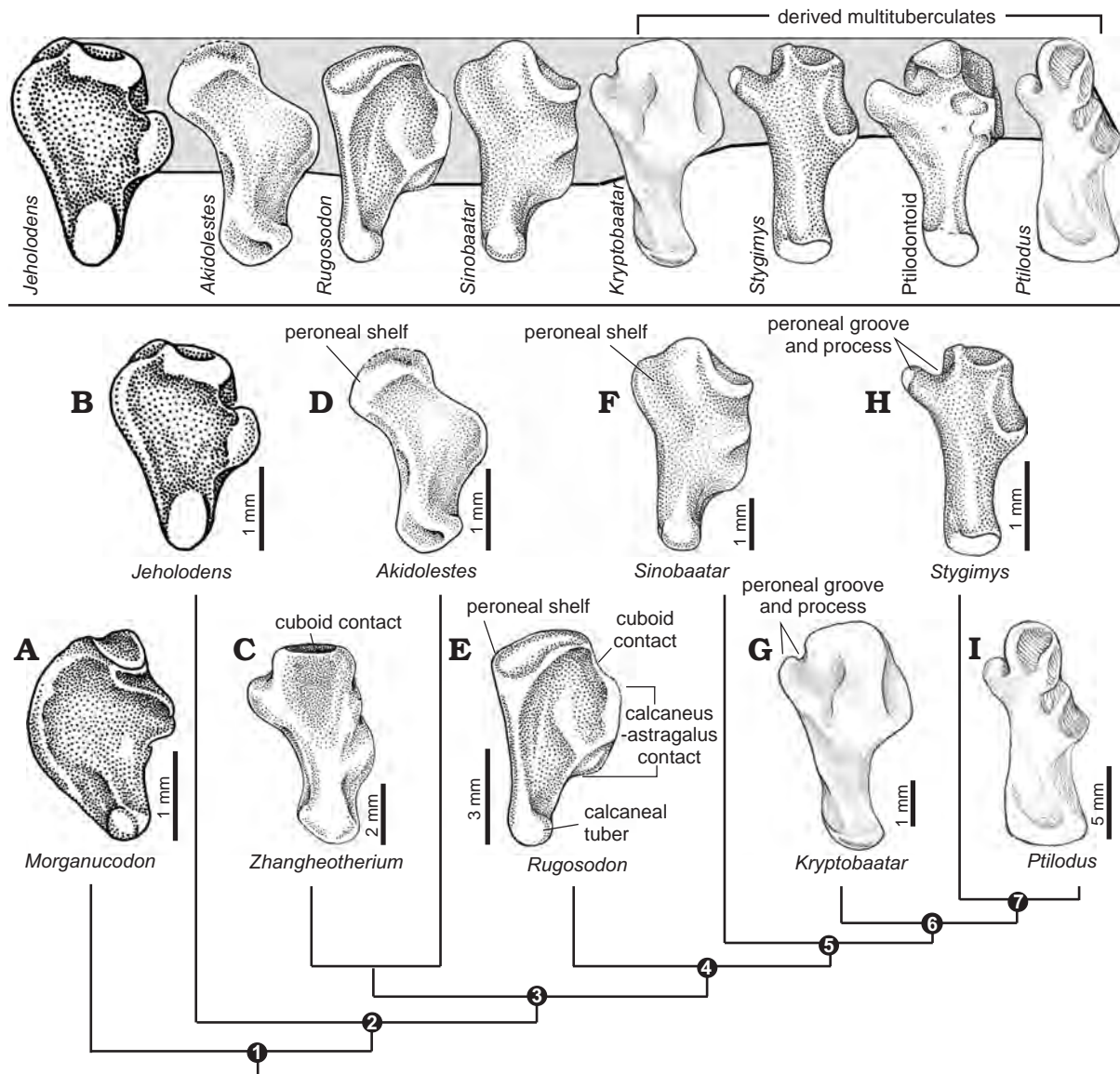
Fig. 8. Morphological disparity and evolutionary pattern of calcanei among multituberculates and their outgroups. **A**. Basal mammaliaform *Morganucodon* in ventral view. **B**. Euriconodont *Jeholodens* in ventral view. **C**. Spalacotherioid *Zhangheotherium* in ventral view. **D**. Spalacotheriid *Akidolestes* in ventral view. **E**. Eaulchoffatiid multituberculate *Rugosodon* in dorsal view. **F**. "Plagiaulacidan" multituberculate *Sinobaatar* in dorsal view. **G**. Djadochtatherian multituberculate *Kryptobaatar* in dorsal view. **H**. Eucosmodontid multituberculate *Stygimys* in ventral view. **I**. Ptilodontid multituberculate *Ptilodus* in ventral view. Proportional changes in evolution of the calcaneus (upper panel): the distal part of the calcaneus becomes narrower, and the proximal part (the calcaneal tuber) is elongate in the more derived taxa. Drawings are either original to this study or adapted with modification from Luo and Wible (2005), Chen and Luo (2013), Zhou *et al.* (2013), and Yuan *et al.* (2013). Several are composite drawing from photos published by Szalay (1994), Kielan-Jaworowska and Gambaryan (1994), Hurum and Kielan-Jaworowska (2008), and Bolortsetseg (2008). Cladogram based on the Adam's consensus tree of Yuan *et al.* (2013). Nodes (1) Mammaliaformes; (2) Theriimorpha; (3) Theriiformes (in part); (4) Multituberculata; (5) clade ("plagiaulacidans" + Cimolodonta); (6) Cimolodonta; (7) unnamed clade.

Functional developmental interpretation of parafibula. — In the development of extant monotremes, the parafibula is a separate embryonic element and then in the later growth stages becomes fused completely to the proximal end of the fibula, to become the enlarged parafibular process (Pearson and Davin 1921; Barnett and Lewis 1958; Vickeryous and Olsen 2007). In marsupials, the parafibula is a separate ossification associated with the proximal end of the fibula in development, and it remains as a separate, small bone in adults (Pearson and Davin 1921; Barnett and Lewis 1958; Lessertisseur and Saban 1967; Argot 2002; Kielan-Jaworowska and Gambaryan 1994). A hypertrophied parafibula, either fused or a separate bone as in *Rugosodon* (Fig. 5), is similar in shape to the fully fused to the fibula in monotremes. Thus *Rugosodon* and

monotremes only differ in whether the parafibulo-fibular suture is fused, or not. The large parafibula, with or without the adult suture to fibula, can provide more area for origination of the peroneal muscles, the M. gastrocnemius lateralis, the M. tibialis posterior, and the M. extensor digitorum hallucis (Lessertisseur and Saban 1967; Kielan-Jaworowska and Gambaryan 1994; Argot 2002; Gambaryan *et al.* 2002). The gastrocnemius and the tibialis posterior join the Achilles tendon on the calcaneal tubercle for plantar-flexion of the pes (Kielan-Jaworowska and Gambaryan 1994; Chen and Luo 2013). The peroneal muscles (especially M. peroneus longus) have the function of rotating and everting the foot via the peroneal shelf or the peroneal groove of the calcaneus (Szalay 1994; Kielan-Jaworowska and Gambaryan 1994; Argot 2002; Szalay and Sargis 2005).

Most placental mammals lack a separate parafibula (Pearson and Lewis 1921; Lessertisseur and Saban 1967). Accordingly, they have smaller bone surface area for muscles attached to the proximal end of the fibula (Evans 1995; Neveu and Gasc 2002). By contrast, in marsupials, the presence of a parafibula can augment the attachment area for origination of several muscles to dorsiflex (or extend) the metatarsals (*e.g.*, M. extensor hallucis longus) and to plantarflex pedal digits (*e.g.*, M. peroneus longus) (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994; Szalay 1994). In monotremes, the fused parafibula process of the fibula (Vickeryous and Olsen 2007) adds a significantly expanded surface of origination for these muscles (Gambaryan *et al.* 2002).

In this light, we interpret that, with a larger parafibula, the proximal region of fibula including the parafibula would have had a broader attachment of the muscles in *Rugosodon* than in mammals with a smaller parafibula or without a parafibular process of the fibula. We further speculate that, with this extra bony element of the parafibula, there would be a greater volume of muscles for plantarflexion, eversion and dorsiflexion of the ankle, in locomotion.

The parafibula shows systematic variation among multituberculates. It is larger in *Rugosodon* and *Sinobaatar* than in the cimolodontan multituberculates (including *Ptilodus*; Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008; Bolortsetseg 2008). Currently, it is not yet feasible to assess the further differences of muscles resulting from the large (and un-fused) parafibulae of *Rugosodon* and *Sinobaatar* versus the smaller parafibula of other, derived multituberculates (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994, fig. 44). The functional differences of disparate sizes of the parafibula among multituberculates can only be understood after the skeletomuscular differences of the parafibula of disparate sizes among marsupials are more fully explored (Argot 2002).

Upper ankle joint. — The upper ankle joint (UAJ, *sensu* Szalay 1994) of *Rugosodon* is highly mobile (Fig. 7), as in other multituberculates (Jenkins and Krause 1983; Szalay 1993; Kielan-Jaworowska and Gambaryan 1994). The medial distal condyle and the lateral distal condyle of the tibia (*sensu* Jenkins and Krause 1983) are, respectively, in contact with the medial astragalo-tibial facet and the lateral astragalo-tibial facet of the astragalus (Fig. 7). The main movement of the upper ankle joint involves pivoting of the peg-like medial condyle on the medial astragalar facet and gliding between a spiral lateral condyle in the distal end of the tibia with the curved lateral astragalar facet. With this pivotal rotation the pes as a whole can increase its range of abduction and adduction relative to the crus (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994).

This rotation of the distal end of the crus relative to the astragalus was originally proposed for the Paleogene *Eucosmodon* and *Ptilodus* by Jenkins and Krause (1983; also Krause and Jenkins 1983) and for Late Cretaceous multituberculates (Kielan-Jaworowska and Gambaryan 1994; Szalay 1994). Because the observable features of the tibio-astragalar articulation in *Rugosodon* are identical to those of *Eucosmodon* and *Ptilodus*, we can now interpret the function of the upper ankle joint in *Rugosodon* accordingly (Fig. 7). The wide range of possible movement of the lateral tibial condyle relative to the medial tibial condyle, and the lack of constraint by the fibula on the upper ankle joint facilitate rotation (both abduction and eversion) of the hind foot at this joint (Jenkins and Krause 1983, fig. 1). For *Ptilodus*, Jenkins and Krause (1983; see also Krause and Jenkins 1983) suggested that the foot, in normal stance, would be capable of abduction of 30 to 40 degrees (longitudinal axis of the foot passing through MT III deviated from a sagittal plane). We interpret that *Rugosodon* was capable of a similar range of eversion, although we are unable to quantify the scope of this eversion, due to the fact that the medial and lateral distal condyles of tibia are partially obscured by their association with the astragalus.

Movement at the UAJ depends on the absence or presence of the fibular malleolus. An absence of this structure would be permissive for the movement, while the presence (or the size variation of this structure if present) would tend to limit this movement. Historically, there was uncertainty as to how the distal end of

the fibula would be involved in crural rotation at the UAJ, as pointed out by Szalay (1993). This previously unclear issue can now be clarified by the *in situ* preservation of the fibula with the tarsals in *Rugosodon* (Fig. 4) and in *Sinobaatar* (Z-X L, personal observation). The distal fibula has a contact with the calcaneus, in addition to its contact with the astragalus. However, it lacks a distinctive lateral malleolus, thus this contact does not constrain the range of the upper ankle joint movement. The wide cruro-tarsal rotation is, at least, a functional adaptation of paulchoffatiids (Yuan *et al.* 2013) through the Paleogene multituberculates (Krause and Jenkins 1983). A fibular malleolus was identified in one specimen of *Kryptobaatar* by Kielan-Jaworowska and Gambaryan (1994, fig. 8), and a similar structure is also described in another specimen of *Kryptobaatar* by Bolortseg (2008). However, the distal malleolus is absent in *Chulsanbaatar* and *Catopsbaatar* (Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008). It is possible that the range of cruro-tarsal rotation at the upper ankle joint is more limited in *Kryptobaatar*, but less constrained in other contemporary multituberculates. For multituberculates as a whole, we suggest that the degree of possible rotation at the upper ankle joint may be variable in different taxa.

Lower ankle joint. — The lower ankle joint (LAJ, *sensu* Szalay 1993) is between the astragalus and the calcaneus. The astragalus and the calcaneus are in juxtaposition horizontally and side-by-side in *Rugosodon*: the astragalus is not superposed on top of the calcaneus (Figs 2, 4, 6, 9, 10). This is also the case in the eobaatarid *Sinobaatar* (Hu and Wang 2002, fig. 1). Similarly, the Late Cretaceous *Kryptobaatar*, *Chulsanbaatar*, and *Catopsbaatar* lack a direct superposition of the astragalus on top of the calcaneus, although this absence of superposition was somewhat obscured by the fact that the metapodials and phalanges are strongly abducted toward the calcaneal tuber, preserved *in situ* in these fossils (Kielan-Jaworowska and Gambaryan 1994, figs 6, 25; Hurum and Kielan-Jaworowska 2008, figs 11, 13). For *Ptilodus*, in which the tarsals preserved in three dimensions are more reliable for this assessment, the astragalus was reconstructed as obliquely overlapping on the calcaneus (Krause and Jenkins 1983), although the exact extent of this overlap may be quite limited, as compared to therians. The calcaneo-astragalar facet of the astragalus overlaps the calcaneus, but the sustentacular facet of the astragalus is juxtaposed side-by-side with the calcaneus (Jenkins and Krause 1983, fig. 1). The superposition of the astragalus on top of the calcaneus, by both the calcaneo-astragalar facet and the sustentacular facet, as seen in extant therians (*sensu* Jenkins 1970; Szalay 1993), is not developed in *Ptilodus* or *Eucosmodon*. Fossils of *Rugosodon* and *Sinobaatar* can now extend this plesiomorphic condition (juxtaposition of the astragalus and calcaneus) to the basalmost taxa of the multituberculate clade (Figs 9, 10).

Jenkins and Krause (1983) interpreted that, in *Ptilodus* and *Eucosmodon,* the LAJ was capable of pivoting at the sustentacular facets of the astragalus and calcaneus. The calcaneus has translational movement relative to the astragalus, at the calcaneo-astragalar facets. Taken together, this movement can facilitate the plantarflexion and inversion of distal pedal elements (Krause and Jenkins 1983). Although the sustentacular and calcaneo-astragalar facets of the calcaneus and the astragalus are only partially exposed in the *Rugosodon* type specimen, the exposed aspects of the astragalus and the calcaneus appear to be similar to those of *Ptilodus* and *Eucosmodon*. By extension, we speculate that *Rugosodon* may be similar in mechanical function of the joint between the astragalus and the calcaneus, as proposed previously for other multituberculates (Jenkins and Krause 1983; Kielan-Jaworowska and Gambaryan 1994).

Astragalo-navicular joint. — The grooved or saddle-shaped anterior surface of the astragalar head would permit hinge-like rotation of the navicular relative to the astragalus in dorso-ventral direction, permitting significant dorso- and plantarflexion of the navicular to the astragalus, and also side-to-side movement, especially abduction (Fig. 7). This enhances the mobility of the hind foot in general.

We interpret the navicular to have been aligned distal to the astragalus in *Rugosodon* (Fig. 9A). By contrast, the navicular is more ventro-distal to the astragalus in some Late Cretaceous and Paleogene multituberculates (Fig. 9B). In three-dimensional preservation of the astragalus in some multituberculates (*Eucosmodon*, Szalay 1994, figs 5.8, 5.9; *Catopsbaatar*, Hurum and Kielan-Jaworowska 2008, fig. 12; *Kryptobaatar*, Bolortseg 2008, figs 36, 37), the navicular facet is more ventrally inclined, facing ventro-distally in plantar view. The navicular is also positioned ventro-distal to the astragalus in several intact pedes (Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008).

Calcaneo-cuboid joint. — In a majority of multituberculates, the calcaneo-cuboid joint faces medio-distally ("antero-medially") in the dorsal view of the pes (Figs 7, 8). But the dorso-ventral orientation of the calcaneus-cuboid joint can show systematic variation among multituberculates (Fig. 9A$_1$ *versus* Fig. 9B$_1$). The plesiomorphic pattern of the calcaneo-cuboid joint is a vertical orientation of its surface in the dorsal-ventral
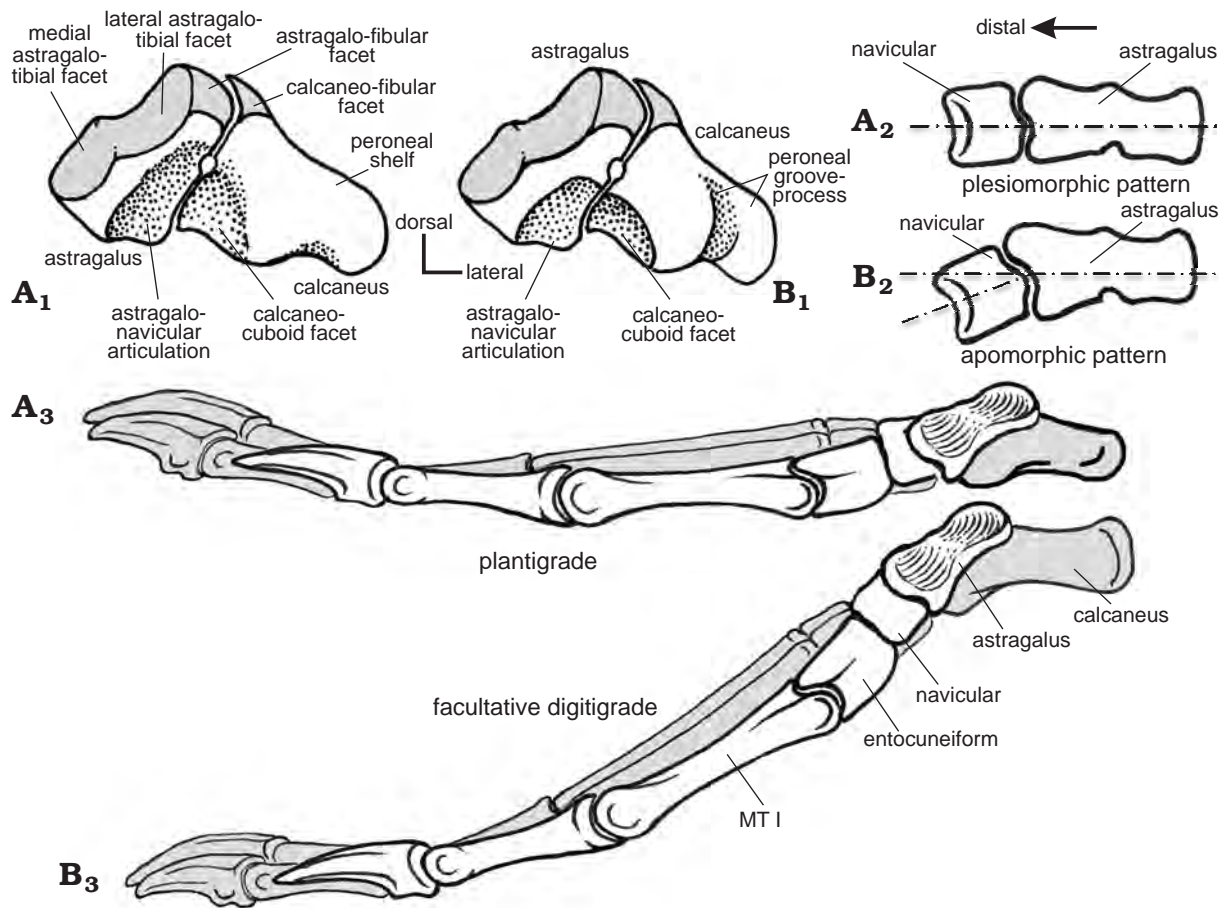
Fig. 9. Schematic patterns of the astragalo-navicular articulation among multituberculates. **A**. Plesiomorphic pattern: the astragalus and the calcaneus in juxtaposition. The groove-like astragalo-navicular contact is oriented more vertically and less inclined on the distal end of the astragalus. The calcaneo-cuboid contact is also more vertically oriented and less inclined on the distal end of the calcaneus. The peroneal shelf is not differentiated into the peroneal process separated by a groove. A_1, distal ("anterior") view of the astragalus with a more dorsally placed navicular contact, and the calcaneus with a more dorsally placed cuboid contact (stylistic drawing after Szalay 1993, fig. 9.11); A_2, schematic alignment of the navicular and the astragalus; A_3, the plesiomorphic astragalo-navicular alignment tends to be correlated with the plantigrade pedal posture. **B**. Apomorphic pattern of some derived multituberculates. B_1, distal ("anterior") view of the astragalus with a more ventrally placed and inclined navicular contact, and the calcaneus with a more ventrally inclined cuboid contact as well (stylistic drawing after Szalay 1993, fig. 9.11); B_2, schematic alignment of the more ventrally positioned and inclined navicular to the astragalus; B_3, the derived condition of the astragalo-navicular alignment tends to be correlated with the facultative digitigrade pedal posture, as reconstructed for derived multituberculates of the Late Cretaceous (*e.g.*, Kielan-Jaworowska and Gambaryan 1994, fig. 54). MT, metatarsal.

direction. The cuboid facet of calcaneus of *Rugosodon* appears to be this type: the calcaneo-cuboid facet is vertically oriented on the calcaneus (Fig. $9A_1$). But in dorsal view, the calcaneo-cuboid contact is oriented medio-distally from the long axis of the calcaneus (Fig. 7). This interpretation needs to be confirmed when additional specimens with separated calcaneus and cuboid become available for *Rugosodon*.

An apomorphic pattern involves positioning of the calcaneo-cuboid joint surface on the antero-medio-ventral side of the calcaneus (Fig. $9B_1$). In this pattern of orientation, the cuboidal contact surface is more ventrally inclined, and is extensively visible on the ventral aspect of the calcaneus, as shown in the Cretaceous ptilodontoid calcanei (Szalay 1994, fig. 5.8) and the eucosmodontid *Stygimys* (Krause and Jenkins 1983, fig. 26; also Kielan-Jaworowska and Gambaryan 1994, fig. 55; Kielan-Jaworowska *et al.* 2004). We interpret this type of calcaneo-cuboid articulation to have been more conducive for the distal tarsal bones to plantarflex and to invert, relative to the calcaneus.

The ventrally tilted calcaneo-cuboid joint, combined with the above-mentioned flexion at the astragalo-navicular joint, augments the scope of flexion of the metatarsal and phalanges of digit I. Increased plantarflexion would be compatible with a digitigrade stance, at least facultatively, for the standing pedal posture.
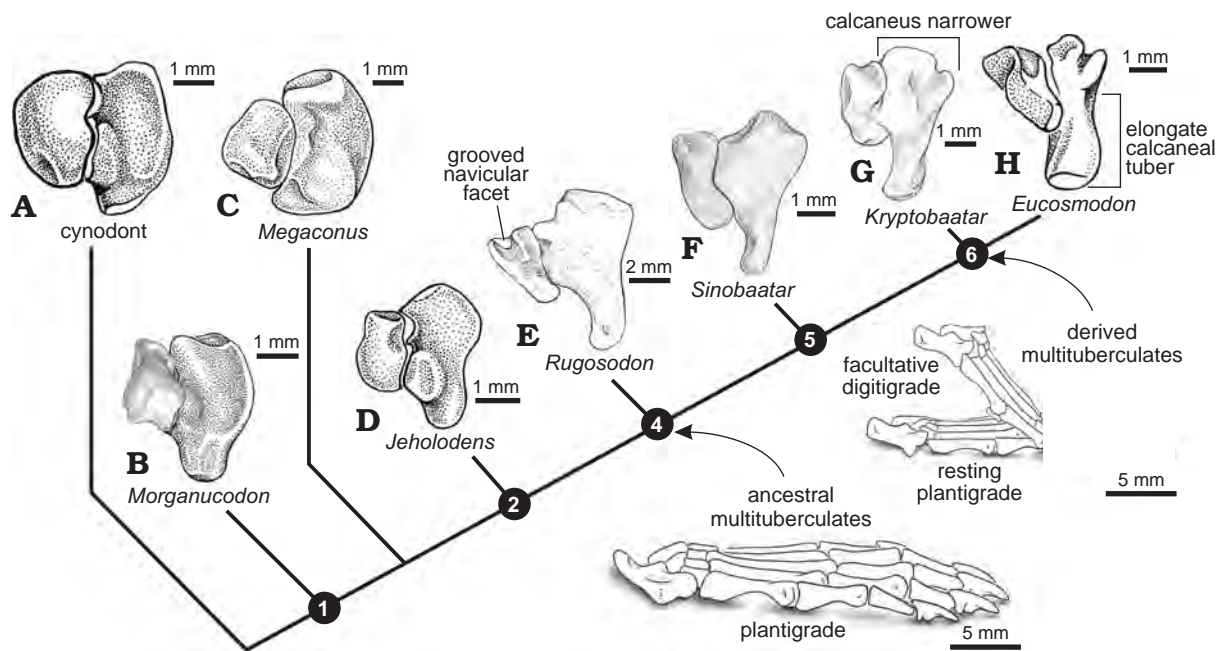
Fig. 10. Evolutionary pattern of the astragalus, the calcaneus, and pedal posture among multituberculates and their outgroups. **A**. Manda cynodont. **B**. Basal mammaliaform morganucodontan, *Morganucodon*. **C**. Basal mammaliaform haramiyidan, *Megaconus*. **D**. Basal mammalian triconodontan, *Jeholodens*. **E**. Basal multituberculate paulchoffatiid, *Rugosodon*. **F**. Multituberculate *Sinobaatar*. **G**. *Kryptobaatar*, a djadochtatherian multituberculate. **H**. *Eucosmodon*, a ptilodontoid multituberculate. We hypothesize that multituberculates (node 4) ancestrally have a wide distal region of calcaneus and relatively short calcaneal tuber that are plesiomorphies. These are related to a plantigrade pedal posture, a functionally generalized feature. In the derived clade (node 6) including Cretaceous djadochtatherians of Cretaceous through ptilodontoids and taeniolabidids of the Paleogene, the distal calcaneus becomes narrower and the calcaneal tuber becomes more elongate. The narrower calcaneus and elongate calcaneal tuber, among other features, have a longer in-lever for plantarflexion at the ankle, and help achieve a facultatively digitigrade stance. A–C from Zhou *et al.* (2013); D, H from Ji *et al.* (1999); E–G are original to this study. Cladogram nodes (1) Mammaliaformes; (2) Theriimorpha; (4) Multituberculata; (5) unnamed clade ("Plagiaulacidans"+Cimolodonta); (6) Cimolodontans. Cladogram node designation is the same as in Fig. 8.

Entocuneiform-MT I joint. — *Rugosodon* is identical to Late Cretaceous and Paleogene multituberculates in the saddle-shaped distal surface of the entocuneiform, reciprocated by a curved groove of the proximal end of MT I (Fig. 6C; see also Krause and Jenkins 1983; Szalay 1994; Kielan-Jaworowska and Gambaryan 1994). This joint is permissive of a vertical rotation of MT I to the entocuneiform, which could further amplify the dorso- and plantar-flexion of the phalanges of pedal digit I (Fig. 7D). In extant *Didelphis* (Szalay 1994), the long tendon of M. peroneus longus inserts on the plantar base of MT I, and pulls to flex pedal digit I at the saddle shaped entocuneiform-metatarsal joint. In the multituberculate reconstruction by Kielan-Jaworowska and Gambaryan (1994, fig. 57), the tendon of M. peroneus longus passes in the peroneal groove onto the plantar side of the pes and inserts on the plantar base of MT I. The M. extensor digitorum hallucis inserts on the dorso-distal part of MT I, for the extension of pedal digit I (Fig. 7). M. peroneus longus and the M. extensor digitorum hallucis are antagonistic muscles for plantarflexion and dorso-extension of digit I, but both muscles originated from near the enlarged parafibula at the knee joint in *Rugosodon* (Fig. 6).

We note that, in *Rugosodon*, MT I was not habitually abducted at the entocuneiform joint. Pedal digit I is not divergent from other pedal digits. In the articulated foot bones of *Sinobaatar*, pedal digit I is not divergent either (personal observation; see also Hu and Wang 2002). In *Kryptobaatar*, *Chulsanbaatar*, and *Catopsbaatar*, for which most pedal bones are intact, MT I is not divergent (Kielan-Jaworowska and Gambaryan 1994; Hurum and Kielan-Jaworowska 2008). Therefore we suggest that multituberculates did not have divergent digit I or an opposable hallux (Fig. 6), as previously speculated by Simpson and Elftman (1928). Rather, pedal digit I was facultatively capable of a wider range of abduction, thanks to the development of the reciprocal saddle joint of the entocuneiform permissive of such abduction of MT I (Jenkins and Krause 1983, fig. 1). The enhanced mobility and wide range of abduction, plantar- and dorsoflexion of MT I is a derived condition in multituberculates as a whole, unique among Mesozoic mammal clades (Jenkins and Krause 1983).

PEDAL POSTURE

Pedal abduction and eversion. — In both feet of *Rugosodon*, *in situ* metatarsals are not strongly abducted laterally from the tarsals; neither is MT V strongly abducted from the more central digit rays. This appears to be a habitual and resting posture of the metatarsals with respect to the tarsals for paulchoffatiids, a basal clade of multituberculates. Because the Paleogene multituberculates show no eversion of the pes either (Krause and Jenkins 1983; Szalay 1993), we interpret the ancestral multituberculate condition to have not involved either habitual eversion or abduction in a resting posture.

We interpret that metatarsals were capable of a range of eversion and abduction relative to the calcaneus, at lease in some multituberculate taxa. In the holotype of *Sinobaatar lingyuanensis* (IVPP V12517), the metatarsals are preserved in a strongly everted position (Hu and Wang 2002, fig. 1; Wang *et al.* 2003, fig. 200). However, in another specimen of *Sinobaatar* (NGMC3100), the foot is preserved with distal pedal bones along the axis of the crus and the calcaneus, and there is no eversion of metatarsals from the tarsals, thus different from the type specimen of *Sinobaatar lingyuanensis*. Different degrees of abduction of the metatarsals preserved in different specimens of *Sinobaatar* are not conflicting with each other. This suggests that metatarsals of this taxon were capable of a range of everting positions relative to tarsals.

Kielan-Jaworowska and Gambaryan (1994) interpreted that, in some Late Cretaceous multituberculates, metatarsals were habitually abducted and everted, such that the proximal end of MT V would have contacted the peroneal process of the calcaneus, in a standing and resting posture. This was based on *Kryptobaatar* and *Chulsanbaatar* whose *in situ* metatarsals are strongly flexed. MT I–V are also strongly adducted toward the plantar midline of the pes. Kielan-Jaworowska and Gambaryan (1994, fig. 54) argued that this was the habitual posture in standing pose, an opinion that was further expanded by Hurum and Kielan-Jaworowska (2008, p. 563).

As shown by the *Sinobaatar* fossil materials, the metatarsals can be abducted and everted relative to the calcaneus in one specimen (Wang *et al.* 2003) but show little or no abduction in others (*e.g.*, NGMC3100). Such a strong eversion/abduction as seen in some multituberculates may not be the habitual standing posture (Hu and Wang 2002). Instead, it may represent the outer limit of the permissible abduction and eversion, for a range of facultative eversion. The degree of facultative eversion in multituberculates is also partly dependent on cruro-tarsal rotation at the UAJ, as the latter joint movement can augment overall pedal abduction and eversion.

Pedal posture. — We propose a plantigrade standing pedal posture for *Rugosodon*, based on several cruro-pedal features. The plantigrade pedal posture is defined by the cruro-tarsal joint as the primary joint of flexion of the foot. But for a digitigrade pedal posture, the primary joint of flexion is the metatarso-phalangeal joint, and the inter-phalangeal joints, in standing position (Carrano 1997). Plantigrade, digitigrade, and unguligrade stances are represented by a continuum of postural grades among placental mammals. Nonetheless, there are some qualitative differences that can help to distinguish these grades of posture (Carrano 1997).

Plantigrade therian mammals are characterized by several osteological characters. Commonly they have less restrictive structure of the cruro-tarsal joint, which is capable of a wider range of lateral rotation (abduction and adduction), and less parasagittal (fore-aft) rotation arc at the tibio-tarsal joint than digitigrade mammals (Wang 1993; Carrano 1997). Within the placental carnivoran clade, the arboreal plantigrade forms have a lesser trochlear arc than the cursorial digitigrade forms (Wang 1993). Plantigrade mammals tend to have a shorter calcaneal tuber and a longer proximal part of the calcaneus relative to the overall calcaneal length, than digitigrade mammals (Carrano 1997). Plantigrade mammals tend to have a relatively wider sustentacular region than digitigrade mammals of the same clade (Polly 2008; Polly and MacLeod 2008). Also, plantigrade mammals tend to have a wider spread of metapodials, with MT I and MT V more abducted from the longitudinal axis of the foot, in contrast to the more convergent metapodials with side digits (MT I and MT V) adducted toward the pedal axis in digitigrade mammals (Carrano 1997).

We offer another observation: that plantigrade mammals tend to have a greater combined breadth of the calcaneus and the astragalus, as evidenced by the transversely wide astragalus and calcaneus in extant monotremes, which are plantigrade. By contrast, extant mammals with a digitigrade stance are characterized by a narrower combined width of the calcaneus and the astragalus, thanks to a more complete superposition of the astragalus over the calcaneus (Jenkins 1970; Szalay 1993), in addition to the narrower width of

each bone. We note that extant therian mammals with plantigrade stance lack the inclined orientation of the astragalo-navicular and the calcaneo-cuboid joints that can lift the calcaneus and the astragalus up from the substrates, in habitual standing posture.

Rugosodon has a combination of the characteristics for plantigrade posture: the calcaneal body is medi-olaterally wide and dorso-ventrally compressed, and the peroneal shelf is also wide. The calcaneal tuber is short relative to the calcaneal length. The calcaneo-cuboid joint is vertical (not so much inclined). Finally, the metatarsals are divergent (with medial and lateral metatarsals abducted from the midline of the foot), as preserved in both pedes. These plantigrade features are also present in *Sinobaatar lingyuanensis* (Hu and Wang 2002; Wang *et al.* 2003) and in other *Sinobaatar* specimens (Z.-X. Luo, personal observation).

PHALANGEAL PROPORTIONS

It is now feasible to use the segment proportions of the pedal digits to estimate the substrate preference of an extinct mammal, by morphometric comparison with extant mammals having known substrate preferences and locomotor adaptations (Zheng *et al.* 2013; Bi *et al.* 2014). As initially proposed for the manus (*e.g.*, Lemelin 1999), the phalangeal index is the sum of lengths of the proximal and intermediate phalanges divided by the length of metacarpal of the same digit (commonly digit III) (Kirk *et al.* 2008). Zheng *et al.* (2013) extended this metric to the pedal bones, and estimated the likely substrate preferences of extinct mammals by comparing their phalangeal indices to those of extant mammals with known habits and substrate preference. In general, the higher the phalangeal index, the more likely the pes would have a capacity for gripping or branch-walking, related to climbing function and arboreal adaptation (Kirk *et al.* 2008; Zheng *et al.* 2013; Bi *et al.* 2014). The pedal phalangeal index of *Rugosodon* is 114%. This is higher than *Sinobaatar* at 97%, which was likely a terrestrial mammal (Zheng *et al.* 2013). The phalangeal index value of *Rugosodon* and *Sinobaatar* are close to those Mesozoic mammals considered to be terrestrial, such as *Jeholodens* (Table 1).

EVOLUTIONARY PATTERNS

In the first study to address limb functional anatomy of multituberculates, Simpson and Elftman (1928, p. 4) interpreted that the pes of *Eucosmodon* "is pentadactyl and plantigrade, of grasping type with partially opposable hallux." Although it is now clear that multituberculates did not have an opposable hallux, Simpson and Elftman (1928) were correct in proposing that *Eucosmodon* was plantigrade, as an exemplar of multituberculate pedal posture. The question of plantigrade vs. digitigrade pedal postures was not explicitly discussed by Krause and Jenkins (1983). However, it is implicit in their discussion on the grasping capability of the pes, the tibio-astragalar rotation, and their graphic reconstruction of divergent and spread digit rays that *Ptilodus* and *Eucosmodon* had a plantigrade posture (see also Granger and Simpson 1929, fig. 23).

The plantigrade pedal posture is also phylogenetically plesiomorphic for multituberculates as a whole, by comparison to outgroups that are independently inferred to have been plantigrade by osteological characters. In current phylogenies, multituberculates are the sister group to the trechnotherian clade. The basal-most taxa of trechnotherians, *Zhangheotherium* and *Akidolestes*, have a dorso-ventrally flattened and mediolaterally wide calcaneal body (Luo and Ji 2005; Hurum *et al.* 2006). *Akidolestes* has a short calcaneal tuber (Li and Luo 2006; Chen and Luo 2013). Outside the multituberculate-trechnotherian clade (Figs 8, 10: node 2), eutriconodonts (Ji *et al.* 1999; Hu 2006) also have a wide calcaneus (Fig. 8). Outside crown Mammalia (Fig. 8: node 1), *Morganucodon*, *Agilodocodon* and the haramiyid *Megaconus* have similarly plesiomorphic calcaneal structures (Jenkins and Parrington 1976; Szalay 1994; Zhou *et al.* 2013; Meng *et al.* 2015; Luo *et al.* 2015). Recent discoveries of tarsals in these stem mammaliaform have augmented the earlier evidence from *Megazostrodon* (Jenkins and Parrington 1976, fig. 18) that mammaliaforms as a whole are plantigrade (Zhou *et al.* 2013).

While the basal taxa of Multituberculata, such as *Rugosodon* and *Sinobaatar*, had the plesiomorphic plantigrade posture, not all multituberculates were plantigrade. Pedal posture of more derived multituberculates was more varied, and may have been digitigrade, if only facultatively. Kielan-Jaworowska

Table 1. Pedal phalangeal measurements (mm) and indices for digit III of *Rugosodon eurasiaticus* and comparison with other Mesozoic mammals.

Comparative Mesozoic mammaliaforms	Hypothesized substrate preference	Metatarsal length	Proximal phalanx length	Intermediate phalanx ength	Pedal phalangeal index	Specimens/ references
Agilodocodon scansorius	arboreal?	3.91	2.89	2.33	134%	BMNH1138
Eomaia scansoria	arboreal?	4.35	3.15	2.4	128%	CAGS01-IG1A
Jeholodens jenkinsi	terrestrial?	3.92	2.48	1.88	111%	GMV 2139A
Maotherium sinensis	terrestrial?	7.3	4.1	3.15	99%	Rougier *et al.* 2003
Rugosodon eurasiaticus	terrestrial?	9.59	6.48	4.47	114%	BMNH1143
Sinobaatar lingyuanensis	terrestrial?	6.3	3.2	2.8	95%	Zheng *et al.* 2013
Sinodelphys szalayi	arboreal?	2.9*	2.5*	2.3*	165%	CAGS00-IG03

* In the type specimen of *Sinodelphys szalayi*, the pedal bones are associated but partially displaced relative to each other; thus the length measurements of metatarsal, proximal phalanx and intermediate phalanx are provisional.

and Gambaryan (1994, fig. 54) reconstructed a digitigrade pedal posture for several Late Cretaceous multituberculates: *Kryptobaatar*, *Chulsanbaatar*, and *Nemegtbaatar*. The plantar flexure of the calcaneus-cuboid and the astragalus-navicular is preserved intact (or nearly so) in *Kryptobaatar*, *Chulsanbaatar*, and *Catopsbaatar* (Hurum and Kielan-Jaworowska 2008, p. 563), as well as in a new and un-named multituberculate (Bolortsetseg 2008). Given a strong pedal plantarflexion, the calcaneus, when held horizontal, is lifted from the substrate (Fig. 9B, Fig. 10: node 6). The primary contact to the substrate would be by metatarsals, or metatarsal-phalanges in a digitigrade posture (Kielan-Jaworowska and Gambaryan 1994, fig. 54).

The digitigrade hypothesis for Cretaceous multituberculates is supported by the tightly adducted metatarsals in intact feet (Kielan-Jaworowska and Gambaryan 1994; Bolortsetseg 2008; Hurum and Kielan-Jaworowska 2008). These are different from the more divergent digit rays of *Rugosodon* (Yuan *et al.* 2013) and of extant therians having plantigrade posture (Szalay 1994; Carrano 1997). Furthermore, these Late Cretaceous multituberculates show a more elongate calcaneal tuber and a more bilaterally compressed calcaneal body than in *Rugosodon* and *Sinobaatar* (Figs 8–10).

Based on the flexed foot in Late Cretaceous multituberculates, Kielan-Jaworowska and Gambaryan (1994, fig. 55) also re-interpreted *Eucosmodon* to have had a strongly flexed tarsus and a digitigrade pedal posture. By our re-evaluation, however, the case for digitigrady in *Eucosmodon* is not strong, although we would agree that *Eucosmodon* could have been facultatively digitigrade during at least some phases of active locomotion.

In terms of evolution of pedal structure and function (Figs 7–10), the basal-most known *Rugosodon* has many diagnostic features of multituberculates as a whole. These are correlated with enhanced mobility in the cruro-tarsal rotation at the UAJ, and high mobility in the astragalo-navicular joint, and in plantarflexion and dorsiflexion of MT I at its joint to the entocuneiform. Thus, the earliest evolution of multituberculates was accompanied by new cruro-pedal locomotor functions (Fig. 7, Fig 10: node 4).

However, a majority of the calcaneal characters of the Jurassic *Rugosodon* and Early Cretaceous *Sinobaatar* are plesiomorphic compared to other multituberculates. These calcaneal features happen to be related to inferred plantigrade pedal posture. Further evolution of the calcaneal structures for versatile functions occurred in a more derived subclade of multituberculates (Fig. 10: node 6). The most prominent apomorphic feature is the elongation of a more bilaterally compressed calcaneal tuber, relative to the calcaneus length in derived multituberculates (Fig. 8). A longer calcaneal tuber increases the in-lever for the gastrocnemius and other muscles to pull the Achilles tendon on the calcaneal tuber. The narrower proximal part of the calcaneus in such derived multituberculates as *Kryptobaatar* and *Eucosmodon* (Krause and Jenkins 1983) has been hypothesized to correlate with a more digitigrade pedal posture (Kielan-Jaworowska and Gambaryan 1994), or to a facultatively digitigrade posture (Fig. 9, Fig. 10: node 6). This interpretation can be supported by comparative evidence from placental mammals that digitigrade taxa tend to have a narrower proximal part of the calcaneus than do plantigrade taxa of the same group (Wang 1993; Carrano 1997; Polly 2008; Polly and MacLeod 2008).

In the derived multituberculates, the peroneal process and groove are separate structures. The tendon of M. peroneal longus has been reconstructed as passing through the peroneal groove (Kielan-Jaworowska and Gambaryan 1994). These bony characters and their soft-tissue correlates are clearly apomorphic, by comparison to the undifferentiated peroneal shelf of *Rugosodon* and *Sinobaatar*, and most of the outgroups to multituberculates (Fig. 8). In the latter taxa, the tendon of M. peroneus longus passed through the gap between the peroneal shelf, the cuboid, and the proximal end of MT V, but without a distinctive peroneal groove.

In both configurations of the course for the tendon of M. peroneal longus, it inserts on the plantar base of MT I and the M. peroneal brevis tendon inserts on the plantar base of MT V, as exemplified by extant didelphid marsupials (Szalay 1994). These structures are correlated with the functions in the eversion of the metatarsals, plus some plantarflexion in didelphids. However, the functional difference of the tendon passage in a distinct groove, or without a groove, is still unclear.

The more disparate morphologies of the tarsals of the derived multituberculates (Fig. 10: node 6) with potentially more diverse locomotor functions are also consistent with the independent observations on dentition that the Late Cretaceous multituberculates evolved a great disparity of dental patterns and more diverse feeding functions before the radiation of ptilodontoids and taeniolabidoids in the Paleocene (Wilson *et al.* 2012).

SUMMARY

- The new fossil of *Rugosodon* provides diagnostic cruro-tarsal characters for multituberculates as a whole, and shows that multituberculates developed novel structures of the astragalus, the navicular and the entocuneiform that increased the mobility of the all joints of these bones, very early in their phylogenetic history.
- *Rugosodon* shows plesiomorphic features of the calcaneus and the cuboid. This helps to establish the ancestral condition from which the more derived djadochtatherian multituberculates of the Late Cretaceous and taeniolabidoids and ptilodontoids of the Paleogene evolved more apomorphic calcaneal features that can be correlated with more versatile functions of the ankle.
- Multituberculates have a relatively wide range of morphologies of the tarsals and presumed pedal postures. We propose that the ancestral pedal posture of multituberculates was plantigrade without a strong abduction of metatarsals, whereas some of the derived multituberculates of the Late Cretaceous and Paleogene evolved facultative digitigrady and a wider range of pedal abduction and eversion.
- *Rugosodon* had a sprawling (crouched) hind limb posture and habitually flexed knee. It was more likely a terrestrial than an arboreal mammal, based on its pedal phalanges.

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FIRST JURASSIC MAMMALS OF GERMANY: MULTITUBERCULATE TEETH FROM LANGENBERG QUARRY (LOWER SAXONY)

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Two multituberculate molars from the Kimmeridgian of the Langenberg Quarry near Goslar (Lower Saxony, Germany) represent the first Jurassic mammals from Germany. An upper M1 with cusp formula 5L/4B is characterized by strongly ornamented enamel and is assigned to *Teutonodon langenbergensis* gen. et sp. n. within the plagiaulacid line. A second specimen preserving two large and one small cusp is interpreted as a lingual fragment of an eobaatarid m1. It extends the stratigraphic range of Eobaataridae from the Early Cretaceous to the Late Jurassic (Kimmeridgian) The new findings expand the geographic range of multituberculates to Central Europe.

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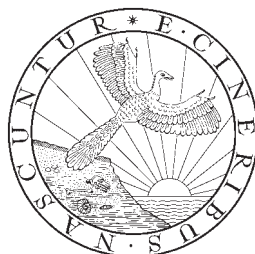
INTRODUCTION

During Jurassic times, Germany was largely covered by epicontinental seas, and Jurassic strata of the Germanic Basin and northwest German Jurassic basin (Lower Saxon Basin) have mainly produced marine fossils. Terrestrial vertebrates such as the small juvenile theropod dinosaurs *Juravenator* Göhlich *et* Chiappe, 2006 and *Sciurumimus* Rauhut *et al.*, 2012 from the Solnhofen area in southern Germany are rare exceptions. Even in the Solnhofen area, which has yielded a reasonable number of terrestrial vertebrates during more than 200 years of extensive collecting, a mammalian specimen has never been detected. The Jurassic lagoons of the Solnhofen area were apparently too far from the coast (Ziegler 1990) for a regular input of terrestrial faunal elements. In northern Germany, the Upper Jurassic (Kimmeridgian) is developed as shallow marine to continental deposits (Pieńkowski *et al.* 2008). A relatively recently discovered locality for terrestrial vertebrates in northern Germany, the Langenberg Quarry near Goslar (Lower Saxony), has now produced the first Jurassic mammalian remains from Germany.

Institutional abbreviation.—NLMH, Niedersächsisches Landesmuseum, Hannover, Germany.

GEOLOGIC SETTING

All described material was found in the Langenberg Quarry, a classic and well-studied outcrop exposing excellent sections of Upper Jurassic shallow marine strata (Lotze 1968; Pape 1970; Fischer 1991) near the town of Goslar, Lower Saxony, northern Germany (Fig. 1). The beds are tilted to a near vertical, slightly overturned position and the quarrying proceeds along strike, exposing the beds only in cross section and
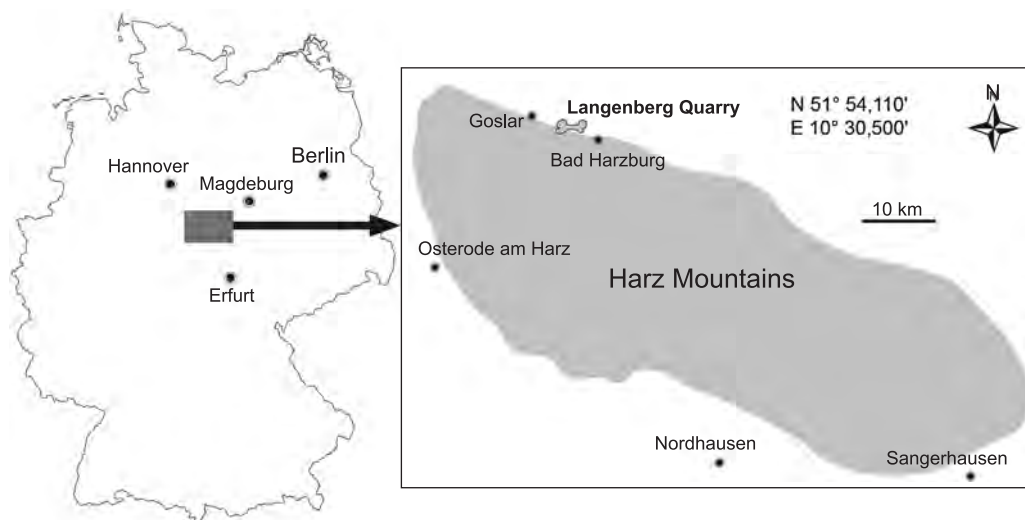
Fig. 1. Geographic position of the Langenberg Quarry at the northern rim of the Harz Mountains in Lower Saxony (Germany).

not along bedding planes. The dominant deposits are impure carbonates which grade into marls. Sediment composition and faunal content of invertebrates can vary with water depth and be influenced by water salinity, but there is no evidence of subaerial exposure (Lotze 1968; Pape 1970). The sediments in the quarry are well dated biostratigraphically and range from late Oxfordian to late Kimmeridgian in age (Lotze 1968; Pape 1970; Fischer 1991). After the stratigraphic subdivision of Fischer (1991), most of the terrestrial vertebrate remains (including the sauropod dinosaur *Europasaurus* Mateus *et al.*, 2006 in Sander *et al.* 2006 and probably the mammal teeth described herein) were found in bed 83, and not in bed 93 as incorrectly stated in recent publications (Sander *et al.* 2006; Carballido and Sander 2013; Marpmann *et al.* 2014). This bed is a light grey-greenish marly limestone. It has been assigned to the "Mittleres Kimmeridge", a northwest-German equivalent to the lower part of the upper Kimmeridgian of the international chronostratigraphic time scale (Schweigert 1999; Lallensack *et al.* 2015).

Paleogeographically, the Langenberg Quarry is located in the Lower Saxony Basin, which covered much of northern Germany in Late Jurassic and Early Cretaceous times and that was surrounded by several large palaeo-islands (Ziegler 1990), the source of the clastic components in the sediment.

FOSSIL VERTEBRATES FROM THE LANGENBERG QUARRY

The Langenberg Quarry is especially well known as the only locality where the abundant and exquisitely three-dimensionally preserved material of the dwarf sauropod dinosaur *Europasaurus holgeri* has been found (Sander *et al.* 2006; Carballido and Sander 2013; Marpmann *et al.* 2014). The quarry also yielded a number of isolated teeth which belong to several groups of theropod dinosaurs (Gerke and Wings 2014) as well as natural track casts of large theropods (Lallensack *et al.* 2015).

Beds 56, 73, and 83 also have produced exceptional material of non-dinosaurian vertebrates (Wings and Sander 2012). This includes the three-dimensionally preserved articulated skeleton of a small pterosaur, which has been described as the first dsungaripterid from the Kimmeridgian of Germany (Fastnacht 2005), the teeth and skeletons of a new taxon of the small non-marine atoposaurid crocodilian *Theriosuchus* Owen, 1879 (Thies *et al.* 1997; Karl *et al.* 2006), and the associated remains of a partial skeleton of a paramacellodid lizard (Richter *et al.* 2013). Diverse turtle material (including several skulls) has been found as well and comprises cf. *Thalassemys*, *Plesiochelys* Rütimeyer, 1873, and possibly a new taxon (Jansen and Klein 2014). In addition to abundant reptilian teeth (OW, personal observations), microvertebrate remains from the Langenberg include a diverse fish fauna represented mainly by isolated teeth of marine chondrichthyans and osteichthyans (Thies 1995; Mudroch and Thies 1996; Mudroch 2001).

TAPHONOMY

Almost all of the fossil material from terrestrial vertebrates (including both mammalian teeth described herein) was recovered after regular blasting operations in the Langenberg Quarry. Despite the large number of bones and teeth known from *Europasaurus*, the general distribution of bones and teeth in bed 83 is scarce. The skeletal remains seem to have been accumulated in certain areas, probably lenses or channels (OW, personal observations). The bone-bearing sections of bed 83 are usually 30–50 cm thick and also contain a large number of well-rounded micritic intraclasts. The combination of bone material and intraclasts is also important for recognizing blocks of this specific layer in the quarry heap after the blasting.

All herein described material was found near the coordinates: N 51°54,110', E 10°30,500' in October 2014. Because the blocks were not found in situ, it remains possible, although very unlikely, that the finds come not from bed 83, but from another bed nearby. They can, however, be certainly assigned to the lower part of the upper Kimmeridgian.

Both mammalian teeth (NLMH 105650; NLMH 105651) have been found isolated in the fine-grained marly limestone matrix, but the typical micritic intraclasts as well as isolated bones of turtles and crocodilians as well as a large number of crocodilian teeth (>100) and fish teeth were found directly associated. Most of the associated reptilian bones are very well preserved, indicating limited transport and quick

Fig. 2. NLMH 105650, holotype of the plagiaulacid-line multituberculate *Teutonodon langenbergensis* gen. et sp. n. (marked by circle) *in situ*, close to the vertebra of the crocodilian cf. *Goniopholis* during preparation (October 21, 2014).

burial. Almost all teeth are well-preserved and show no evidence of abrasion by postmortem transport. The two mammalian teeth (NLMH 105650 and NLMH 105651) were found in the same sediment block with a total diameter of approximately 30 cm. NLMH 105650 was found during preparation of a dorsal vertebra of the semiaquatic crocodilian cf. *Goniopholis* (Fig. 2) in the Dinosaurier-Park Münchehagen. NLMH 105651 was discovered during picking the screen-washed concentrate from the sediment matrix at the Universität Bonn. Interestingly, NLMH 105650 is almost undamaged; only one root was broken during preparation. Its two large delicate, yet fully preserved roots support the interpretation that there was very little transport before burial and suggest that the habitat was nearby.

MATERIAL AND METHODS

The present work describes two isolated mammalian teeth, NLMH 105650 and NLMH 105651, housed in the geosciences collections of the Niedersächsisches Landesmuseum in Hannover, Germany. The teeth were examined with a Zeiss Discovery V20 Stereomicroscope. Both teeth were scanned with the Micro-CT v|tome|x s 240 scanner (GE Sensing and Inspection Technologies Phoenix|x-ray) at the Steinmann-Institut of the Universität Bonn (Supplementary Online Material available at http://www.palaeontologia.pan.pl/SOM/pp67-Martin_etal_SOM.pdf).

The SEM images of the sputter coated cast of NLMH 105650 were made using a Camscan MV 2300 (Camscan, Cambridge, UK). For molding the specimen the silicone Provil® novo Light regular (EN ISO 4823, type 3, light; Heraeus Kulzer, Hanau, Germany) was used. The cast was made using epoxy resin RenLam® M-1, hardener Ren® HY 956, and pigment Araldit® DW 0137 (Huntsman Advanced Materials, Offenbach am Main, Germany). Systematics and general nomenclature of multituberculates follow Kielan-Jaworowska *et al.* (2004). For terminology of cusps see Fig. 3.

SYSTEMATIC PALAEONTOLOGY

Mammalia Linnaeus, 1758

Multituberculata Cope, 1884

Plagiaulacid line

Family indet.

Genus *Teutonodon* gen. n.

LSID urn:lsid:zoobank.org:pub:AAB91665-4045-403F-BA29-B9EE46D87EFD

Etymology: After Teutones, Germanic tribe of antiquity. In the Middle Ages, Teutonia was the common name for the geographical area of Germany.

Diagnosis. — As for the type and only species.

Distribution. — As for the type and only species.

Teutonodon langenbergensis sp. n.

(Figs 3, 4A–H)

Etymology: After the Langenberg, the hill between Goslar and Bad Harzburg, where the Langenberg Quarry is located.

Holotype: NLMH 105650, upper right M1 (Figs 3, 4A–H).

Type locality and horizon: Langenberg Quarry near the town of Goslar, Lower Saxony, northern Germany. N 51°54,110', E 10°30,500'. Bed 83 (after Fischer 1991), a light grey-greenish marly limestone within the Sünteln-Formation. Based on ostracodes and rare finds of ammonites, it has been assigned to the "Mittleres Kimmeridge", a northwest-German equivalent to the lower part of the upper Kimmeridgian of the international chronostratigraphic time scale (Schweigert 1999; Lallensack *et al.* 2015).

Differential diagnosis. — M1 cusp formula 5L/4B. Enamel strongly ornamented with pits and grooves. Cusp bases coalescent, increasing in size from front to back on the lingual side. Lingual cusp row strongly worn. Differs from the allodontid line by coalescent cusps and ornamented enamel. Differs from paulchoffatiid line by the presence of an incipient posterolingual ridge (strongly worn). Differs from M1 of Ptilodontidae and Taeniolabidae by the presence of only two rows of cusps. Differs from M1 of Plagiaulacidae, Eobaataridae, and *Janumys* Eaton *et* Cifelli, 2001 by a higher number of cusps. Differs from M1 of Albiobaataridae by a larger size and lower number of cusps.

Description. — The shape of the tooth crown of NLMH 105650 (Figs 3, 4A–D) is rectangular with the lingual side longer and more strongly worn than the buccal side. The lingual side comprises five cusps which are all strongly worn with the dentine exposed (except for the anteriormost cusp). The cusps increase in size from front to back, but the remaining base of cusp L4 appears slightly larger than that of cusp L5. Besides the apical wear of the cusps, the entire lingual flank of M1 is worn flat with an elongated field of dentine exposed at the base of cusp L4/5 in the vicinity of the poorly developed posterolingual ridge. The buccal flanks of the lingual cusps are also strongly worn with longitudinal striations. There are four buccal cusps of which the anteriormost (cusp B1) and posteriormost (cusp B4) are smaller than cusps B2 and B3. The buccal cusps are worn only on their lingual side within the longitudinal valley of the crown. Otherwise they are unworn and show a typical plagiaulacid pattern of enamel crests extending from their apices. The cusps of both sides are sitting close together with confluent bases. The longitudinal valley of the crown is V-shaped and is oriented in antero-lingual direction.

Fig. 3. Schematic drawing of the occlusal surface of NLMH 105650 with terminology of cusps. Dotted pattern illustrates exposed dentine.

The anterior side of M1 is flat with a slight indentation at the buccal side for accommodation of the preceding premolar. The distal side is rounded with the buccal flank angled at about 45° and the lingual flank at 25°, giving the posterior end of the tooth crown a somewhat asymmetric appearance. The buccal flank is slightly damaged.

The M1 has two large roots that are slightly curved in lingual direction and a small root between the two larger roots at the labial side.

Measurements. — Length = 2.51 mm, width = 1.73 mm.

Family **Eobaataridae** Kielan-Jaworowska *et al.*, 1987

Gen. et sp. indet.

(Fig. 4I–N)

Included specimen: NLMH 105651, lingual fragment of right lower m1.

Locality: Langenberg Quarry near the town of Goslar, Lower Saxony, northern Germany. N 51° 54,110', E 10° 30,500'.

Description. — NLMH 105651 is interpreted as a lingual fragment of a right lower eobaatarid cheek tooth, most probably a m1, with three cusps in a row. The two anterior coalescent cusps are large and of
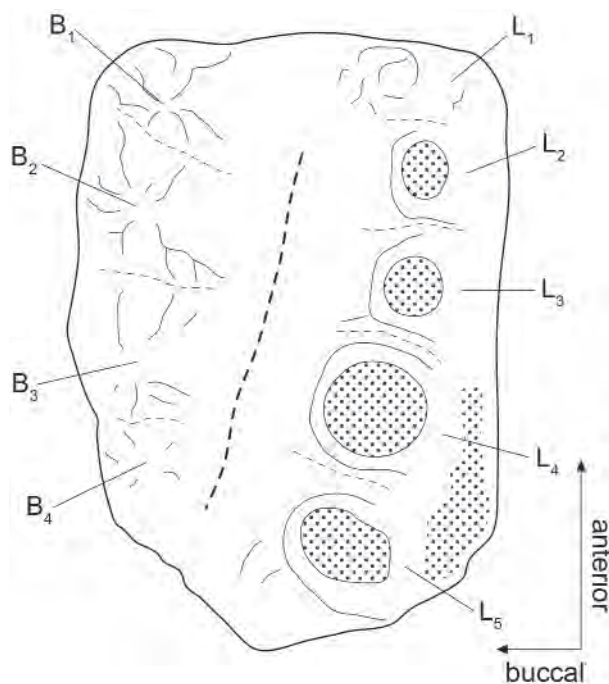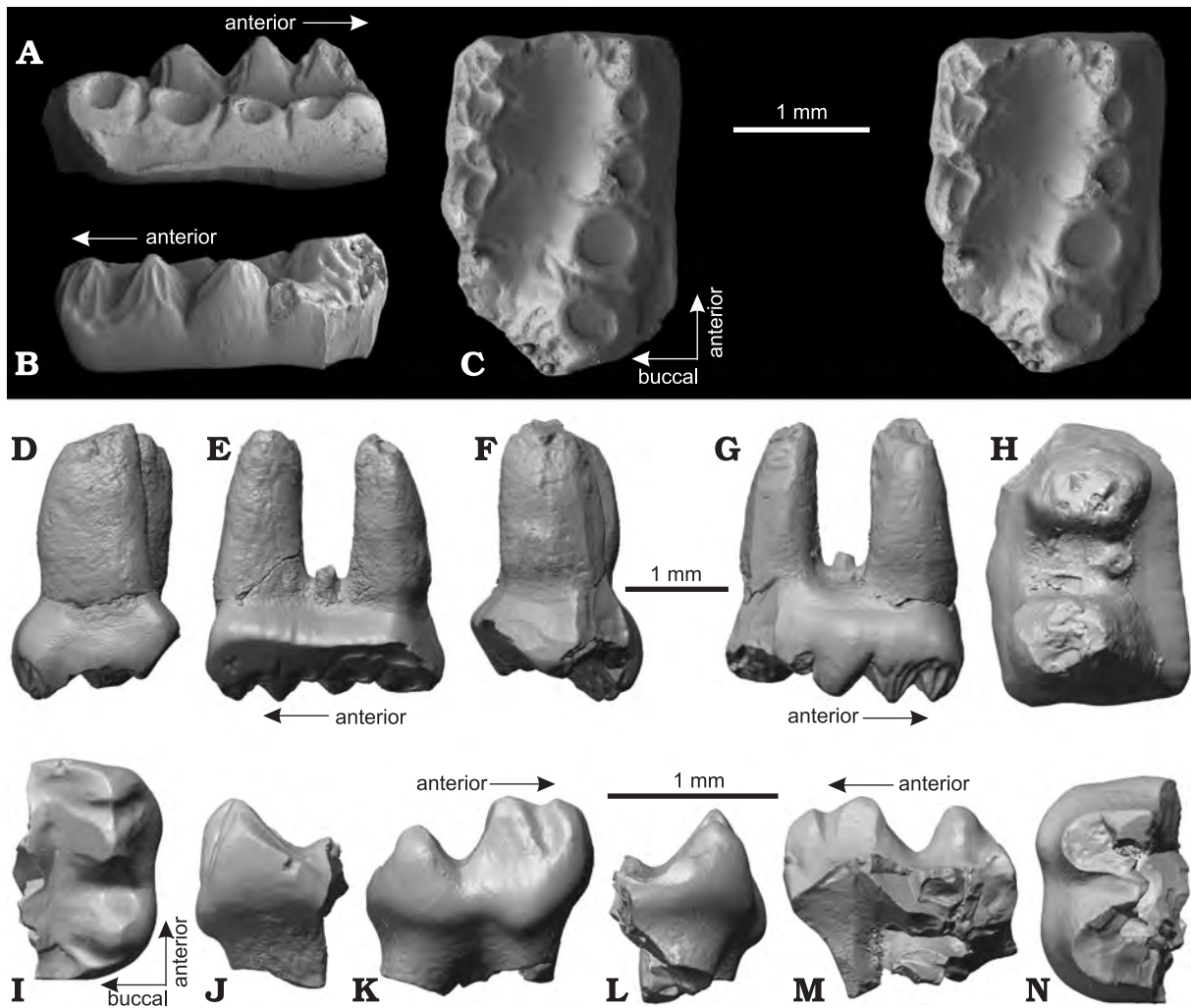
Fig. 4. SEM images (A–C) and digital models (D–N) of right upper M1 of *Teutonodon langenbergensis* and indeterminate eobaatarid right lower m1 from Langenberg quarry. **A–H**. *Teutonodon langenbergensis* (NLMH 105650, holotype), in lingual (**A**), labial (**B**), and occlusal (**C**, stereo-pair) views of tooth crown and anterior (**D**), lingual (**E**), posterior (**F**), labial (**G**), and cervical (**H**) views of entire tooth. **I–N**. Indeterminate eobaatarid m1 (NLMH 105651), in occlusal (**I**), anterior (**J**), labial (**K**), posterior (**L**), and cervical (**N**) views, and lingual view of broken side (**M**).

similar height, the posterior cusps is much lower and separated by a deep notch. The anteriormost cusp is re-curved posteriorly and separated from the following cusps by two shallow grooves on the lingual and buccal side. The tooth originally had two rows of cusps with a deep V-shaped longitudinal valley in between. The preserved cusps are worn on the buccal side, particularly the middle cusp, and their lingual aspect is unworn. The V-shaped longitudinal valley is anteriorly and posteriorly open. The tooth has two roots of similar size and the crown is bulging somewhat lingually.

Measurements. — Length = 1.38 mm, preserved width = 0.93 mm, width of preserved cusp row (buccal edge of crown to midline of the V-shaped longitudinal valley) = 0.62 mm.

DISCUSSION AND COMPARISONS

Following Kielan-Jaworowska and Hurum (2001) "Plagiaulacida" are grouped into three lineages, the allodontid line, the paulchoffatiid line, and the plagiaulacid line. "Plagiaulacida" represent a paraphyletic array of more plesiomorphic multituberculates than Cimolodonta and occur in Europe from the ?Middle Jurassic (Bathonian) or Late Jurassic (Kimmeridgian) to Early Cretaceous (Barremian). In North America, they are recorded from the Late Jurassic to the Early–Late Cretaceous boundary, in Asia from the Late

Jurassic (Oxfordian) to the Early Cretaceous, and in northern Africa from the Early Cretaceous (?Berriasian) of Morocco (Kielan-Jaworowska *et al.* 2004 and references therein).

NLMH 105650. — An affiliation of *Teutonodon langenbergensis* gen. et sp. n. (NLMH 105650) with the allodontid line can be ruled out because allodontids lack enamel ornamentation and have well separated molar cusps. So far, allodontid-line taxa have been recorded only from the Late Jurassic Morrison Formation (see Kielan-Jaworowska *et al.* 2004) and earliest Cretaceous Lakota Formation (Cifelli *et al.* 2014) in the western USA.

Teutonodon differs from Portuguese paulchoffatiids and from Chinese *Rugosodon* Yuan *et al.*, 2013 in possessing molar cusps of similar height and by a posterolingual ridge on M1 (Hahn and Hahn 2000; Yuan *et al.* 2013). This ridge is present, albeit strongly worn, on NLMH 105650. In NLMH 105650, the bases of the cusps vary in diameter, but the heights of the cusps are almost equal as evident from the unworn buccal cusp row. Paulchoffatiids have been recorded from the Kimmeridgian Guimarota beds and the Early Cretaceous (Barremian) Lourinhã-Formation of Portugal (Hahn and Hahn 2000).

Plagiaulacids are characterized by a tendency of molar cusps to coalesce, as well as ornamented enamel with grooves and pits. Within the Late Jurassic to Early Cretaceous Plagiaulacida, an upper M1 is only known for *Bolodon osborni* Simpson, 1928 which has a cusp formula of 3:4 (Hahn and Hahn 2004). The molars of Plagiaulacidae and Early Cretaceous Eobaataridae generally have a lower number of cusps than seen in NLMH 105650 (Hahn and Hahn 2004). The albionbaatarids *Proalbionbaatar plagiocyrus* Hahn *et* Hahn, 1998 from the Late Jurassic and *Albionbaatar denisae* Kielan-Jaworowska *et* Ensom, 1994 from the Early Cretaceous have much smaller M1s with a higher number of cusps. The Late Cretaceous *Janumys erebos* Eaton *et* Cifelli, 2001 was interpreted as related to the plagiaulacid line, based on P4, M1, m1, and m2, which are all smaller than NLMH 105650. M1 of *Janumys erebos* is more elongated than NLMH 105650 and its cusp formula is 3-4:4.

The *Paracimexomys*-group represents the most plesiomorphic (informal) group of Cimolodonta. Although it comprises taxa with ornamented enamel, the ornamentation is much weaker than in NLMH 105650. Stratigraphically, the *Paracimexomys*-group has been recorded from the Aptian–Albian to Maastrichtian of North America and the Late Cretaceous (?Maastrichtian) of Europe (Rădulescu and Samson 1986; Eaton and Nelson 1991; Cifelli 1997). Given the differences in enamel ornamentation and the lower stratigraphic occurrence, an affiliation of NLMH 105650 with the *Paracimexomys*-group is unlikely.

NLMH 105651. — The tooth fragment most closely resembles the lingual portion of right m1 of *Eobaatar magnus* Kielan-Jaworowska *et al.*, 1987 (pl. 2: 2) from the Early Cretaceous (Aptian or Albian) of Mongolia, but is 20% smaller. Eobaataridae have been reported from the Valanginian of southeastern England (Wadhurst Formation, Cliff End), the early Barremian of Spain (Camarilla Formation, Galve; Pié Pajarón; Uña), the Barremian of China (Yixian Formation, Liaoning Province), and the Aptian or Albian of Mongolia (Höövör Beds, Gobi Desert) (Woodward 1911; Simpson 1928; Crusafont-Pairó and Adrover 1966; Kielan-Jaworowska *et al.* 1987; Hahn and Hahn 2001; Hu and Wang 2002). Eobaataridae are characterized by ornamented enamel and coalescing cusps at the lower molars (Kielan-Jaworowska *et al.* 2004, p. 316). NLMH 105651 shows coalescence of the two anterior cusps, but enamel ornamentation is not evident. However, in *Eobaatar* Kielan-Jaworowska *et al.*, 1978 enamel ornamentation is mainly present at the labial portion of the lower molars (Kielan-Jaworowska *et al.* 1987, pl. 2: 1, 2), whereas the lingual portion is smooth.

CONCLUSIONS

The presence of multituberculate teeth at the Langenberg Quarry extends the occurrence of plagiaulacid-line taxa to the Late Jurassic of northern Germany. One specimen serves as the holotype for a new taxon, *Teutonodon langenbergensis*. The presence of this taxon in the Late Jurassic of northern Germany is not surprising, as members of the plagiaulacid line have been hitherto known from the Late Jurassic to Early Cretaceous of North America (Morrison and Lakota formations), Europe (southern England, Portugal, Spain), and Asia (China, Mongolia) (Kielan-Jaworowska *et al.* 2004; Cifelli *et al.* 2014). A second, fragmentary specimen compares most favorably with Eobaataridae (*e.g.*, *Eobaatar magnus*) known otherwise from the Early Cretaceous of Europe and Asia. The record of the first Jurassic mammals from Germany demonstrates the potential of the Langenberg Quarry for further discoveries of terrestrial vertebrates, including the exciting possibility of a major stratigraphical range expansion for eobaatarid multituberculates.

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EARLIEST KNOWN MAMMALIAN STAPES FROM AN EARLY CRETACEOUS EUTRICONODONTAN MAMMAL AND IMPLICATIONS FOR EVOLUTION OF MAMMALIAN MIDDLE EAR

JIN MENG and SHILIN HOU

The earliest known mammalian stapes with unequivocal morphology from an Early Cretaceous eutriconodontan, *Chaoyangodens lii*, is described. The stapes is roughly rectangular in dorsal view with parallel crura and equal width on both the distal and proximal ends. The stapes has a large stapedial foramen and a prominent process that is interpreted as for insertion of the stapedius muscle (PISM). The PISM is homologized with the proximal end of the interhyal, instead of the dorsal process of the sauropsid extrastapes; the latter is fused to the crista parotica of the otic capsule as the tympanohyal in mammals. The morphology of the stapes is probably characteristic of the transitional mammalian middle ear and supports the notion that the rod-like, perforated stapes with a broad end-on contact with the incus is a primitive stapes condition for mammals. During the evolution of mammalian middle ear, the distal end of the stapes and the PISM reduced the size, along with reduction of other ear ossicles. Because the stapedius muscle is absent in monotremes, the columelliform-imperforate stapes of monotremes probably lacks the homologue of the PISM.

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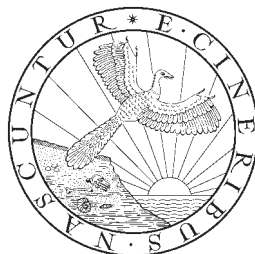
INTRODUCTION

The definitive mammalian middle ear (DMME) (Allin and Hopson 1992) in mammals (Rowe 1988) differs from other extant tetrapods in having a unique middle ear that consists of multiple ossicles. In contrast, the middle ear of non-mammalian amniotes has one ossicle, the stapes (or columella auris). The evolution of the DMME has been a subject that has attracted enormous attention since at least Reichert (1837) and Gaupp (1908, 1913) and still remains as an interesting topic in the study of mammalian evolution. Incorporation of the malleus-incus complex into the middle ear during the early evolution of mammals resulted in an increased bandwidth of hearing and was thus a great biological advantage in mammals (Fleischer 1978). Significant progress has been made recently in documenting middle ear morphologies in Mesozoic mammals, including the ossified Meckel's cartilage, the malleus (= the articular and prearticular), incus (= quadrate) and ectotympanic (= angular) (Wang *et al.* 2001; Meng *et al.* 2003, 2011; Luo *et al.* 2007; Ji *et al.* 2009; Luo 2011). Based on these recent discoveries, the transitional mammalian middle ear (TMME) has been hypothesized as an intermediate stage between the mandibular middle ear, as represented in *Morganucodon* (Kermack *et al.* 1973, 1981), and the DMME in all extant mammals (Allin and Hopson 1992).

In addition to new discoveries made in paleontology, evolution of the mammalian middle ear has also continued to attract considerable attention from developmental and molecular studies that focus on the homology and gene expression of middle ear ossicles and related structures (Maier 1990; Zeller 1993; Mallo 1998, 2001, 2003; Sánchez-Villagra *et al.* 2002; Tucker *et al.* 2004; Wilson and Tucker 2004; O'Gorman 2005; Takechi and Kuratani 2010; Anthwal *et al.* 2013; Gillis *et al.* 2013; Kitazawa *et al.* 2015). More interestingly, paleontological findings and results of developmental biology converge in revealing not only the homology of the middle ear ossicles but also development of structural details of the ossicles, such as the manubrium as a neomorphic outgrowth of the malleus (Allin and Hopson 1992; Clack and Allin 2004; Meng *et al.* 2011; Anthwal *et al.* 2013).

However, the aforementioned developmental and paleontological studies have focused primarily on the ear ossicles that are transformed mandibular elements of non-mammalian cynodonts. In contrast, the stapes of Mesozoic mammals remains little known and less investigated, as already pointed out by Novacek and Wyss (1986). Although the stapes was discovered in the mid 16th century (Mudry 2013), its homology is still a controversial subject in developmental and evolutionary biology. The stapes has been known as the most conservative element of the middle ear ossicles, with its essential form and ontogeny being traceable across vertebrates (Goodrich 1930; Eaton 1939; Romer 1941; Westoll 1943; Parrington 1949, 1955, 1979; Tumarkin 1968; Fleischer 1978; Lombard and Bolt 1979; Novacek and Wyss 1986; Allin and Hopson 1992; Clack and Allin 2004). As Eaton (1939, p. 117) concluded: "The crossopterygian hyomandibular bone, evolving into the tetrapod stapes, retains its original morphological relations largely unchanged, even to mammals." In addition, the articulation between the stapes and incus in mammals represents the quadrate-hyomandibular joint that was present in ancestral amniotes (Kitazawa *et al.* 2015).

The stapes is rarely preserved in early mammals because of its small size and fragility. Among known Mesozoic mammals, there is one nearly complete stapes reported from a Late Cretaceous eutherian (Archibald 1979). Fragments of the stapes were reported from the Late Cretaceous multituberculate *Kryptobaatar* (Rougier *et al.* 1996a) and *Chulsanbaatar* (Hurum *et al.* 1996) and from Early Cretaceous eutriconodonts (Luo *et al.* 2007; Meng *et al.* 2011). Except for the stapes from a Late Cretaceous eutherian (Archibald 1979), the unambiguous morphology of the stapes remains poorly known in Mesozoic mammals and most of their close relatives, such as *Haldanodon* (Lillegraven and Krusat 1991; Ruf *et al.* 2013), *Morganucodon* (Kermack *et al.* 1981), and *Sinoconodon* (Crompton and Luo 1993). As yet, there is no convincing evidence of the stapes known from eutriconodontans.

Because of the scant fossil record, the ancestral condition of the stapes in mammals and transformation of the mammalian stapes during evolution of the mammalian middle ear has remained contradictory (Novacek and Wyss 1986; Meng 1992). It is posited that the rod-like, perforated stapes is the most likely ground plan for derivation of the mammalian stapes and that it probably persisted in "triconodonts" because of its common occurrence in cynodonts and other tetrapods (Novacek and Wyss 1986). Here we report the stapes with unequivocal morphology from the Early Cretaceous eutriconodontan *Chaoyangodens lii* Hou *et* Meng, 2014. It is the earliest known mammalian stapes, given current phylogenetic placements of the eutriconodontans within Mammalia (Luo *et al.* 2002, 2007; Kielan-Jaworowska *et al.* 2004; Rowe *et al.* 2008; Yuan *et al.* 2013; Zheng *et al.* 2013; Bi *et al.* 2014; Krause *et al.* 2014). The morphology of the stapes supports the notion

that the rod-like, perforated stapes is a primitive condition for mammals. It provides new evidence about the stapes morphologies during the evolution of the mammalian middle ear, from the mandibular middle ear to the TMME and then to DMME. It also raises the issue on the homology of the process for insertion of the stapedius muscle in therians, a feature to which little attention has been paid.

Institutional abbreviations. — JTZ, Ji-Zan-Tang Paleontological Museum, Chaoyang, Liaoning Province, China; MGL, Museu Geológico de Lisboa, Lisbon, Portugal.

MATERIAL AND METHODS

The holotype specimen of *Chaoyangodens lii* Hou *et* Meng, 2014 (JZT005-2010) is a skeleton from the lacustrine beds of the Yixian Formation at the Dawangzhangzi locality, Lingyuan, western Liaoning, China (Hou and Meng 2014, p. 548, fig. 1). The age of the strata has been generally considered as Early Cretaceous, but the radiometric dates vary from 122.2 Ma (Smith *et al.* 1995; Wang *et al.* 1999) to 124.6 Ma (Swisher *et al.* 1999, 2002). Other mammals from this locality include the multituberculate *Sinobaatar lingyuanensis* Hu *et* Wang, 2002, the trechnotherian *Akidolestes cifellii* Li *et* Luo, 2006, the metatherian *Sinodelphys szalayi* Luo *et al.*, 2003, and the eutherian *Eomaia scansoria* Ji *et al.*, 2002.

The skeletal specimen is preserved as a split slab of laminated siltstone, with the skeleton being primarily in slab A. The dorsal side of the skull is exposed and the right stapes is preserved in close approximation to the basicranial region of the skull and posterior to the petrosal (Fig. 1). No other ear ossicle has been detected from the crushed specimen. The miniscule stapes is mainly in slab A (Fig. 1B$_1$), with its impression in slab B (Fig. 1B$_2$).

In referring to Mammalia, we adopt the crown mammal concept (Rowe 1988), noting that different definition for mammals have also been used (Kielan-Jaworowska *et al.* 2004). Measurements were made using a microscope equipped with a reticule etched with divisions of 0.01 mm.

DESCRIPTION

The holotype is crushed so that detailed morphology of the skull is difficult to obtain, but the skull length measures 33.7 mm from the rostrum tip to the posterior edge of the occipital condyles (Hou and Meng 2014, fig. 1). The ossified Meckel's cartilage (OMC) is preserved in anatomical position on the medial side of each mandible (Fig. 1A). As in other euriconodonts, including *Repenomamus* (Wang *et al.* 2001; Meng *et al.* 2003), *Gobiconodon* (Li *et al.* 2003), *Yanoconodon* (Luo *et al.* 2007), and *Liaoconodon* (Meng *et al.* 2011), the OMC is rod-like with a blunt posterior end and tapers anteriorly; its anterior portion is loosely lodged in the Meckelian groove on the medial surface of the dentary.
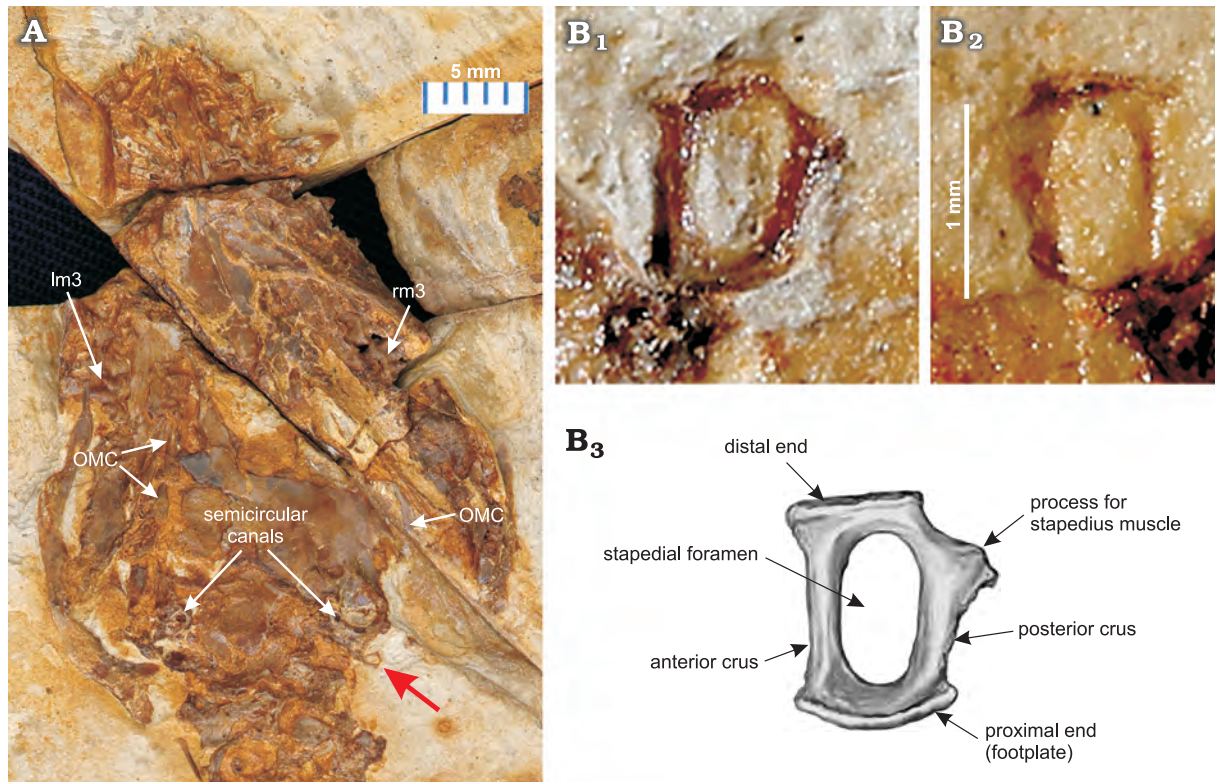
Fig. 1. The skull and right stapes of an Early Cretaceous eutriconodontan *Chaoyangodens lii* Hou *et* Meng, 2014 (JZT005-2010) from Liaoning, China (Hou and Meng 2014). **A**. Dorsal view of the skull with the red arrow pointing to the stapes. **B**. Right stapes (B$_1$, preserved in slab; B$_2$, mostly impression); B$_3$, drawing in dorsal view. Abbreviations: lm3, left m3; OMC, ossified Meckel's cartilage; rm3, right m3.

The ear region on each side of the skull is in poor preservation, but can be identified by exposed cross sections of the semicircular canals. More detailed description of the holotype specimen was presented in Hou and Meng (2014). The morphology and profile of the stapes are well exposed. It is bicrurate and has a large oval stapedial foramen, sufficient for a functional stapedial artery, but it cannot be known whether the artery was present in life. Due to the crushed nature of the specimen there is no cranial structure available for identification of the artery. The stapes measures 1 mm in length, with a maximum width (including the process for insertion of the stapedius muscle) of 0.9 mm. The distal end (in articulation with the incus) and proximal end (the footplate) have the same width, 0.63 mm. This is interpreted as the rostrocaudal length of the stapedial footplate, which approximates the maximum diameter of the footplate. The stapes length as a percentage of skull length is 2.97%, and the skull length to the stapedial footplate diameter ratio is 53.5.

The two crura are nearly parallel and equidistant from the footplate margin, which gives the stapes a rectangular shape in dorsal (lateral) view (Fig. 1B). We interpret the distinctive process on one of the crura as the process for insertion of the stapedius muscle (PISM). In extant mammals the PISM, where present, is on the posterior crus and closer to the stapedial head (Fig. 2C–E); thus, the crus bearing the PISM in *Chaoyangodens* should be the posterior crus and the end of the stapes closer to the PISM is the distal (lateral) end of the stapes (Fig. 1). For those taxa in which the stapedius muscle inserts directly to the stapes head, the process is absent (Doran 1878; Segall 1970; Fleischer 1973; Henson 1974; Novacek and Wyss 1986). The PISM of *Chaoyangodens* is prominent compared to those of extant mammals (Fig. 2), suggesting that the stapedius muscle was relatively large. The homology of this process will be discussed below.

The anterior crus is straight and slightly thinner than the posterior one, as in other mammals (Fig. 2); its cross section is circular judging from the exposed rounded surface of the crus. The posterior crus is slightly curved and arcs posteriorly. The ends of the stapes are almost equal in its width, with the distal end slightly flaring out. The proximal view of the footplate is not available owing to the condition of the specimen preservation. From the exposed edge, the footplate has a slightly convex outline, in contrast to the straight distal end. On slab A the original edge of the footplate slightly projects out from the rest of the stapes. Judging from the exposed portion of the bone, the footplate is most likely an elongate oval with its long axis passing the crura.
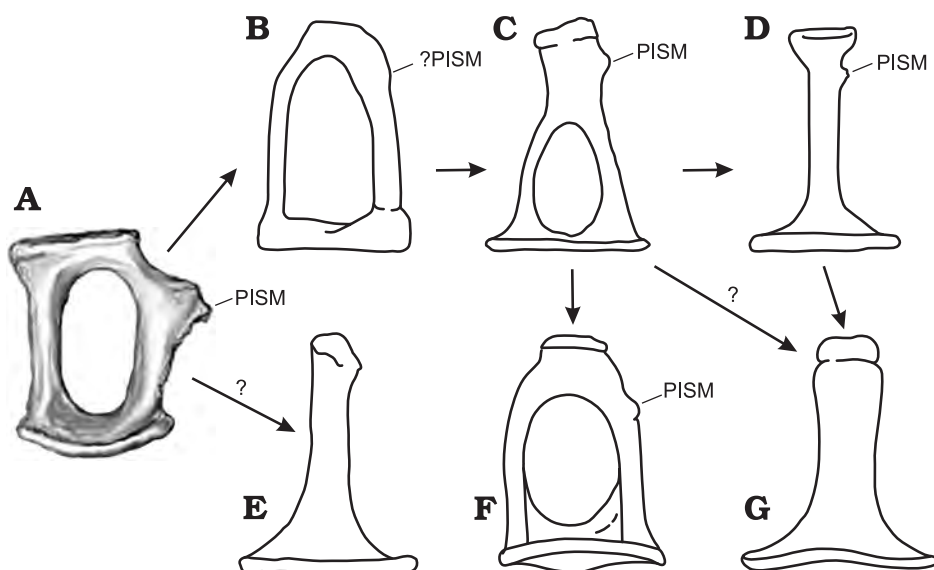
Fig. 2. Comparison and hypothetic transformations of mammalian stapes. **A**. The stapes of *Chaoyangodens lii*, which represents the stapes condition in the TMME and is probably ancestral to those of extant mammals. **B**. The stapes of a Late Cretaceous "unguiculate" eutherian (Archibald 1979). **C**. *Philander* (= *Metachirops*). **D**. *Notoryctes*. **E**. *Orycteropus*. **F**. *Manis*. **G**. *Ornithorhynchus*. B is from Archibald (1979) and C–G from Novacek and Wyss (1986; also see Doran 1878; Segall 1970; Fleischer 1973).

CHARACTER ANALYSES

Shape of the stapes. — The skull of *Chaoyangodens* preserves the ossified Meckel's cartilage, which indicates presence of the TMME, in which the incus fully functioned for hearing. The shape of the stapes must reflect its articulation with the incus. The broad distal end of the stapes indicates that the incudostapedial articulation is sizable and that the incus probably did not have a slender long process and a restricted lenticular process (Doran 1878; Segall 1970; Fleischer 1973; Henson 1974; Novacek and Wyss 1986). This is evidenced by the morphology of the incus in the eutriconodontan *Liaoconodon* (Meng *et al.* 2011). As Meng *et al.* (2011) pointed out, the incus of *Liaoconodon* is proportionally larger than those of extant mammals and its long process is actually shorter than its short process, suggesting that the long process homologous with those of extant therian mammals was not fully developed in *Liaoconodon*.

For early mammaliaforms there are two hypotheses for the stapes-quadrate (incus) articulation: The stapes has a broad end-on-end contact with the quadrate; or it has a restricted contact with the quadrate and simultaneously maintains contact with the tympanic membrane by an extrastapes, as discussed in many studies (*e.g.*, Westoll 1943, 1944; Hopson 1966; Allin 1975, 1986; Parrington 1949, 1979). The former hypothesis appears to be favored because in all therapsid groups the stapes is considerably reduced in size and retains an end-on contact with the quadrate (Allin 1975; Allin and Hopson 1992). The end-on broad contact between the quadrate and the stapes is usually reflected by a broad distal end of the stapes, as in *Brasilitherium*, *Thrinaxodon*, *Exaeretodon*, *Probainognathus*, *Pachygenelus*, and *Haldanodon* (Watson 1953; Estes 1961; Bonaparte 1966; Allin 1975; Parrington 1979; Kermack *et al.* 1981; Novacek and Wyss 1986; Lillegraven and Krusat 1991; Allin and Hopson 1992; Crompton and Luo 1993; Crompton 1995; Rodrigues *et al.* 2013; Ruf *et al.* 2013).

In *Morganucodon* only the proximal part (footplate) of the stapes is known, but a broad distal end of the stapes is reconstructed to articulate with the stapedial process of the quadrate and to prevent the medial displacement of the latter (Kermack *et al.* 1981). A partial stapes of *Sinoconodon* was figured in Crompton and Luo (1993, figs 4.11–4.12), in which it seems that only the anterior crus and partial distal end of the stapes are preserved and visible. From what can be seen, the stapes of *Sinoconodon* probably has a broad distal end.

The stapes of *Chaoyangodens* does not readily fit any of the stapes shapes categories recognized by Novacek and Wyss (1986). The parallel crura and rectangular or columellar outline is somewhat comparable to the columelliform-perforate ("rod-like") stapes that is generally distributed among non-mammalian

cynodonts, such as *Probainognathus*, *Pachygenelus*, and *Brasilitherium* (Novacek and Wyss 1986; Allin 1973; Allin and Hopson 1992; Luo and Crompton 1994; Crompton, 1995; Rodrigues *et al.* 2013). The columelliform-perforate stapes is proportionally large and relatively massive in those non-mammaliaforms. In this regard, the delicate and small stapes with slender crura of *Chaoyangodens* is more similar to the bicrurate stapes of mammals (Novacek and Wyss 1986). However, the stapes of *Chaoyangodens* differs from the bicrurate stapes in having a broad distal end and roughly parallel crura that give the stapes a rectangular outline in dorsal (lateral) view. Most distinctively, it has a prominent PISM.

Although the stapes of *Chaoyangodens* has a broad distal end, it does not show any sign of an extrastapes, similar to those of non-mammalian cynodonts as illustrated by Allin (1975, pls 4, 5) and Allin and Hopson (1992, p. 594, fig. 28-5; p. 595, fig. 28-6). Compared to other mammals, the stapes of *Chaoyangodens* is most similar to that of the Late Cretaceous "unguiculate" eutherian (Archibald 1979) in having a large stapedial foramen, nearly parallel proximal portions of the crura, and an elongate oval (narrow) footplate. The "unguiculate" eutherian stapes differs from that of *Chaoyangodens* in being proportionally long in relation to its width and in having its distal end narrowed to form the head. Whether the "unguiculate" eutherian stapes has the process for insertion of the stapedius muscle is uncertain (Archibald 1979). Judging from the thickened posterodistal region of the stapes, it is possible that the process was present; if so, it would have been small and near the head of the stapes.

There are numerous variations in the stapes morphology of extant mammals (Doran 1878; Segall 1970; Fleischer 1973; Henson 1974; Novacek and Wyss 1986), but the distal end of the stapes is almost invariably restricted to form the restricted head, and is significantly narrower than the proximal end or the footplate (Meng 1992). This condition is also applicable to multituberculates where the stapes is known: it can be either columelliform as in the Tertiary *Lambdopsalis* (Meng 1992) or stirrup-shaped as interpreted in the Late Cretaceous *Kryptobaatar* (Rougier *et al.* 1996a). A narrow stapedial head conforms to the shape of the incus. In therian mammals, the incus usually has a slender, long stapedial process (*crus longum*) that ends as a restricted lenticular process; the latter often bends at a right angle to the long process and articulates to the narrow head of the stapes (Doran 1878; Segall 1970; Fleischer 1973; Henson 1974; Novacek 1993).

Size of the stapes. — In understanding the trend of stapes reduction during mammalian evolution, the relative size of a stapes is usually judged by comparing the footplate diameter and stapes length to the length of the skull. The ratio of skull length to the footplate diameter is useful in that the latter can be estimated from the size of the fenestra vestibuli in specimens that do not have the stapes preserved, although the dimensions of the footplate are slightly smaller than those of the fenestra vestibuli because the annular stapedial ligament connecting the footplate to the fenestra vestibuli is not preserved in fossils. However, it should be cautioned that, in non-mammalian synapsids, the rim of the large footplate overlaps the rim of the smaller fenestra vestibuli (Allin and Hopson 1992; see below).

The footplate length is about 90% of that of the fenestra vestibuli in *Haldanodon* (Lillegraven and Krusat 1991) and *Brasilitherium* (Rodrigues *et al.* 2013). Where it is known, the stapes is usually robust in non-mammalian cynodonts (Watson 1953; Estes 1961; Estes 1961; Bonaparte 1966; Allin 1975; Parrington 1979; Kermack *et al.* 1981; Novacek and Wyss 1986; Rowe 1988; Lillegraven and Krusat 1991; Wible 1991; Allin and Hopson 1992; Wible and Hopson 1993; Crompton and Luo 1993; Rodrigues *et al.* 2013; Ruf *et al.* 2013). In *Morganucodon* the skull length (26 mm) to the footplate diameter (0.6 mm) ratio is about 43, contrasting with a value of 110 in an adult *Tachyglossus* (Kermack *et al.* 1981), so that these authors considered the size of the stapes in *Morganucodon* to be enormous in comparison with that of monotremes, and thus concluded that the stapes of *Morganucodon* is more comparable with that of non-mammalian therapsids than with modern mammals. In *Haldanodon* the skull length (35 mm) to the footplate diameter (0.993) ratio is about 35.2. This ratio was regarded as the largest known among terrestrial mammals, a primitive feature that *Haldanodon* shares with its cynodont ancestors (Lillegraven and Krusat 1991). A new specimen of the stapes of *Haldanodon* (MGL 6722) has a maximum footplate length of 0.85 mm and the estimated skull length of MGL 6721 (Ruf *et al.* 2013, fig. 1A) is 37 mm, which together yield a ratio of 43.5, similar to that of *Morganucodon*. Based on the measurements from some cynodonts (Parrington 1949), the ratio of the skull length to the maximum width of the footplate (the proximal end) of the stapes is 21.4 for *Thrinaxodon*, 17 for *Galesaurus*, and 24.8 for *Trirachodon*. The same ratio is 22.6 for *Brasilitherium* (Rodrigues *et al.* 2013).

The skull length to the maximum footplate length ratio is 53.5 in *Chaoyangodens*, indicating that the stapedial footplate is significantly smaller than that of non-mammalian cynodonts but larger than those of extant mammals, such as *Tachyglossus*. This ratio suggests a general trend of the stapedial footplate reduc-

tion toward the mammalian condition. However, in mammals with a highly specialized auditory system, such as the multituberculate *Lambdopsalis* (Miao 1988; Meng and Wyss 1995), the stapedial footplate can be proportionally large. The skull length to footplate diameter is less than 35 in *Lambdopsalis* (Meng 1992).

The stapes length to skull length ratio is another parameter of stapes size and has been used as a quantitative character in phylogenetic reconstruction of mammals (Wible 1991). Complete stapes are seldom preserved in early mammaliaforms, such as *Morganucodon* (Kermack *et al.* 1981) and *Haldanodon* (Lillegraven and Krusat 1991; Ruf *et al.* 2013), so that the actual length of the stapes is unknown in these forms. However, the stapes length can be approximated from the distance between the fenestra vestibuli and the quadrate articulation in skulls where relevant elements are in anatomical positions (Wible 1991). Wible (1991; also Wible and Hopson 1993) thus recognized a large stapes as the primitive condition, with stapes length as a percentage of skull length from 7.5 to 13% in non-mammaliaform taxa. Based on actual measurements of the stapes (Parrington 1949), the ratio of stapes length to skull length is 8% for *Thrinaxodon*, 9.4% for *Galesaurus*, and 12.1% for *Trirachodon*. The same ratio is 9% for *Brasilitherium* (Rodrigues *et al.* 2013). The derived condition is a small stapes, with the percentage ranging from 3 to 5.5% in extinct mammaliaform taxa such as *Sinoconodon*, morganucodontids, multituberculates, and *Vincelestes*; and 0.05 to 4.2% in extant mammals (Wible 1991). The percentage ranges of extinct mammaliaforms and extant mammals partly overlap. The actual measurement of the stapes length of the multituberculate *Lambdopsalis* is 2.3 mm (Meng 1992), about 3.3% of an adult skull length, which falls into the overlapping range of the two categories. As a member of the extinct euriconodontans, the stapes/skull length ratio is 2.97% for *Chaoyangodens*, smaller than those of extinct basal mammaliaforms. It is clear that the relative size of the stapes of *Chaoyangodens*, either the footplate diameter or the stapes length, is well in the range typical for extant mammals. The small stapes of *Chaoyangodens* is consistent with the size reduction of other ear ossicles, as revealed in the euriconodontan *Liaoconodon* (Meng *et al.* 2011).

Stapedial foramen. — A columelliform-imperforate stapes, like that of monotremes, was once considered as representing the primitive mammalian condition (Doran 1878; Gregory 1910; Segall 1970). More works, however, favor the stapes perforated by the stapedial foramen to be primitive for mammals (Goodrich 1915, 1930; Kuhn 1971; Henson 1974; Fleischer 1978; Novacek and Wyss 1986; Novacek 1993; Lillegraven and Krusat 1991; Wible 1991; Meng 1992; Wible and Hopson 1993; Gaudin *et al.* 1996; Rougier *et al.* 1996a), for the reason that a perforate stapes is present in many non-mammalian cynodonts close to crown mammals, such as *Thrinaxodon, Exaeretodon, Probainognathus*, *Pachygenelus*, *Brasilitherium*, *Sinoconodon*, *Morganucodon*, and *Haldanodon* (Watson 1953; Estes 1961; Bonaparte 1966; Allin 1975; Parrington 1979; Kermack *et al.* 1981; Novacek and Wyss 1986; Rowe 1988; Lillegraven and Krusat 1991; Wible 1991; Allin and Hopson 1992; Wible and Hopson 1993; Crompton and Luo 1993; Rodrigues *et al.* 2013; Ruf *et al.* 2013). Probably because of its relatively robust construction in non-mammalian cynodonts, the stapes in these forms is better preserved compared to the typical mammalian stapes. Novacek and Wyss (1986) also argued that developmental studies of extant mammals show persistence of the stapedial foramen and reduction or loss of the foramen to form the imperforate stapes, as in *Perameles* sp. and *Dasyurus viverrinus* (see Sánchez-Villagra *et al.* 2002), but there is no case in which the perforate condition is plausibly derived from an imperforate condition. The stapes of *Chaoyangodens* lends additional support to the notion that a perforate stapes is primitive for mammals.

Presence of a sizable stapedial foramen is suggestive, but not conclusive, for presence of the stapedial artery. Because the ear region of JZT005-2010 is poorly preserved, there is no other evidence for the existence of the artery. However, the stapedial artery as a common feature is present during development in almost all extant mammals, although it is lost by the adult stage in all marsupials and in some placentals (Wible 1987; Wible *et al.* 2001). An intrastapedial course of the stapedial artery associated with the rod-like stapes has been considered a primitive condition for mammals (Goodrich 1930; Novacek and Wyss 1986). This hypothesis is consistent with the stapes morphology of *Chaoyangodens* (see cautionary note above in "shape of stapes" section).

Given a phylogeny in which Mammalia includes therians, monotremes, euriconodontans, and multituberculates (Luo *et al.* 2002, 2007; Kielan-Jaworowska *et al.* 2004; Rowe *et al.* 2008); and the mosaic distribution of stapedial morphology within mammals (Doran 1878; Fleischer 1973, 1978; Novacek and Wyss 1986), the columelliform stapes (Fig. 2D) probably evolved by reduction of the stapedial foramen, and did so independently several times within multituberculates, monotremes, marsupials, and placentals.

Stapedial footplate. — In basal mammaliaforms, such as *Morganucodon* (Kermack *et al.* 1981) and *Haldanodon* (Lillegraven and Krusat 1991; Ruf *et al.* 2013), the stapedial footplate is nearly rounded in proximal view. Multituberculates appear to have a similar condition, as evidenced by preserved stapes or the shape of the fenestra vestibuli (Miao and Lillegraven 1986; Wible 1990; Meng 1992; Fox and Meng 1997). In extant mammals, the stapedial footplate is circular in monotremes but varies considerably in therians (Doran 1878; Fleisher 1973; Zeller 1993; Nummela and Sánchez-Villagra 2006). A nearly rounded footplate of the stapes or the fenestra vestibuli has been considered to be a primitive condition in mammals, in contrast to a more elliptical (derived condition) footplate (Segall 1970; Archibald 1979).

The stapedial footplate is probably elongate oval in *Chaoyangodens*. An elongate oval footplate is present in the stapes of various mammals, such as the Cretaceous "unguiculate" eutherian (Archibald 1979), the marsupial *Petaurus breviceps* (Nummela and Sánchez-Villagra 2006), the placental *Tarsius spectrum* (Coleman and Boyer 2011, fig. 6j), and even humans (Quam *et al.* 2014). The footplate shape can be approximated from the fenestra vestibuli for those fossil taxa in which the stapes is not preserved. However, this is only applicable for species in which the stapes fits in the fenestra vestibuli and connects to the rim of the fenestra vestibuli by the annular ligament. Allin and Hopson (1992, p. 596) noted that, in all non-mammalian synapsids, the rim of the large footplate overlaps the rim of the smaller fenestra vestibuli and that this overlapping would have prevented the stapes from being driven into the inner ear. This overlapping relationship means that the size of the footplate is larger than the fenestra vestibuli and that the stapes may not vibrate as an entity in a piston-like manner as in extant mammals; instead, sound pressure waves were propagated along it (Watson 1954). The overlapping footplate-fenestra vestibuli relationship does not seem to be present in *Brasilitherium*, *Haldanodon* (Lillegraven and Krusat 1991; Rodrigues *et al.* 2013; Ruf *et al.* 2013), and *Morganucodon*, as reconstructed by Kermack *et al.* (1981).

Homology of the PISM. — Although the stapes was discovered in the mid sixteenth century (Mudry 2013), its homology still remains controversial. It is known that the three middle ear ossicles are derived from the neural crest and are endochondral bones, of which the stapes originates from the second arch, whereas the malleus (the goniale, which fuses to the malleus, is a dermal bone) and incus are first arch derivatives (Goodrich 1930; De Beer 1937; Crompton and Parker 1978; Kontges and Lumsden 1996; Tucker *et al.* 2004; Chapman 2011; Kitazawa *et al.* 2015). The homology of the stapes can be viewed in two different senses. First, in terms of developmental biology, it remains an open question as to whether the stapes is derived from a unique source of the second branchial (hyoid) arch (Rodríguez-Vázquez 2005, 2009; Rodríguez-Vázquez *et al.* 2006) or is from dual sources, with the footplate originating from the otic capsule and the rest of the stapes representing the dorsalmost derivative of the second branchial arch (Cauldwell and Anson 1942; Anson *et al.* 1960; Masuda *et al.* 1978; Ars 1989; Mallo 1997; Nandapalan and Tos 2000; Whittemore *et al.* 2013). Some authors suggest that development of the stapes is required for formation of the fenestra vestibuli (Rijli *et al.* 1993), whereas others indicate that this ossicle is not essential for formation of the fenestra vestibuli but that the development of the two structures, even if it occurs independently, must be coordinated (Mallo 1997, 2001; Kanzler *et al.* 2000).

Second, from an evolutionary perspective, the views about the homology of the stapes across different vertebrate groups are diverse. Summarizing the work by others (Goodrich 1930; Westoll 1943; Parrington 1979), Novacek and Wyss (1986) pointed out that the hyomandibula in fishes has been broadly homologized with the columella auris in lower tetrapods, and that fine details of structure and function in the hyomandibula of crossopterygians, which seem to be shared by cynodont therapsids and other tetrapods, are identified. These authors consider the homology of these elements at a more general level to be widely accepted. Furthermore, Novacek and Wyss (1986, pp. 41 and 44) thought that "the mammalian stapes is homologous strictly with the 'reptilian' and bird otostapes" and that "the mammalian stapes is homologous with the proximal columella of sauropsids and other tetrapods, but not with the extra-stapedial elements (distal columella) of these forms". On the other hand, Cambas (1983) considered that in mammals, the stapedial footplate and head represent the otic and quadrate processes of the dorsalmost derivatives of the hyoid arch, respectively, and the styloid process (tympanohyal and stylohyal) represents the dorsal and hyoid processes; thus, the columella is the homologue of the stapes and the styloid process. Cambas' work corroborates the hypotheses that the dorsal process of rhipidistians and basal tetrapods may be present in the mammalian styloid process (Goodrich 1930; de Beer 1937) and that the styloid process also includes the homologue of the hyoid process. Presley (1984) also observed that the mammalian blastema shows reasonable homologues of the otic process (stapes), quadrate process (element of Spence), dorsal process (styloid), and hyoid process (stylohyoid) im-
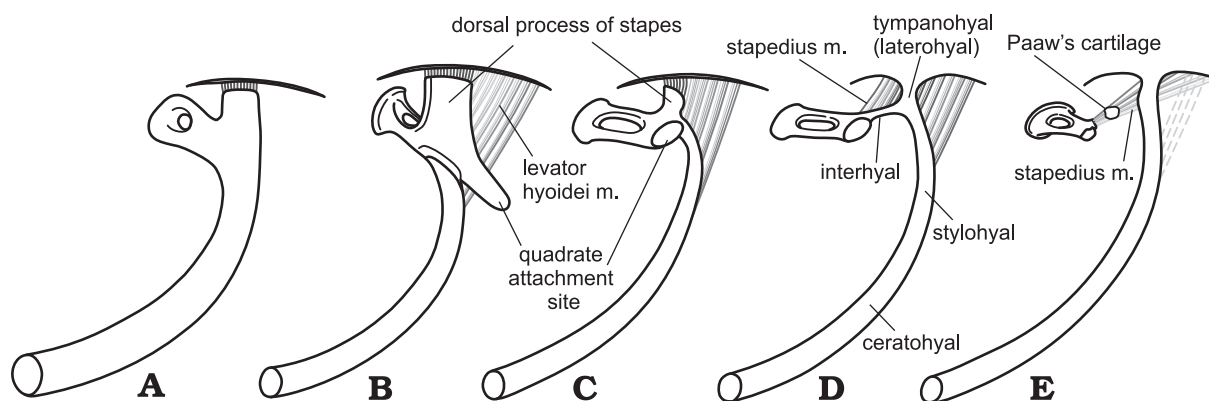
Fig. 3. Diagram showing the development and evolution of the synapsid hyoid arch skeleton, focusing on the stapes and the dorsal process (left side toward anterior aspect). Mesenchymal primordium in a modern mammalian embryo (**A**), compared with adult synapsid conditions (**B–E**). **B**. "*Pelycosaur*" condition with a massive stapes having a strong dorsal process attached to the paroccipital process. **C**. Primitive cynodont condition with a lighter stapes having a smaller dorsal process situated posterodistally. **D**. Hypothetical stage based on ontogeny, with fusion of the dorsal process to the paroccipital process, detachment of the dorsal process and hyoid cornu from the stapes except for a slender ligamentous or cartilaginous connection (interhyal). **E**. Modern mammal condition, with a very light stapes having the dorsal process completely detached; and complete differentiation of the stapedius muscle, with the stapedius tendon and its sesamoid cartilage of Paaw. Abbreviation: m, muscle. Modified from Allin and Hopson (1992: fig. 28.3).

plicit in Westoll's (1943, 1945) analysis. Allin (1975, p. 406) explicitly noted that the mammalian stapes "is the homolog of the stapes proper and at least the proximal portion of the extrastapes of reptiles (including the quadrate process)". Allin and Hopson (1992) further recognized that the primitive synapsid stapes appears to include homologs of parts of the sauropsid extrastapes, particularly the quadrate process and the dorsal process; they further hypothesized that both originated from the extrastapes or hyostapes, noting that all except for the quadrate process are lost or detached in extant mammals.

In addition to the aforementioned views on homology of the stapes, the stapes of *Chaoyangodens* raises yet another issue about the homology of the PISM, which in turn is relevant to the development of the stapedius muscle that functions for protecting the inner ear from overstimulation by excessively loud sound and/ or for frequency tuning (Wever and Bray 1942; Fleischer 1978). The stapes in early mammals and their close relatives is rare in the fossil record, but where it is preserved, studies have often focused on the general morphology of the stapes, its size, the stapedial foramen, and the footplate (Archibald 1979; Novacek and Wyss 1986; Meng 1992). There is little attention paid to the homology of the PISM, perhaps because the process is such a minuscule structure in extant mammals and is unknown among previously-described Mesozoic mammals, except for its possible presence in the Late Cretaceous "unguiculate" eutherian (Archibald 1979). In contrast, Allin (1975; also in Hopson 1966; Parrington 1979; Allin and Hopson 1992) recognized that an ossified dorsal process is present in at least some members of all therapsid groups; in *Thrinaxodon*, for example, the process extends upward from the posterolateral corner of the stapes toward the paroccipital process. In the Late Triassic mammaliamorph *Brasilitherium riograndensis*, a process near the stapedial head was interpreted as most probably serving as the attachment for the stapedius muscle and was compared to the "strong dorsal process" on the stapes of the *Thrinaxodon liorhinus* (Estes 1961). The stapes of *Brasilitherium* has a larger stapedial foramen and is relatively gracile (Rodrigues *et al.* 2013). The dorsal process or PISM is unknown in *Morganucodon* and *Sinoconodon* because of poor preservation of the stapes in those taxa (Kermack *et al.* 1981; Crompton and Luo 1993).

The question now is whether the PISM is homologous with the dorsal process of the adult therapsid stapes or with another derivative of the second branchial arch. Based on de Beer (1937) and Presley (1984), Allin and Hopson (1992) explained the development and evolution of the synapsid second branchial arch that is relevant to the stapes and related structures (Fig. 3). More detailed and recent developmental studies of the stapes focusing on the human embryo (Rodríguez-Vázquez 2005, 2009; Rodríguez-Vázquez *et al.* 2006) are also illustrative on the homology of the PISM. The general developmental pattern of the stapes is that, during early embryonic stages, the mesenchymal blastema of the second branchial arch in sauropsids and mammals has two processes, the medial and lateral, at its dorsal end. The medial process ossifies in sauropsids as the stapes proper (the otostapes) and in mammals as the entire stapes (Fig. 3). The medial process, called the

stapedial anlage in Rodríguez-Vázquez (2005), is a unique combination with two distinct parts: the dorsal part that forms the footplate and the ventral part that is crossed by the stapedial artery during embryonic development and forms the crura and the head of the stapes. The lateral process, which is part of the Reichert's cartilage (Rodríguez-Vázquez, 2005), chondrifies as the dorsal process of the sauropsid extrastapes and fuses to the crista parotica of the otic capsule as the tympanohyal (laterohyal) in mammals (Hanson *et al.* 1962; Cambas 1983; Allin and Hopson 1992; Rodríguez-Vázquez 2005, 2009). In mammals, the homology of the tympanohyal and the dorsal process are supported by their topographic relationships to the jugular vein and hyomandibular branch of the facial nerve, and the articulation with the crista parotica (Cambas 1983; Rodríguez-Vázquez 2005, 2009).

In mammals, a mesenchymal condensation, the interhyal (*interhyale*), temporarily connects the embryonic stapes with the dorsal process (or the cranial end of Reichert's cartilage) in an early stage of development. The interhyal has a thicker proximal part (the stapedial portion), which becomes the tendon of the stapedius muscle and, sometimes, a sesamoid cartilage (of Paaw) within this tendon; whereas the thinner distal (external) part disappears at the beginning of the fetal period. Rodríguez-Vázquez (2005, p. 172) also observed that the stapedius muscle develops independent of the interhyal and joins the interhyal at a later stage of development, so that "the muscle and tendon must therefore have different origins, in contrast to the opinion given by Hanson *et al.* (1962) and Louryan (1993)". Based on the developmental evidence, the PISM of mammalian stapes is most probably homologous with the ossified proximal (stapedial) end of the interhyal on which the tendon of the stapedius muscle attaches, and is not homologous to the dorsal process of the sauropsid extrastapes.

DISCUSSION

In extant mammals and their synapsid kin, the stapes distally articulates with the incus (quadrate). This articulation is conservative and represents the quadrate-hyomandibular joint that was present in ancestral amniotes but was lost in diapsids (Kitazawa *et al.* 2015). The general evolutionary trend for the stapes is its reduction in size from a massive one in non-mammalian cynodonts to a miniscule one to comply with the reduced incus, the malleus, and the ectotympanic bones in mammals. Reduction of the stapes size decreases its mass, and the stapes is in fact the lightest of the ear ossicles (Fleischer 1978). The stapes in extant mammals is characterized by a narrow distal end (the head) so that for stapes with two crura, the crura are not parallel to each other but distally converge in various ways to the head. For those with a narrow columelliform shaft, the head is as wide as, or only slightly wider than, the shaft (Fig. 2D, F, G). This morphology perhaps represents the latest stage of mass reduction of the stapes during the evolution of the mammalian middle ear, which, along with modifications of the incus and malleus, functions for highly sensitive airborne hearing. As recognized by Fleischer (1978), it is much easier to tune a vibrational system, with the stapes being a mass-spring system, to high frequencies if the mass involved is small. Moreover, through the tension of the stapedius muscle, the stapes can be somewhat tilted. Whether this is for protecting the inner ear from overstimulation or for change of frequency response of the ear is unclear, but the articulation between incus and stapes has to allow for some lateral give (Fleischer 1978). A restricted stapedial head seems necessary or at least efficient for such flexibility at the incudostapedial articulation.

The stapes is poorly represented in the Mesozoic fossil record, making it difficult to understand its evolutionary transition within early mammals. Archibald (1979) thought that the perforate stapes is likely the primitive mammalian condition, but he also considered both the columelliform stapes of monotremes and the stirrup-like stapes of the Late Cretaceous "unguiculate" eutherian (Fig. 2) to be derived compared to that of *Didelphis*. The new evidence from *Chaoyangodens*, however, favors an alternative hypothesis that the Late Cretaceous eutherian stapes is probably more primitive than that of *Didelphis* and that the columelliform stapes of monotremes may have evolved independently from that of therians (Fig. 2). Furthermore, the stapes of *Chaoyangodens* lends support to the notion that the rod-like stapes with a broad distal end is a primitive condition for mammals (Novacek and Wyss 1986; Meng 1992; Rougier *et al.* 1996a). From the mandibular middle ear to the TMME the stapes reduces in size, falling in the size range of extant mammals. However, because of the relatively broad distal end, as in *Chaoyangodens*, tension of the stapedius muscle at the TMME stage may work differently from those of the DMME, in that the stapes may not be tilted and

the incudostapedial articulation has less flexibility to allow for any lateral give (Fleischer 1978). From the stapes of the TMME to that of DMME of mammals, the most distinct change is the restriction of the distal end of the stapes. Given the diverse phylogenetic hypotheses of mammals (see Meng 2014 and references therein) and the poor fossil record of the stapes in early mammals, it is difficult to map on any phylogeny how the stapes evolved within major clades of mammals. It is highly possible that the stapes with a restricted (narrow) head evolved independently more than once to give rise to a variety of stapes forms in mammalian subgroups (Doran 1878; Fleischer 1973, 1978; Novacek and Wyss 1986).

The interesting issue about the stapes of *Chaoyangodens* is the presence of a distinctive PISM. As noted above, the embryologic evidence of extant mammals shows that the PISM and the dorsal process (tympano-hyal) are two different structures, although both are derivatives of the second branchial arch. The PISM is probably homologous with the proximal (stapedial) end of the interhyal instead of the dorsal process of the sauropsid extrastapes. It follows that, if the stapes has the dorsal process, as interpreted in *Thrinaxodon*, the PISM and the tympanohyal would be absent. Similarly, if the tympanohyal is formed at the basicranial region in Mesozoic mammals, as has been interpreted for multituberculates (Wible and Hopson 1995; Rougier *et al.* 1996a; Wible and Rougier 2000) and eutriconodontans (Wible and Hopson 1993, 1995; Rougier *et al.* 1996b; Wang *et al.* 2001; Meng *et al.* 2003), there should be no expression of the dorsal process on the stapes in those forms. For *Brasilitherium riograndensis*, if the process on the stapes is for the attachment of the stapedius muscle, as interpreted by Rodrigues *et al.* (2013), then it should not be the dorsal process, but the PISM. Because the stapes of non-mammaliaform cynodonts lacks the PISM, the development of the PISM and the stapedius muscle would represent innovative structures acquired during the evolution of the mammalian middle ear. Whether the stapedius muscle is for protecting the inner ear from overstimulation or for tuning of sound vibrations, this structure works only with a gracile stapes, probably including taxa such as *Brasilitherium riograndensis*, and is perhaps suggestive for high frequency hearing.

The distinctive PISM of *Chaoyangodens* suggests that the interhyal was less reduced than that of any known adult individuals of extant mammals and that the stapedius muscle was relatively larger than that of extant mammals. Whether similar structures were present in basal mammaliaforms was unclear. However, the stapedius muscle may be inferred from presence of the fossa for the stapedius muscle on the petrosal, which in turn is suggestive of the PISM. The fossa for the stapedius muscle is known in eutriconodontans (Wible and Hopson 1993; Rougier *et al.* 1996b), consistent with presence of the PISM in the eutriconodontan *Chaoyangodens*. The stapedius fossa is not illustrated in the petrosal of *Morganucodon* (Wible and Hopson 1993, 1995), but a deep pit anterior to the paroccipital process and immediately posterior to the rod (the crista interfenestralis) separating the fenestrae cochleae and vestibuli was posited as possibly housing the levator hyoidei muscle; the latter is found in monotremes and is the homologue of the stapedius muscle (Kermack *et al.* 1981). Rougier *et al.* (1996b), following Crompton and Sun (1985), interpreted this feature as an indicator of the stapedius muscle in *Morganucodon*, and noted that a similar depression on the crista interfenestralis occurs in tritylodontids, *Sinoconodon*, *Dinnetherium*, *Megazostrodon*, and *Haldanodon*. The stapedius fossa (stapedial muscle fossa) and the site possibly for the attachment of the tympano-hyal were identified in *Haldanodon* (Ruf *et al.* 2013) and *Dryolestes* (Luo *et al.* 2012). In *Brasilitherium riograndensis*, neither the tympanohyal nor the fossa for the stapedius muscle were reported (Rodrigues *et al.* 2013). Absence of the two structures, if confirmed with better material, would favor interpretation of the process on the stapes of *B. riograndensis* as the dorsal process, not the PISM.

In some extant therian mammals, the PISM is small and close to the head (Fig. 2), which probably represents a vestige of the ossified proximal base of the interhyal. In others, the PISM is absent or the stapedius muscle inserts directly to the head so that there is no discernable process on the posterior crus of the stapes (Doran 1878; Segall 1970; Henson 1974; Fleischer 1978; Novacek and Wyss 1986; Novacek 1993). This may be interpreted as reduction or non-ossification of the proximal interhyal in adult therian stapes. However, lack of the PISM in monotremes may require a different interpretation because monotremes do not have the stapedial muscle (Fleischer 1978). Presley (1984) also noted that there is no true stapedius muscle in adult monotremes and that this is probably secondary, owing to the very specialized pattern of the ossicles. Based on the work of Edgeworth (1931, 1935), Wible (1991), and Wible and Hopson (1993) pointed out that the levator hyoidei muscle, from which the stapedius muscle is derived, is present in monotremes, but it takes origin from the ventral edge of the paroccipital process in *Ornithorhynchus* and from the squamosal in *Tachyglossus*. Thus, lack of the stapedius muscle and the PISM on the stapes of monotremes suggest the possibility that the stapes of monotremes does not include the part homologous to the interhyal.

CONCLUSIONS

Of the middle ear ossicles reported from a handful of Mesozoic mammals, the stapes remains the least known. The discovery of the stapes from the Early Cretaceous eutriconodontan *Chaoyangodens* (Hou and Meng 2014) provides the first unambiguous morphology for the structure in eutriconodontans and is the earliest known mammalian stapes. The stapes of *Chaoyangodens* is reduced in size compared to those of non-mammalian cynodonts and is within the size range of extant mammals. Reduction of the stapes is consistent with the reduced incus and malleus as observed in the TMME of the eutriconodontan *Liaoconodon* (Meng *et al.* 2011). The stapes of *Chaoyangodens* has nearly parallel crura and a large stapedial foramen, supporting the notion that the rod-like stapes, penetrated by a large stapedial foramen, is a primitive condition for mammals. The broad distal end of the stapes in *Chaoyangodens* indicates an end-on broad contact with the incus, a primitive retention of the condition seen in basal mammaliaforms. Reduction of the distal end of the stapes to form a narrow head of the stapes in the DMME of extant mammals likewise reduces the mass of the stapes and allows flexibility at the articulation between the stapes and the incus. These modifications of the stapes would contribute to sensitive hearing of high-frequency airborne sounds and are derived features present in extant mammals. The process identified as the PISM on the posterior crus of the stapes remains prominent in *Chaoyangodens*. Based on embryological studies of extant mammals, the distinct PISM of *Chaoyangodens* is hypothesized to be homologous with the ossified proximal end of the interhyal and is probably present in close relatives of mammals that have the stapedius muscle (as reflected by presence of the fossa for the stapedius muscle). The PISM and the stapedius muscle attached to it are probably innovative structures that developed during the evolution of cynodonts toward mammals. Absence of the PISM and lack of the stapedius muscle in monotremes may suggest that the stapes of monotremes does not have the homologue of the PISM. The stapes of *Chaoyangodens* indicates that, during the evolution from the mandibular middle ear to the TMME, the stapes conforms to the change of other ossicles in size and mass reduction. From the TMME to DMME, the stapes reduces its distal end to form a restricted head and the PISM is reduced to a vestige or becomes completely indiscernible.

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ADDENDUM

While this paper was in press, a study by Gaetano and Abdala (2015) appeared, in which the authors presented excellent documentation of the stapes in gomphodont cynodonts and discussed the broader implications for structure of the middle ear among non-mammaliaform cynodonts. Although Gaetano and Abdala's work is largely consistent with some previous observations on the stapes of non-mammaliaform cynodonts, as summarized herein, the authors raised an issue in interpreting the function of the dorsal process present on some stapes they reported. According to Gaetano and Abdala, the dorsal process is a triangular-shaped lamina pointing dorsally or dorsomedially from the dorsolateral portion of the posterior crus in non-mammaliaform cynodonts (except for some specimens of *Thrinaxodon*) and is well-suited for the insertion of a small ligament or muscle, such as Paauw's cartilage or the stapedial muscle. The authors interpreted that the stapedial muscle connected the stapes, by attachment to the dorsal process, to the paroccipital process in basal cynodonts (see Gaetano and Abdala 2015, for detailed discussion and references). This interpretation differs from what we advocate in our paper: we interpret the dorsal process and PISM as different structures based on developmental evidence. If both structures are interpreted as serving for attachment of the stapedial muscle among different groups of cynodonts, then the homology of either the bony process on the stapes or the muscle presumably attached to it, or both, needs to be further investigated within a phylogenetic framework, as well as within embryological context bearing on development of the stapes. Further data and research are needed to address this intriguing homology issue.

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CRANIODENTAL ANATOMY OF A NEW LATE CRETACEOUS MULTITUBERCULATE MAMMAL FROM UDAN SAYR, MONGOLIA

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The multituberculate *Mangasbaatar udanii* gen. et sp. n., represented by two specimens from Udan Sayr locality in the Gobi desert (Mongolia), is a derived member of a speciose group of Late Cretaceous Mongolian multituberculates (LCMM), clustering together with large-size forms such as *Catopsbaatar*, *Tombaatar*, and *Djadochtatherium*, forming a monophyletic group. *Tombaatar sabuli* is the sister taxon and shares with the new form the dental formula, overall dental morphology, and approximate size. The new multituberculate has a very large middle ear cavity, housing a petrosal and promontorium that are deeply sunk into the braincase. The expansion of the middle ear cavity seems to be absent among basal LCMM, only developing among members of Djadochtatherioidea, and to an extreme degree in the Udan Sayr multituberculate and *Tombaatar*. Among living mammals, enlarged middle ear cavities confer enhanced low frequency audition and are often found in fossorial species, such as golden moles, and several groups of rodents adapted to open, arid environments. Burrowing is a possible behavior for the new mammal and its closest relatives with similarly expanded middle ear regions and an arid environment has been proposed for the sediments where most LCMM are found. The new taxon further demonstrates the morphological, and possibly ecological, diversity among multituberculates.

Key words: Multituberculata, Djadochtatherioidea, skull structure, phylogeny.

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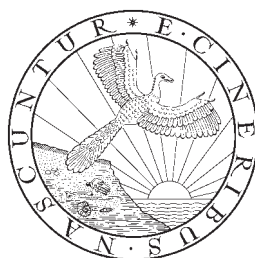
INTRODUCTION

Since 1990, the American Museum of Natural History (AMNH) and the Mongolian Academy of Sciences have been prospecting the Mesozoic outcrops of Mongolia in search of fossil vertebrates. This new project is the heir of a similar series of expeditions organized by the AMNH during the 1920s that recovered some of the first early mammals from Central Asia (Gregory and Simpson 1926; Simpson 1928a, b; Matthew *et al.* 1928, 1929). The recent American-Mongolian expeditions (1990 to the present) have followed that tradition and results have been plentiful, including the discovery of one of the richest Mesozoic localities in the world, Ukhaa Tolgod (Norell *et al.* 1994; Novacek *et al.* 1994; Dashzeveg *et al.* 1995, 2005; Dingus *et al.* 2008). The Cretaceous localities of Mongolia, especially those of the Djadochta and similarly-aged Barun Goyot formations (Shuvalov 2000; Jerzykiewicz 2000; Dashzeveg *et al.* 2005; Dingus *et al.* 2008), are exceptionally rich in well-preserved small vertebrates in comparison to those in other parts of the world. During 1940–1980 most of the paleontological exploration of Central Asia was undertaken by joint Russian-Mongolian and Polish-Mongolian expeditions that resulted in the discovery of new Cretaceous localities in the Nemegt Valley, raising the bar regarding specimen quality and allowing for much more detailed anatomical work than previously possible (Clemens *et al.* 1979; Lillegraven *et al.* 1979). Professor Kielan-Jaworowska, in whose memory the present volume is compiled, was the leader of the Polish expeditions, a prolific and accomplished scientist who for years shaped the debate on early mammalian evolution (see summary and review in Kielan-Jaworowska *et al.* 2004; Kielan-Jaworowska 2013). With very few exceptions, the most complete Late Cretaceous mammalian skeletons known to date have been recovered from those Mongolian localities (Kielan-Jaworowska 1969a, b, 1970, 1974, 1975a, b, c, 1977, 1978, 1979, 1984a, b, 2013; Kielan-Jaworowska and Sochava 1969; Kielan-Jaworowska and Dashzeveg 1978; Kielan-Jaworowska and Trofimov 1980; Kielan-Jaworowska and Gambaryan 1994; Gambaryan and Kielan-Jaworowska 1995; Kielan-Jaworowska and Hurum 1997, 2001; Kielan-Jaworowska *et al.* 2005). Multituberculates are the most common mammalian specimens collected in the Cretaceous localities of Mongolia. The Late Cretaceous Mongolian Multituberculates (LCMM) are the best-known specimens of multituberculates and currently eleven genera are recognized (Wible and Rougier 2000; Kielan-Jaworowska and Hurum 2001, 2005; Kielan-Jaworowska *et al.* 2004). To those we add a new one here.

Multituberculates possess the longest fossil record of all mammals, extending from the early middle Jurassic to the late Eocene (Prothero and Swisher 1992; Freeman 1976, 1979; Kielan-Jaworowska *et al.* 2004). Several recent studies (Zheng *et al.* 2013; Zhou *et al.* 2013; Bi *et al.* 2014) have opened discussion regarding the timing of certain events within the basal branches of the mammalian tree, namely the origin of the very first mammals via the relationships between Haramiyidae and Allotheria (including multituberculates). It is at present unresolved if multituberculates are closely related to haramiyids, eleutherodontids and other forms with cusps in line, and while multituberculates are consistently regarded as mammals in recent studies (Bi *et al.* 2014; Luo *et al.* 2015; Meng *et al.* 2015), opinions differ regarding haramiyids and eleutherodontids.

Multituberculates are also one of the best-represented groups of Mesozoic mammals: over five hundred partial or complete skulls and skeletons have been collected from Ukhaa Tolgod since 1993. However, the taxonomic diversity in Ukhaa Tolgod and other localities of the Djadochta Formation is relatively low, the fauna being dominated by medium-sized forms such as *Kryptobaatar dashzevegi* Kielan-Jaworowska, 1970 (Wible and Rougier 2000). The specimens described here are from a different locality, Udan Sayr (Fig. 1), which is considered to be somewhat younger than traditional localities like the Flaming Cliffs, probably corresponding to the Barun Goyot Formation (Jerzykiewicz and Russell 1991; Kielan-Jaworowska *et al.* 2004) and of late Campanian age. A few tantalizing mammalian specimens have been collected at Udan Sayr, including basal metatherians (Trofimov and Szalay 1994; Szalay and Trofimov 1996), eutherians, and multituberculates (Bolortsetseg 2008).

The collection of complete or nearly complete specimens of LCMM led to a revival in the study of multituberculate phylogeny (Simmons 1993; Miao 1993; Rougier *et al.* 1997; Kielan-Jaworowska and Hurum 1997, 2001; Kielan-Jaworowska *et al.* 2002, 2005), which excepting a few publications (Ladevèze *et al.* 2010; Smith and Codrea 2015) has subsided in recent years. One of the most notable results of the work on the late 1990s and early 2000s has been the recognition of an endemic LCMM clade, Djadochtatheria, later reclassified as superfamily Djadochtatherioidea Kielan-Jaworowska *et* Hurum, 1997 (Rougier *et al.* 1997; Kielan-Jaworowska and Hurum 1997; Kielan-Jaworowska and Hurum 2001). Multituberculate cranial anatomy has been monographically treated in two instances: Miao (1988) described the taeniolabidoid

Fig. 1. Map of Mongolia with location of the Udan Sayr locality, Gobi Desert, Mongolia.

Lambdopsalis bulla Chow et Qi, 1978 and Wible and Rougier (2000) described *Kryptobaatar dashzevegi*. Later, Kielan-Jaworowska *et al.* (2005) provided a revised description of *Catopsbaatar* Kielan-Jaworowska, 1994 with a high level of detail, and even more recently a CT study of the ear region of a cf. *Tombaatar* skull from a Djadochta equivalent in China was presented by Ladevèze and co-authors (Ladevèze *et al.* 2010). *Kryptobaatar* is a member of Djadochtatherioidea consistently recovered in a relatively basal position in the group and is a suitable generalized LCMM to serve as interpretative baseline for understanding the evolution of Djadochtatherioidea. On the other hand, *Tombaatar sabuli* Rougier *et al.*, 1997 is thought to be a much derived member of this clade, but the fragmentary skull so far described is quite poorly preserved and Ladevèze *et al.* (2010) described only the ear region in any detail. The well-preserved specimens described here are closely related to *Tombaatar* and provide a substantial amount of new information (of the jaw, ear region and basicranium in particular) about this highly-derived group. A detailed knowledge of a generalized form, such as *Kryptobaatar*, and derived forms, such as *Tombaatar* and allies, illuminates the range of morphological diversity for Djadochtatherioidea in particular and multituberculates in general.

GEOLOGICAL SETTING AND MATERIAL

The holotype and refered specimen were found in the easternmost exposures of Udan Sayr (Fig. 1). Following current Mongolian legislation, precise coordinates are only available to qualified researchers. General coordinates for Udan Sayr are 43° N, 103° E, about 65 kilometers west of Bayan Dzag in Umnugovi Province, Mongolia. Udan Sayr was first discovered by the Soviet Mongolian Paleontological Expedition in the 1980s (Benton *et al.* 2000) and two joint expeditions have worked there, one between the Mongolian Academy of Sciences (MAS) and the American Museum of Natural History and another between the MAS and Hayashibara Museum of Natural Sciences. The former expedition collected the holotype of *Mangasbaatar* from Udan Sayr in 1997. Exposures of Udan Sayr are scattered across an area of more than 60 km^2. The lower

strata consist of fluvial sandstones and mudstones and with dinosaur footprints being the most common fossils, whereas the upper strata, where the holotype was found, consist of alternating red beds of cross-stratified and structureless sandstone (Watabe *et al.* 2010). The types of the ceratopsian dinosaur *Udanoceratops tschizhovi* (Kurzanov 1992; Dong and Currie 1993) and *Asiatherium reshetovi* Szalay *et* Trofimov, 1996, a basal metatherian (Rougier *et al.* 1998, 2015; Davis *et al.* 2008; Bi *et al.* 2014), are also from Udan Sayr.

The cross-stratified beds are likely eolian in origin, and the lithology and sedimentary structures of these beds and the structureless sandstones are very similar to exposures of the Djadochta Formation at Bayan Dzag and Ukhaa Tolgod (Gradziński *et al.* 1977; Jerzykiewicz and Russell 1991; Jerzykiewicz *et al.* 1993; Loope *et al.* 1998; Dingus *et al.* 2008), and for this reason previous workers have concluded that the beds at Udan Sayr are also Djadochta Formation (Saneyoshi *et al.* 2008; Watabe *et al.* 2010). The occurrence of two typical Djadochta taxa, *Protoceratops andrewsi* and *Pinacosaurus* sp. at Udan Sayr is consistent with this conclusion (Watabe *et al.* 2010; Handa *et al.* 2012). Preliminary magnetostratigraphic analyses of the Djadochta Formation from Bayan Dzag and Tugrigeen Shiree suggest that this formation was deposited during a period of rapidly changing polarity between 71 to 75 Mya (Dashzeveg *et al.* 2005).

The specimens were collected in friable red sandstones that vary from fine to medium in grain size. As in the Djadochta and Barun Goyot formations, the fossils are frequently complete including, in some instances, articulated specimens of which *Asiatherium* (Trofimov and Szalay 1996) is a good example. Isolated skulls are frequently included in harder carbonate concretions, which often result from the erosion of a partial skeleton. The postcranium associated with the specimen PSS-MAE 141 formed the core of a Ph.D. thesis and has been described elsewhere (Bolortstseg 2008), while PSS-MAE 142 shows portions of the skeleton enclosed in a concretion.

The skull morphology of multituberculates is distinct from that of other mammals and different authors have used various organizational schemes to describe them with a rather elaborate, sometimes incompatible nomenclature (Gidley 1909; Simpson 1937; Kielan-Jaworowska 1971; Kielan-Jaworowska *et al.* 1986, 2002, 2005; Gambaryan and Kielan-Jaworowska 1995; Wible and Rougier 2000; Kielan-Jaworowska and Hurum 2005). We follow the nomenclature of Wible and Rougier (2000) as developed in their glossary, incorporating recent additions by Kielan-Jaworowska *et al.* (2005). The term "Lateral Flange" has been used to denote two slightly different portions of the multituberculate braincase. Kielan-Jaworowska *et al.* (2005) followed earlier usage by Kielan-Jaworowska (1971), against that used by Rougier, Wible and Hopson (Rougier *et al.* 1992, 1996a; Wible and Hopson 1993; Wible and Rougier 2000; Rougier and Wible 2006). Kielan-Jaworowska *et al.* (2005) reported that Wible and Rougier (2000, pp. 40, 94) endorsed the interpretations of Kielan-Jaworowska (1971) of "Lateral Flange"; that is not so. The referred pages, in particular Wible and Rougier (2000, p. 40), are an almost textual use of Hopson's personal communication (Kielan-Jaworowska *et al.* 2005, pp. 488–489) defining his interpretation of "Lateral Flange". Here, "Lateral Flange" refers to the thickened lower edge of the anterior lamina that, in multituberculates, is inturned (medially directed) and contacts the promontorium.

The preliminary comparison and evaluation of the morphological features of the new specimens from Udan Sayr strongly suggest that they are members of Djadochtatherioidea, an endemic Late Cretaceous multituberculate clade of Asia (Rougier *et al.* 1997; Kielan-Jaworowska and Hurum 1997; Kielan-Jaworowska *et al.* 2003), representing fairly derived members of that clade (see analysis below). In fact, these new specimens are similar to *Catopsbaatar catopsaloides* from the classic Late Cretaceous locality of Kheermin Tsav (Kielan-Jaworowska 1994; Kielan-Jaworowska *et al.* 2002, 2005) and to the type of *Tombaatar sabuli* (Rougier *et al.* 1997), a species from the Mongolian Late Cretaceous locality of Ukhaa Tolgod (Dashzeveg *et al.* 1995; Novacek *et al.* 1997). *Tombaatar* was identified by Rougier *et al.* (1997) and Kielan-Jaworowska and Hurum (1997), as closely related to another large LCMM, *Catopsbaatar catopsaloides* (Kielan-Jaworowska 1974, 1994). *Tombaatar*, *Catopsbaatar*, and a third form, *Djadochtatherium* Simpson, 1925 are diagnosed by a relatively large suite of derived characters (Rougier *et al.* 1997; Kielan-Jaworowska and Hurum 1997; Kielan-Jaworowska *et al.* 2002, 2005) that are also present in this new species. Therefore, following Rougier *et al.* (1997) and Kielan-Jaworowska and Hurum (1997, 2001), this study accepts the existence of a group formed by the large-sized LCMM and will discuss the affinities of these specimens in this context.

The specimen PSS-MAE 141 consists of a skull (Figs 2–10), lower jaws (Figs 11–14), and postcranial elements (Bolortsetseg 2008). The skull has been dorsoventrally compressed, resulting in a moderate loss of height and a general oblique deformation of the skull to the left when viewed from the front. Missing are portions of the right zygomatic arch and basicranium. Only remnants of the skull roof elements are pre-

served. The sutures, however, can be followed in most instances. The left lower jaw is nearly complete with full dentition, while the dentary and three teeth are all that remain of the right lower jaw.

A second specimen, PSS-MAE 142, attributed to the hypodigm, is represented by an incomplete skull (Figs 15–18) and postcranial skeleton. The specimen includes a good portion of the rostrum, palate, braincase, fragments of both glenoids, and an isolated right premaxilla. The lower jaws are only partially preserved. The right lower jaw is a fragment showing p3–m2, while on the left only the m2 has been recovered. The postcranium includes most dorsal lumbar vertebrae, an articulated segment of the caudal series, fragmentary shoulder girdle and forelimbs, and nearly complete pelvis and hind limbs.

Institutional abbreviations. — AMNH, American Museum of Natural History, New York, NY, USA; PSS-MAE, Paleontological and Stratigraphic Section (PSS) of the Geological Institute, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; YPM-PU, Peabody Museum of Natural History, Princeton University Collection, Yale University, New Haven, CT, USA; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

SYSTEMATIC PALEONTOLOGY

Class **Mammalia** Linnaeus, 1758

Subclass **Allotheria** Marsh, 1880

Order **Multituberculata** Cope, 1884

Superfamily **Djadochtatherioidea** Kielan-Jaworowska *et* Hurum, 2001

Family **Djadochtatheriidae** Kielan Jaworowska *et* Hurum, 1997

Genus *Mangasbaatar* gen. n.

Type and only species: *Mangasbaatar udanii*, new species.

Etymology: *Mangas*, transliteration from Mongolian: Mangas is a mythological monster of Mongolian folklore; *baatar*, transliteration from the Mongolian for hero, a suffix commonly used to designate Mongolian multituberculates; *udanii*, after the locality Udan Sayr where the specimens were found. Udan: probably a corruption of the Mongolian Ulaan, meaning red: red wash, or gulch, which describes the locality well.

Holotype: PSS-MAE 141, an almost complete skull and jaws (Figs 2–14).

Referred material: PSS-MAE 142, an incomplete skull and jaws associated with a fairly complete postcranium (Figs 15–18).

Locality: Udan Sayr, 85 km northwest of Bulgan-Somon, Umuni Gobi Aimak (southern region), Mongolia, from beds of similar lithology and age as the Barun Goyot Formation.

Diagnosis for monotypic genus and species: Large-sized multituberculate similar to *Tombaatar* and *Catopsbaatar*, but differing from other Late Cretaceous Mongolian Multituberculates in lacking the P2. *Mangasbaatar* shares with *Tombaatar* the proportions of the M1 and a similar cusp formula for the M1 (one extra cusp in each of the rows for *Mangasbaatar*), but differs in the slightly larger skull size, smaller size of the P1, and different M1 to M2 length ratio (1.78 *Mangasbaatar*, 1.46 *Tombaatar*). The M1 in *Mangasbaatar* is proportionately 20% longer than in *Tombaatar*. *Mangasbaatar* resembles *Catopsbaatar*, but differs from *Tombaatar* and *Djadochtatherium*, in having broad flat nasals. The frontals and parietals in *Mangasbaatar* are strongly convex, but less so in *Catopsbaatar* (the condition is unknown in *Djadochtatherium* and *Tombaatar*). The proportionally longer molars in *Mangasbaatar* determine that the root of the zygomatic arch is approximately at the level of the posterior root of the P4/M1 embrasure. *Mangasbaatar* resembles *Catopsbaatar* in this feature, but *Tombaatar*, and probably *Djadochtatherium*, share the primitive condition with the root of the zygomatic arch more anteriorly positioned at the level of the anterior root of the P4. All of the large-sized LCMM share a posterior position for the orbit, a derived feature absent in more generalized LCMM. The ear region of most LCMM lodges large tympanic sinuses. *Mangasbaatar*'s development of these features is extreme and similar to an as yet undescribed specimen of *Tombaatar* (PSS-MAE 60). *Catopsbaatar* has this sinus complex, although it is less developed. In Djadochtatherium the relevant portion of the skull is not known. *Mangasbaatar* shares with other LCMM except *Tombaatar* the premaxilla as the only element forming the alveolus for P3. *Mangasbaatar* shares with *Djadochtatherium* and *Catopsbaatar* the presence of a polygonal p4. It also shares with *Catopsbaatar*, but not with *Djadochtatherium*, an almost vertical anterior wall of the diastema in front of the p3. In *Mangasbaatar* the occlusal plane of the lower teeth forms a low angle to the plane of the bottom of the lower jaw similar to that in *Catopsbaatar*, but different than in *Djadochtatherium*. The p3 still has a more distinctive crown-root junction in *Mangasbaatar*, but it is more "peg-like" in *Catopsbaatar*. *Kryptobaatar*, *Nemegtbaatar* Kielan-Jaworowska, 1970, and *Chulsanbaatar* Kielan-Jaworowska, 1970 retain more primitive conditions for these characters of the lower dentition.
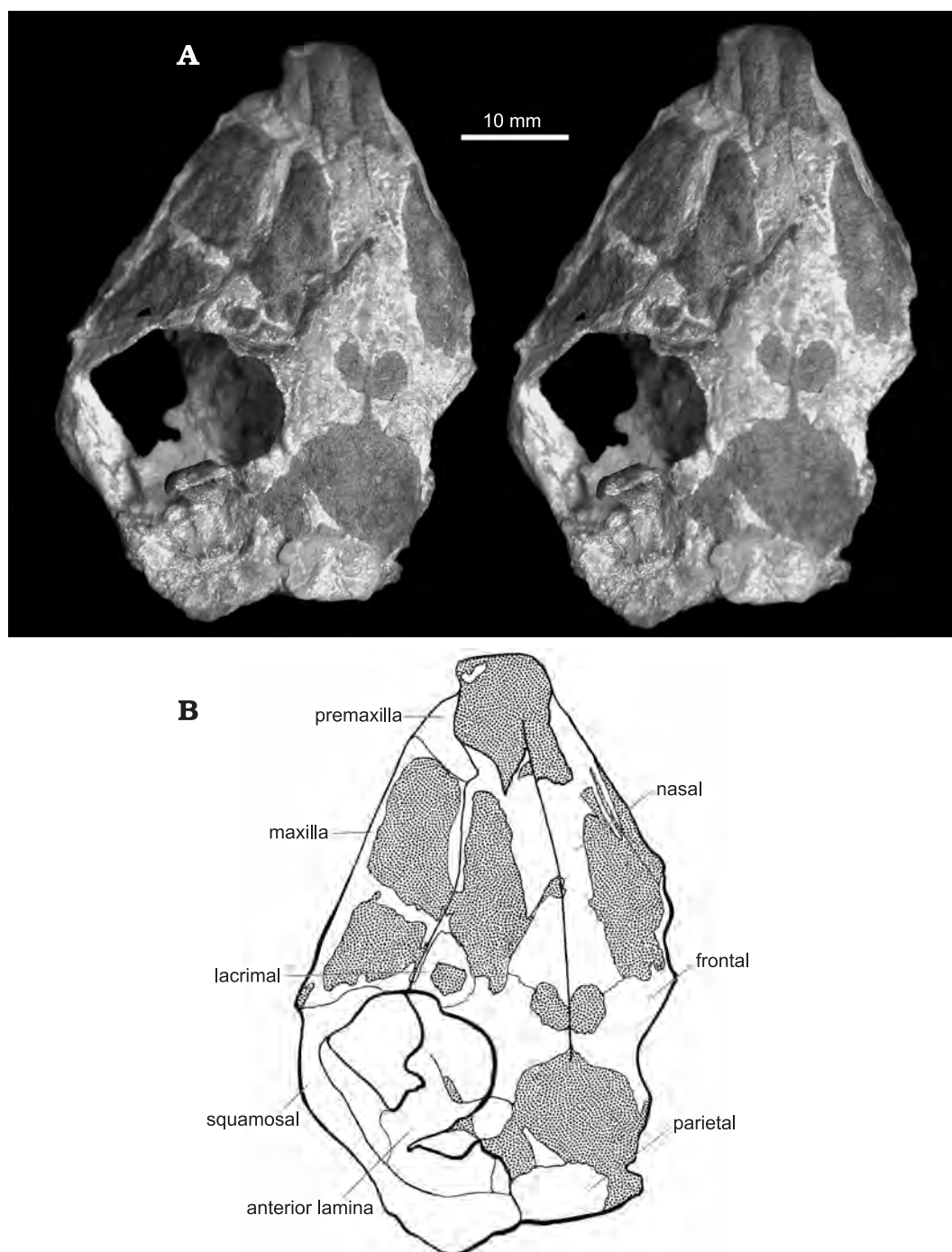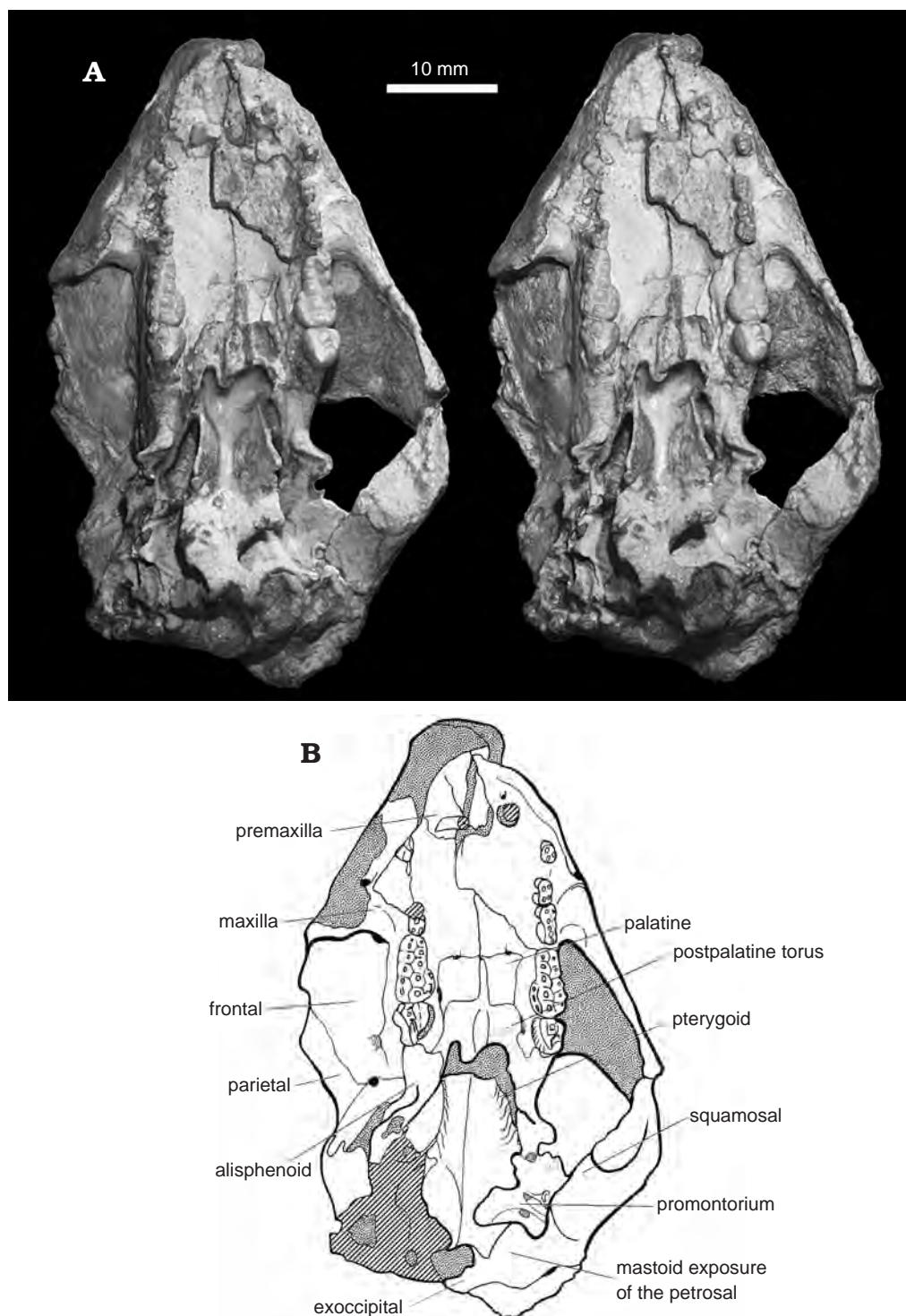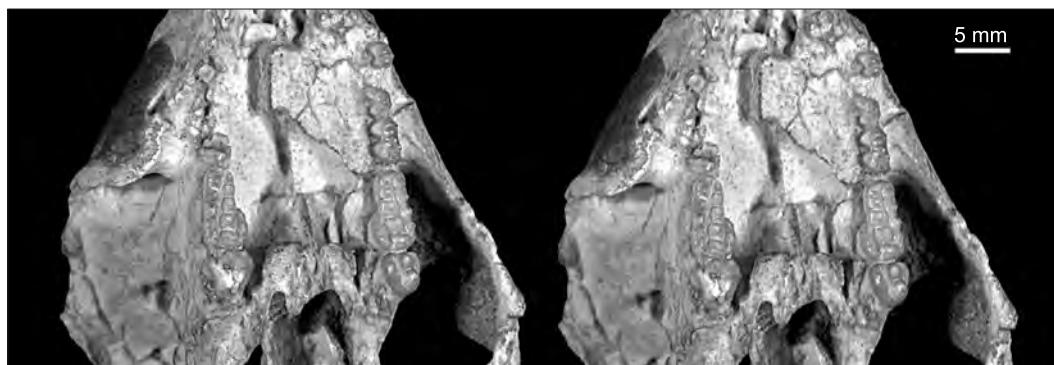
Fig. 2. Holotype of *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 141, Udan Sayr, Late Cretaceous, Mongolia. Stereophotograph of the skull in dorsal view (**A**), and explanatory drawing (**B**). Dotted pattern represents matrix.

DESCRIPTION

General description. — *Mangasbaatar udanii*, with a body mass estimate of 0.879 kg (using formulas by Wilson *et al.* 2012), is one of the largest Late Cretaceous Mongolian multituberculates, and along with *Catopsbaatar* is among the largest mammalian herbivores of the Mesozoic. The two specimens described in this paper are preserved well enough to allow a reconstruction of the skull (Figs 19–22) and jaws (Fig. 23). Presented here is a bone-by-bone description of the skulls and lower jaws of the type specimen, PSS-MAE 141, and the referred specimen, PSS-MAE 142. The postcranial skeleton is described elsewhere (see Bolortsetseg 2008). The type specimen is a young adult with only little wear of the cheek teeth, while the referred specimen is an old adult whose cusps have been worn flat.

Fig. 3. Holotype of *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 141, Udan Sayr, Late Cretaceous, Mongolia. Stereophotograph of the skull in ventral view (**A**) and explanatory drawing (**B**). Dotted pattern represents matrix; parallel lines represent damaged surfaces.

Premaxilla. — The premaxilla is a large bone with both horizontal (palatal) and vertical (facial) processes well developed, forming a substantial portion of the muzzle (Figs 2, 3, 7). The horizontal component forms the anterior portion of the palate and the floor of the nasal cavity. In ventral view of PSS-MAE 141, the point of contact between both premaxillae is obscured by the deformation of this specimen (Figs 3–5). The suture with the maxilla on the rostrum meanders posteromedially from the raised labial margin (*crista premaxillaris* of Kielan-Jaworowska *et al.* 2005). Most of the external surface of the right premaxilla in

Fig. 4. Holotype of *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 141, Udan Sayr, Late Cretaceous, Mongolia. Stereophotograph of the palatal region in ventral view.

PSS-MAE 141 is missing, exposing the broken I2 inside the alveolus. Enough is preserved of the premaxilla however to show that, as in *Tombaatar*, the maxilla extensively overlaps the premaxilla. This feature is also shown by the isolated premaxillae of PSS-MAE 142. The premaxilla lodges the ever-growing I2 that bulges into the nasal cavity.

In ventral view, the premaxilla-maxilla suture does not form the caudal rim of the alveolus for I3, as in *Tombaatar*, but rather runs posterior to this alveolus conforming to the condition present in most members of Djadochtatherioidea. Therefore, the circular alveolus for I3 is fully contained within the premaxilla (Fig. 3). Both alveoli, I2 and I3, are anteroposteriorly aligned along a parasagittal plane. Medial to the I3 alveoli are the large, anteroposteriorly oriented incisive foramina, which are jointly formed by premaxilla and maxilla. As in *Tombaatar*, the premaxilla is perforated by several nutrient foramina anterior to the incisive foramina and there are distinct thickenings of the premaxilla between the alveoli for I2 and I3 (Rougier *et al.* 1997). The crista premaxillaris (Kielan-Jaworowska *et al.* 2005) is well developed, but lacks most of the nutrient foramina seen in *Catopsbaatar*. Only a few are present in PSS-MAE 141 and 142.

The vertical component of the premaxilla, the facial process, forms the lateral wall of the nasal cavity and the lower margin of the external nares. The opening of the nares is oriented directly anteriorly and no indication of a septomaxilla or internarial bar is discernible (Fig. 2), as is found in, for example, the Late Cretaceous multituberculate *Lambdopsalis*. In lateral view, contact with the maxilla is along a rostrally-convex suture posterior to the alveolus of a large I2. A slender posterior process of the premaxilla extends between the maxilla and nasal, ending above P1 (Fig. 7). The narrow extension of the posterior process is similar to *Tombaatar* and *Catopsbaatar* but differs from the blunter process of other members of Djadochtatherioidea.

Maxilla. — The maxilla in multituberculates is a large bone that forms part of the palate, rostrum, and orbital areas. These three portions of the bone define individual processes: the palatal, facial, and orbital, respectively (Figs 3–5, 7, 18). The maxilla contacts the premaxilla anteriorly, the nasals and lacrimals dorsally, and the palatine posteriorly in the palate. Posteriorly in the orbital-temporal area, the maxilla contacts the frontal, the alisphenoid, and possibly the orbitosphenoid. The rostral process of the maxilla is large and is the main bone forming the rostrum. It is convex laterally, reflecting the large size of the maxillary sinuses as seen in multitubereculate serial sections (Kielan-Jaworowska *et al.* 1986; Hurum 1994) and CT scans (Kik 2002; Macrini 2006). This conspicuous lateral bulging of the maxilla gives multituberculates their distinctly triangular-appearing rostrum. The extreme development of this feature is seen in members of Djadochtatherioidea, in which the rostrum and the side of the zygomatic arches become confluent (Rougier *et al.* 1997; Kielan-Jaworowska and Hurum 1997, 2001; Kielan-Jaworowska *et al.* 2004, 2005). The premaxillary-maxillary suture is well preserved only on the left side of PSS-MAE 142 (Fig. 18). The suture forms a long arcuate line that extends posteriorly both at the ventral and dorsal limits. The dominant feature on the rostral process is a large infraorbital foramen that is recessed in a depression and opens into the rostrum at the level corresponding to the diastema between P1 and P3 (Figs 7, 18, 22). The infraorbital foramen is depressed dorsoventrally and its exit forms a deep groove that extends anteriorly under the bulging sides of the maxilla. Thus far, with the sole exception of some specimens of *Catopsbaatar* (Kielan-Jaworowska *et al.* 2005), all LCMM have been described as having only one infraorbital foramen. This is a derived condition shared by all cimolodonts but absent in the Jurassic paulchoffatiids (Simpson, 1928a; Hahn 1985, 1987; Hahn and Hahn 1994). In *Mangasbaatar*, there is a second, small foramen anterior to the main infraorbital

Fig. 5. Holotype of *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 141, Udan Sayr, Late Cretaceous, Mongolia. Stereophotographs of the right and left sides of the palatal region in ventral view detail of the right half of the skull (**A**) and detail of the left side of the skull (**B**).

foramen just described (Fig. 22). This small aperture opens at the level of the P1, or slightly in front of it, and is present bilaterally in PSS-MAE 141 and 142. Given the distribution of the character among the remaining LCMM, it is likely that the presence of this secondary infraorbital foramen in *Mangasbaatar*, and those variably present in *Catopsbaatar*, are a convergence to the primitive morphology. The condition of this character in the closely related *Tombaatar* cannot be ascertained in the type specimen because of the poor preservation of the relevant area, but other available specimens show a single foramen.

The infraorbital canal is broken open on both sides of PSS-MAE 142 so that the communication between the maxillary foramen in the orbit and the infraorbital foramen in the rostrum can be traced. The left side
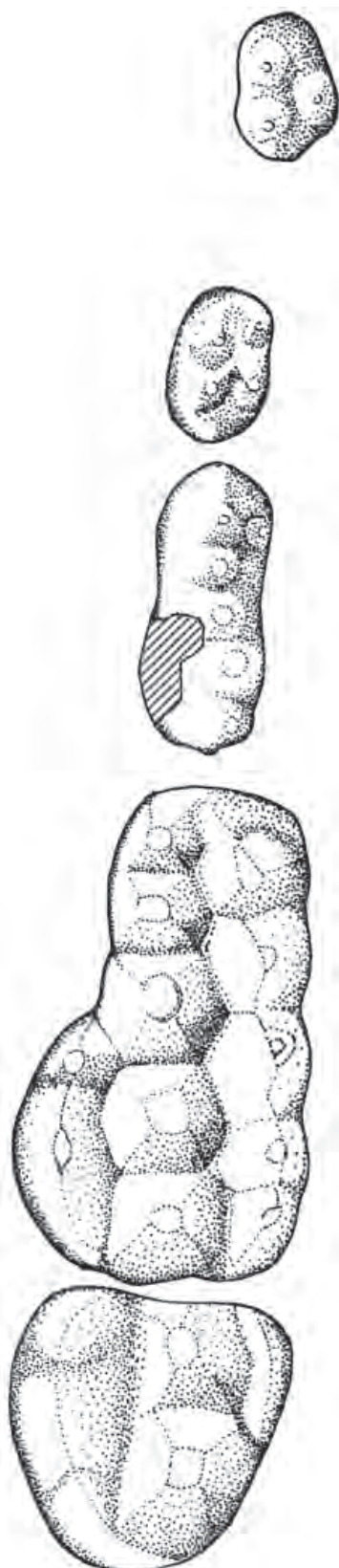
Fig. 6. Holotype of *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 141. Ilustration of the left upper dentition in occlusal view. Parallel lines represent damaged surfaces.

of the specimen has been prepared, revealing several foramina of various sizes that open medially into the interior of the maxilla from the infraorbital canal. These foramina correspond to those described by Rougier *et al.* (1997) in *Tombaatar* and *Djadochtatherium*. These foramina likely correspond to alveolar nerves providing blood and nervous supply to the teeth and maxillary sinus. A similar pattern is known among recent mammals (Sisson and Grossman 1955; Evans and Christensen 1979; Moore and Agur 2002).

The facial process of the maxilla in PSS-MAE 142 is well preserved and shows numerous small nutrient foramina perforating the substance of the bone. A distinctive pattern of small ridges and rugosities mostly oriented anteroposteriorly are present on the lower half of the facial process indicating the area of attachment of superficial facial musculature. The *m. buccinatorius* is, most likely, responsible for the scars mentioned above; this muscle would extend posteriorly to reach the mesial edge of the anterior zygomatic ridge (Fig. 22) for the *pars anterior musculi masseteris superficialis* (see below).

The facial process continues posteriorly to form, together with the lacrimal, the anterior edge of the orbit. As in all other LCMM, *Mangasbaatar* lacks a distinct floor for the orbit, and the maxilla shows inside the orbit a well-developed orbital pocket (Figs 3–5, 16, 17) that extends anteriorly beyond the level of the orbital ridge (Kielan-Jaworowska *et al.* 1986; Gambaryan and Kielan-Jaworowska 1995; Wible and Rougier 2000). This orbital pocket, an important component of the orbital cavity, accounts for approximately one-third of the length of the preorbital region of *Mangasbaatar*. The root of the zygomatic arch marks the anterior extent of the orbital pocket. The zygomatic process of the maxilla is broad, originates at the level of the embrasure between P4 and M1, and extends backward to contact the zygomatic process of the squamosal at roughly the lowest point of the orbit. The dorsal edge of the zygomatic process is concave-convex determining a very peculiar orbital outline (Figs 7, 22), shared with *Tombaatar*. The area forming the orbital edge on the zygoma is slightly convex, becoming concave posteriorly, towards the maxillo-squamosal suture; this arrangement results in a very slender posterior portion of the zygoma. The great height of the zygomatic arch produces a relatively small, dorsally located orbit, positioned in the posterior half of the skull.

Between the root of the zygoma, the infraorbital foramen, and P1–P4, there is a flat area that forms a distinct platform on the lateral surface of the maxilla and dorsal to the teeth. A sharp ridge, the anterior zygomatic ridge, divides this platform. The anterior zygomatic ridge ends directly lateral to the anterior root of P4 and extends posteriorly into the zygoma (although the exact distal extension cannot be determined because of insufficient preservation). Enough is preserved in isolated maxilary fragments of PSS-MAE 142 to show that the ridge is well developed with a lightly rugose apex. What is preserved of the anterior zygomatic ridge conforms to the morphology present in other LCMM, but is longer and narrower than that present in *Catopsbaatar* (Kielan-Jaworowska and Hurum 2005).

In ventral view, the palatal process of the maxilla is preserved in both PSS-MAE 141 and 142 (Figs 3–5, 16, 17). Nevertheless, both specimens are broken and parts of the palate have been displaced and asymmetrically deformed. The result of this deformation is that right and left elements are not always aligned. The sutures are better shown by PSS-MAE 141, but PSS-MAE 142 conforms quite closely to the pattern of the type. The maxillary contribution to the incisive foramina is not well preserved in either
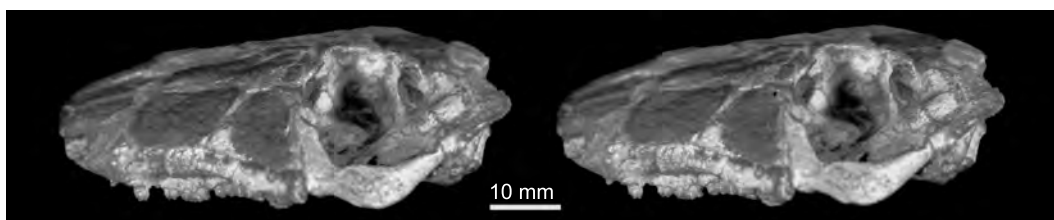
Fig. 7. Holotype of *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 141. Stereophotograph of the left side of the skull in lateral view.
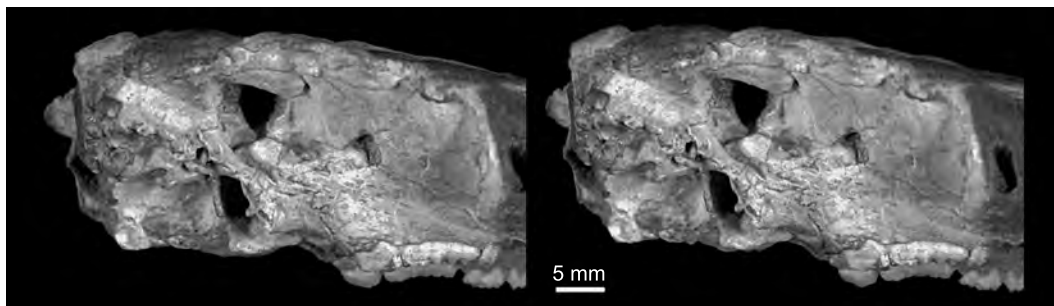

Fig. 8. Holotype of *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 141. Stereophotograph of the right ear region in lateral view.

specimen, though it seems limited to the posteriormost edge of the apertures. The contact of the skull between the premaxilla and maxilla in this region has already been described but, in addition, along the suture on the right side of both PSS-MAE 141 and 142, there is a medium-sized foramen in the suture right behind I3. The anterior portions of the palatine processes of the maxillae are moderately concave, becoming more so posteriorly. This change in curvature of the maxilla is so pronounced that the palate can be considered almost flat at the level of P1 but very deep at the level of M1.

The maxilla contacts the subrectangular exposure of the palatine approximately at the level of the middle of M1 (Figs 5, 17). The contact between maxilla and palatine is made through an inverted L-shaped suture with an anterior transverse component and a posterior parasagittal component. A large foramen can be distinguished at the lateral extent of the transverse suture between the maxilla and the palatine bones. It is the major palatine foramen that grooves the maxilla only in the immediate vicinity of the opening. The foramen probably transmitted the major palatine artery and nerve that in modern mammals supply the roof of the mouth, to finally anastomose with the arteries and nerves reaching the incisive foramen from the nasal cavity, likely branches of the sphenopalatine artery and nasopalatine nerve.

The longitudinal portion of the maxillary-palatine suture runs close to the M2 and the posterior portion of M1. Along the longitudinal portion of this suture, there is a slit-like foramen, interpreted here as the minor palatine foramen, that opens in front of the M2. Kielan-Jaworowska *et al.* (2005) followed earlier interpretations (Kielan-Jaworowska *et al.* 1986) and identified the slit-like foramina, here identified as minor palatine foramina (following Wible and Rougier 2000), as a deep pocket called "palatonasal notch". Examination of CT scans of *Kryptobaatar* skull PSS-MAE 101 reaffirms the interpretation of Wible and Rougier (2000) and is thus followed here for *Mangasbaatar* (Fig. 22).

The maxilla has no contribution to the transverse aspect of the palate along the sagittal suture with the palatine. The maxilla is restricted to the bone immediately around the roots of the molars, the alveolar process. Immediately behind the M2, the maxilla contacts the alisphenoid through a sharply serrated suture (Figs 5, 9, 10, 20, 21).

The maxilla is extensively exposed in the orbitotemporal region (Figs 7, 18, 22); its orbital portion is broad and flat with the ascending process forming the medial wall of the orbit and contacting dorsally the lacrimal. The fronto-maxillary suture is extensive and runs obliquely from the anterodorsal aspect of the orbit to the sphenopalatine foramen, which occupies a posteroventral position in the orbit. After reaching the sphenopalatine foramen, the fronto-maxillary suture becomes approximately horizontal and runs posteriorly along the floor of the temporal area toward the sphenorbital fissure. In the deeper part of the temporal area, the frontal is replaced by the orbitosphenoid in its contact with the maxilla. The maxilla also contacts the alisphenoid in the floor of the temporal region. The suture between these two elements is well shown
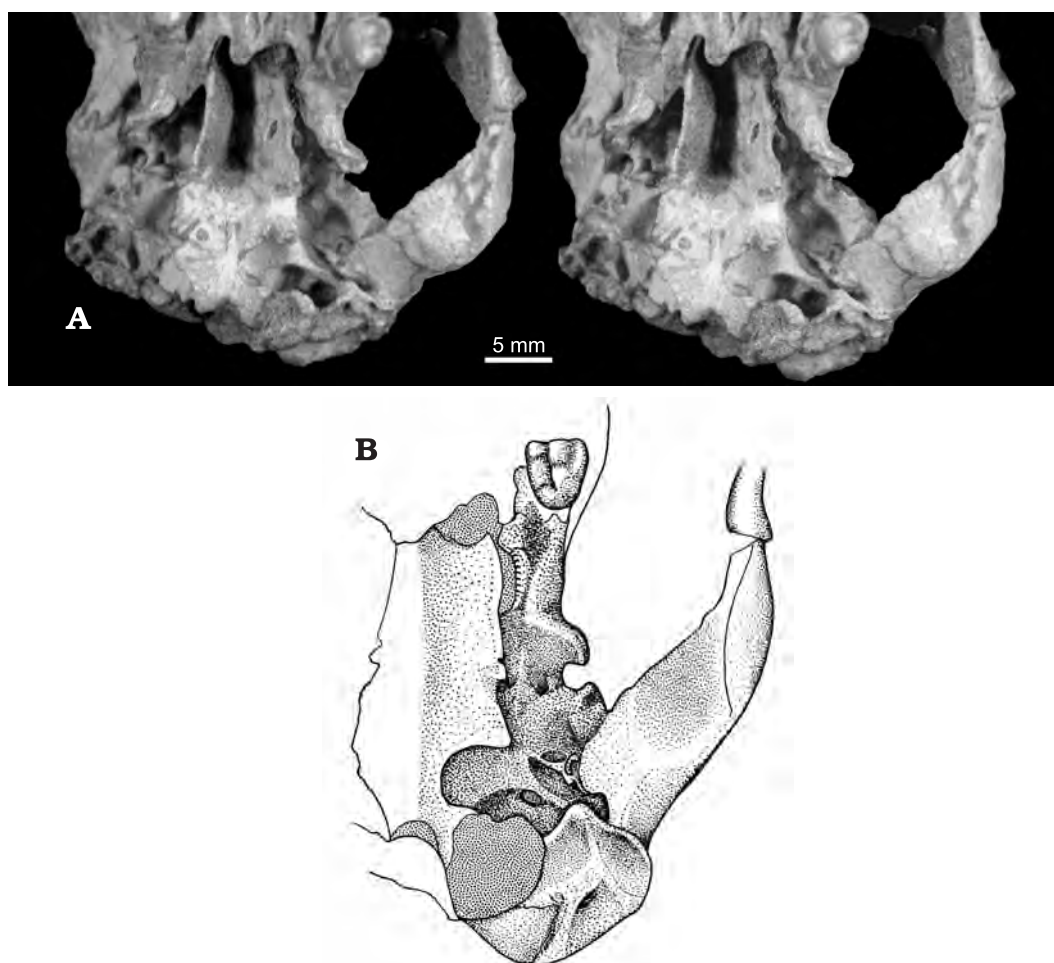
Fig. 9. Holotype of *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 141. Stereophotograph of the basicranium in ventral view (**A**) with explanatory drawing (**B**).

by PSS-MAE 142 (Fig. 18). This serrated contact runs from immediately behind M2 to the lateral edge of the sphenorbital fissure. It follows, from the above-described contacts with the maxilla, that a prong of this bone is wedged between the alisphenoid, frontal, and probably the orbitosphenoid in the floor of the tempo-ral area. This wedge of the maxilla forms a platform, originating in the vicinity of the sphenorbital fissure, which opens and broadens anteriorly to become continuous with the orbital contribution of the maxilla.

The sphenopalatine foramen is large, with a "dumb-bell" shape, and incompletely divided in half by a process that is well preserved only in the right side of PSS-MAE 142 (Fig. 18); the two areas likely repre-sent a proper sphenopalatine foramen and a confluent caudal paltine foramen. The sphenopalatine foramen transmits the sphenopalatine artery and nerve, and the major palatine nerve and artery. Following the pattern in extant mammals (Evans and Christensen 1979), the former pair will occupy the anterodorsal subdivision of the sphenopalatine foramen on its way to the nasal cavity, while the latter pair would occupy the larger posteroventral subdivision of the sphenopalatine foramen on its way to the palate. Along the maxillo-frontal suture on the floor of the orbitotemporal region, there is a broad surface, the sphenopalatine groove, which leads to the sphenopalatine foramen.

As in *Kryptobaatar* (Wible and Rougier 2000) and *Tombaatar* (Rougier *et al.* 1997), there is a small foramen, posteroventral to the sphenopalatine foramen, which transmits the minor palatine nerve and com-panion vessels from the orbit into the minor palatine foramen of the hard palate. This foramen is preserved only on the right side of PSS-MAE 141 (Fig. 8). In the type specimen of *Tombaatar*, the orbital entrance of the minor palatine nerves and vessels and the minor palatine foramina are connected by a groove on the maxilla that is open to the choanae, and therefore leaves no doubts that the "palatonasal notch" transmitted a structure to, or from, the orbit to the palate; the status of this feature is *Mangasbaatar* cannot be ascertained.
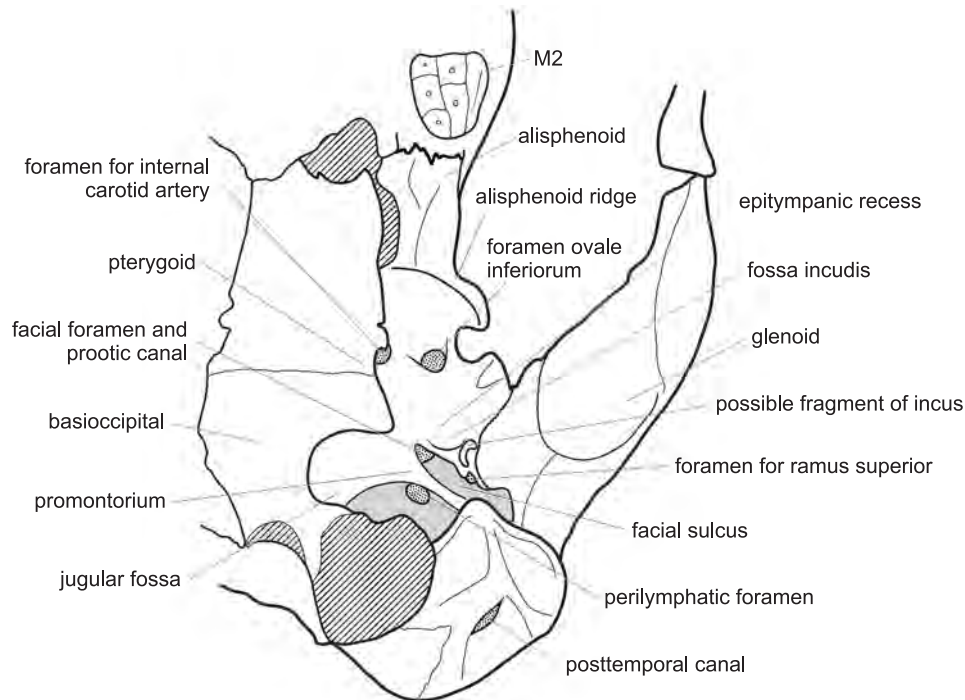
Fig. 10. Holotype of *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 141. Line drawing of the basicranium in ventral view. Light shaded area, common space of the middle ear, eustachian tube, epitympanic recess and exit of V3 branches. Dark shaded area represents a postpromontorial tympanic sinus divided by the crista interfenestralis.

Palatine. — The palatine is well preserved in both PSS-MAE 141 and 142 (Figs 3–5, 16, 17). In *Mangasbaatar* the palatine is exposed only in the palate. There is no orbital exposure of this bone as in most other LCMM, with the possible exception of *Nemegtbaatar* (Hurum 1998a). Right and left palatines meet in the sagittal plane to form a sharp median crest that preserves an open suture throughout its length. The crest becomes taller posteriorly where it meets the robust postpalatine torus. The palatine is essentially flat between the median crest and its lateral contact with the maxilla.

Bordering the ventrolateral margin of the choanae is a massive postpalatine torus (Figs 5, 17). This is an unusually complex structure that resembles that of *Tombaatar*. The torus begins anteriorly at the level of the M1–M2 embrasure, where it rises abruptly from the palate. The torus is formed by two distinct wings, right and left, which project ventrally to the level of the occlusal plane. The wings are concave posteriorly and are limited medially by two sharp crests that result from the bifurcation of the median crest described above in the anterior portion of the palatine. Between these two crests that form the medial edge of the wings of the torus there is a deep recess occupying the midline. The function of this elaborate torus in *Mangasbaatar* is uncertain. The posterolateral corner of the torus extends posteriorly on the sides of the choanae through a "splint"-like process directly medial to the alisphenoid. This posterior extension of the palatine into the choanae is preserved only in PSS-MAE 141.

Nasal. — The nasals are large paired bones that form the roof of the nasal cavity. They are in contact with each other medially, with the premaxillae and maxillae laterally, and with the frontals posteriorly (Figs 2, 15, 19). Erosion of the dorsal surface of PSS-MAE 141 has destroyed most of the nasals, leaving the crest and sutures that projected into the nasal cavity. The overall features of the nasal are preserved mostly as natural molds. Enough remains, however, to show that the nasals become broader posteriorly and are overlapped by the frontals.

In PSS-MAE 141 (Fig. 2), the dorsal surface of the nasal cavity and the paranasal sinuses are exposed because of missing nasals and maxilla. Along the suture between nasal and maxilla, there is a ridge of bone that projects ventrally into the nasal cavity. This roughly parasagittal ridge is the remnant of the nasoturbinal ridge. Throughout its length, the nasal seems to be mostly cancellous bone with only a thin, dense layer of cortical bone. Based on natural endocasts (Rougier and Novacek 1997) and CT scanning of other Mongolian multituberculates like *Kryptobaatar* (PSS-MAE 101), it is likely that those intranasal cavities were con-
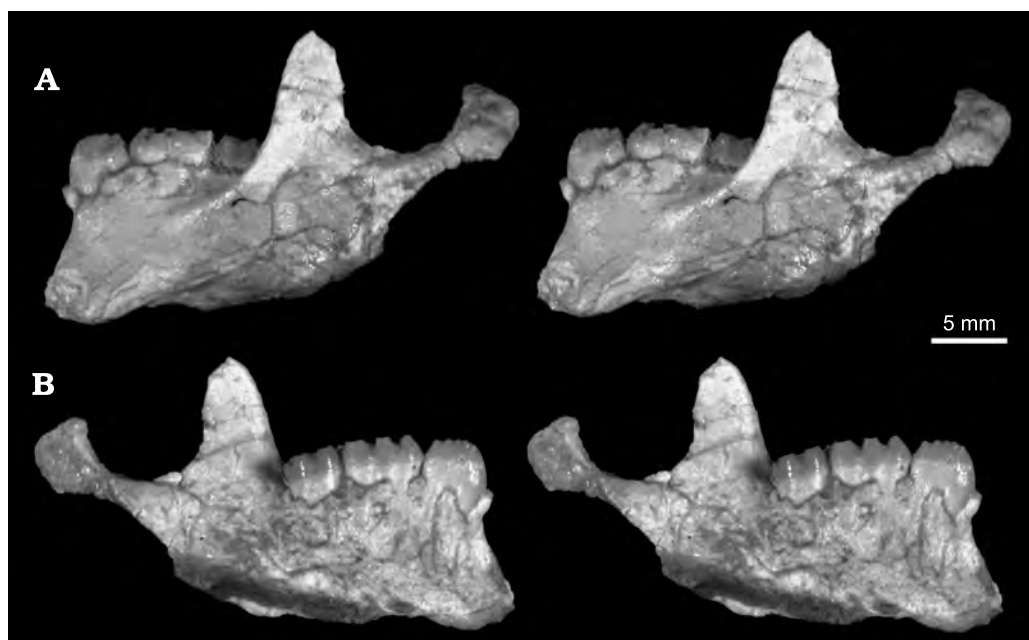
Fig. 11. Holotype of *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 141. Stereophotographs of the left dentary in buccal (**A**) and medial (**B**) views.

nected to the nasal cavity, indicating an extreme degree of pneumatization of the multituberculate skull. The great development of pneumaticity is frequently reflected by the preservation of the specimens. When found as isolated specimens, the skulls are often missing the thin cortical bone forming the outer surface of nasals, frontals and parietals.

In the specimen PSS-MAE 142 (Figs 15, 18), the posterior one-third of the right nasal is well preserved, as is a small portion of the left nasal. Along the midline, right and left nasals are separated by a broad prong of the frontals that extends anteriorly at about the level of the lacrimal. This process of the frontal and the concomitant separation of the back part of the nasals is a primitive feature for mammals, present in various degrees almost universally among Mesozoic forms. *Catopsbaatar* has a more transverse nasal-frontal suture than most other LCMM (Kielan-Jaworowska *et al.* 2005). Not enough is preserved to determine the number of nasal foramina, but judging from the natural endocast it is likely that at least one relatively large foramen was present.

Lacrimal. — Portions of the lacrimal are preserved in both specimens, the most complete being the right side of PSS-MAE 142 (Figs 15, 18, 19, 22). The external exposure of the lacrimal is subrectangular and is wedged in the orbital margin between frontal and maxilla. The nasal contacts the lacrimal along its anteromedial edge. The lacrimal contribution to the orbital mosaic cannot be fully ascertained, but it is clear that it was restricted to the dorsal portions of the orbit without extensive ventral projection. The lac-

rimal was, however, involved in the formation of a very deep orbital pocket and sharp orbital ridge for the attachment of the anterior portion of the anterior portion of the superficial masseter muscle (Gambaryan and Kielan-Jaworowska 1995). Remnants of a bifid nasolacrimal canal are present on the right side of PSS-MAE 142 and most of its course can be traced through the denuded skull roof of the left side of PSS-MAE 141.

Frontal. — Most of the contribution of the frontal to the skull roof is missing in PSS-MAE 141 (Fig. 2); however, the orbital portions of this bone are well preserved (Figs 7, 8). The right frontal in PSS-MAE 142 is mostly complete (Fig. 15). Sutures in the skull roof are well shown by PSS-
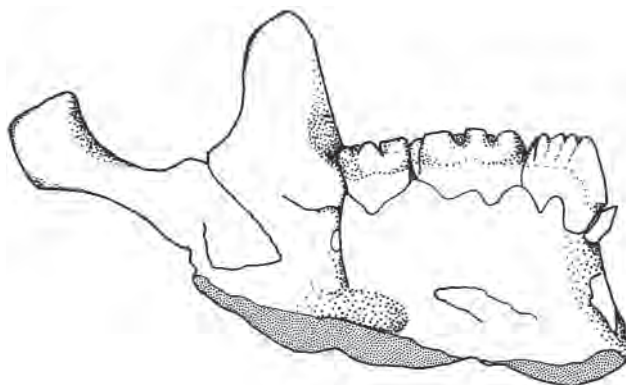
Fig. 12. Holotype of *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 141. Illustration of the dentary in medial view.
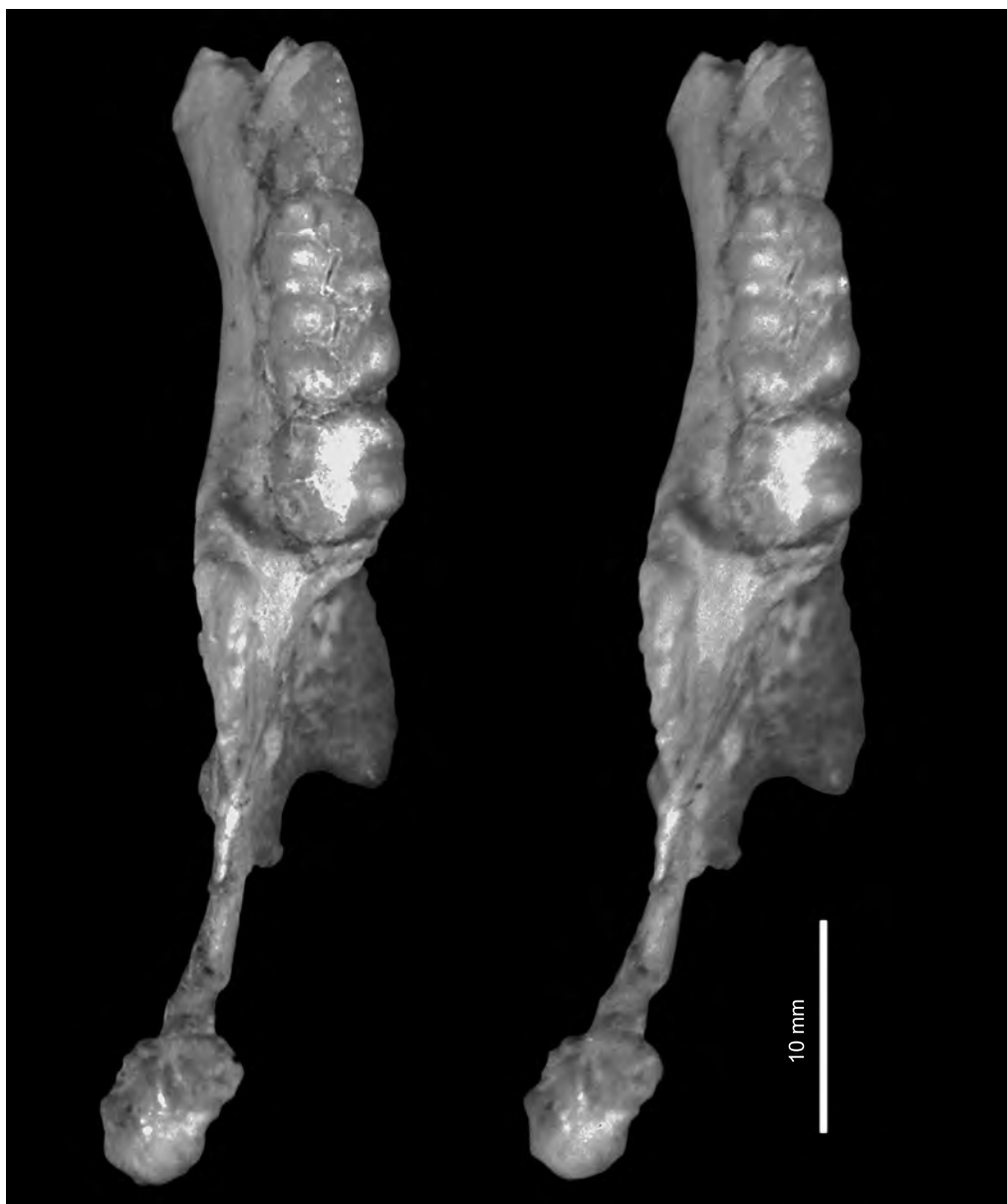
Fig. 13. Holotype of *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 141. Stereophotograph of the dentary in occlusal view.

MAE 142 but those in the orbit are somewhat ambiguous in both specimens, especially in the area near the sphenorbital fissure. The frontal is the largest component of the skull roof and extends roughly from the level of the anterior root of M1 until the posterior one-third of the braincase. This moderately convex bone is slightly raised in the midline where it contacts the frontal from the other side via an open suture. Anteriorly, the frontal is wedged between the nasals and anterolaterally contacts the lacrimal. The parietal demarcates the posterior expansion of the frontal. The frontals contact the parietals through a broad V-shaped suture extending from just in front of the postorbital process backwards (Fig. 15). The frontal forms the dorsal-most portion of the rugose orbital edge. The lateralmost extension of the dorsal orbital rim is damaged in both specimens; however, the right side of PSS-MAE 142 may preserve some evidence of this feature.

In the orbit (Figs 8, 18, 22), the frontal forms most of the posteromedial wall, contacting the orbitosphenoid throughout much of its length and reaching the dorsal-most aspect of the anterior lamina through a narrow process. The frontal-orbitosphenoid suture forms a gentle arch from the floor of the orbitotemporal region to the dorsal portion of the anterior lamina. Approximately in the middle of this arch, there is a large foramen formed jointly by frontal and orbitosphenoid, the ethmoidal foramen; grooves from above and below the foramen lead to it. The one from below, the larger of the two, starts in the sphenopalatine groove and through a
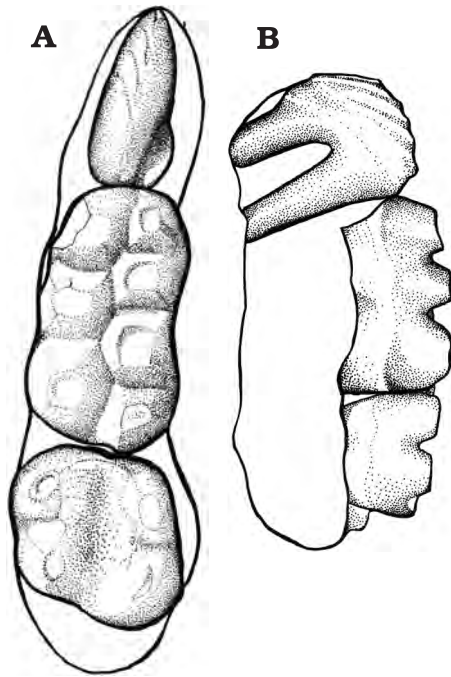
Fig. 14. Holotype of *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 141. Illustrations of the lower dention in occlusal view (**A**) and fragment of the right dentary in lateral view (**B**).

gentle curve reaches the ethmoidal foramen from directly below. This groove follows the likely course of the frontal-orbitosphenoid suture in the area and it was likely occupied by the ethmoidal nerve and artery. The groove reaching the ethmoidal foramen from above has a sigmoid shape and is developed mostly above the frontal-orbitosphenoid suture, in the frontal. This groove is continuous with the anterior opening of the orbitotemporal canal, which is broken open on both sides of PSS-MAE 141. The rostral end of the orbitotemporal canal is formed mostly by the frontal and is completed by the parietal, which forms its roof. The likely occupant of this groove was a large orbitotemporal artery and its accompanying vein. A similar pattern is known in most LCMM including *Kryptobaatar* (Wible and Rougier 2000). The anterodorsal portion of the frontal contributes to the orbital ridge and orbital pocket, which is jointly formed by maxilla, lacrimal, and frontal.

Parietal. — The parietal has been mostly eroded away in PSS-MAE 141 (Fig. 2) but most of it is preserved in the right side of PSS-MAE 142 (Fig. 15). The parietal contributes to the posterior one-third of the braincase and helps separate the orbit from the temporal area by forming a postorbital process. The parietal contacts the frontal anteriorly, through the already described broad "V"-like suture anteroventrally with the anterior lamina, posteroventrally with the squamosal, and posteriorly with the supraoccipital. The parietal is slightly convex dorsally. This feature becomes more pronounced laterally than in the midline. Right and left parietals are separated by a suture that is difficult to trace because of partial fusion between these bones.

Temporal lines, for the attachment of the temporal muscle, are present but are not very sharp and they do not meet each other to form the sagittal crest. Instead, they contact the lambdoidal crest parasagittally. The temporal lines originate from the posterior edge of the postorbital process and extend posteromedially forming a broad arch. The relatively lateral position of the temporal lines implies a proportionally small area for the temporalis muscle, much smaller than that in other forms with a sagittal crest such as *Kryptobaatar* (Wible and Rougier 2000).

The parietals are the sole elements forming the median portions of the lambdoidal crests (*i.e.*, there is no supraoccipital participation). These crests are minimally developed sagittally but flare out and become quite large laterally. This development of the lambdoidal crests begins on the lateral portions of the parietal contribution to these crests and becomes more pronounced in the squamosal/petrosal portion of the crests.

As in all the other LCMM, the postorbital process is formed in its entirety by the parietal. It is preserved in its full length only on the left side of PSS-MAE 141 (Fig. 2). The process is inordinately long at 10.2 mm (measured from the root of the process). A very long process of similar dimensions is present in *Catopsbaatar* (Kielan-Jaworowska 1974, 1994), another large LCMM probably related to both *Tombaatar*, and *Mangasbaatar* (Rougier *et al.* 1997; Kielan-Jaworowska and Hurum 1997).

At the base of the postorbital process is the external opening of the orbitotemporal canal, which has already been described as being formed jointly by the frontal and parietal. The orbitotemporal canal is open internally into to the braincase as shown by the endocast of the skull PSS-MAE 141. The parietal forms the roof of the canal but the canal has no floor and is open internally into the cranial vault, until it reaches the petrosal in the back portion of the braincase (see below).

Squamosal. — The squamosal has sustained damage in both specimens, but the one on the left side of PSS-MAE 141 is the most complete (Figs 2, 7). The squamosal can be subdivided into two portions: the squama abutting the braincase, and the zygomatic process contacting the maxilla and bearing the glenoid fossa. The squamosal contacts the maxilla anteriorly, the petrosal medially, and the parietal dorsally.

As in all other multituberculates, the zygomatic arch is formed mostly by the squamosal and the maxillary bone, with a reduced jugal on the medial side of the zygoma (Hopson *et al.* 1989; Wible and Rougier 2000,
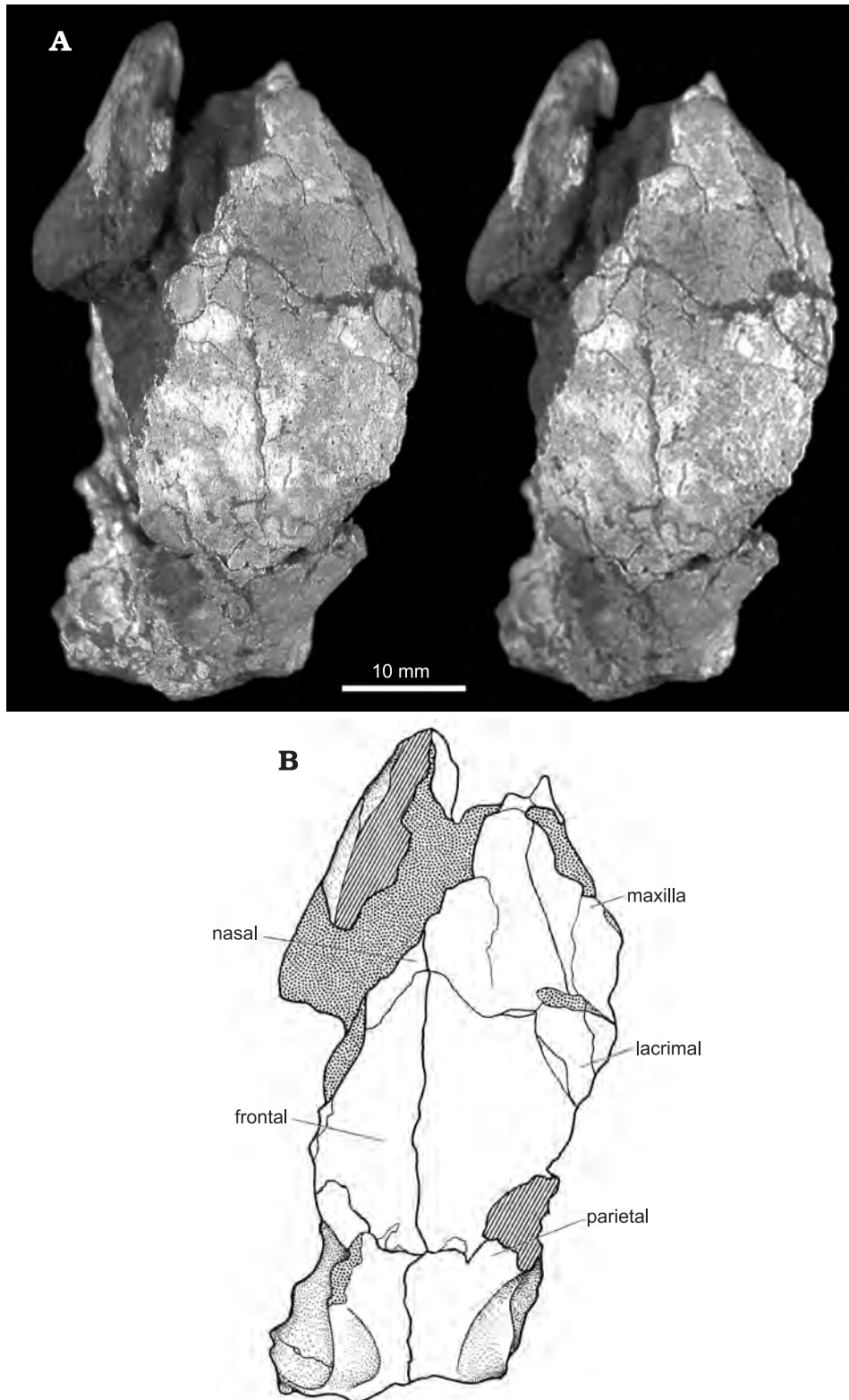
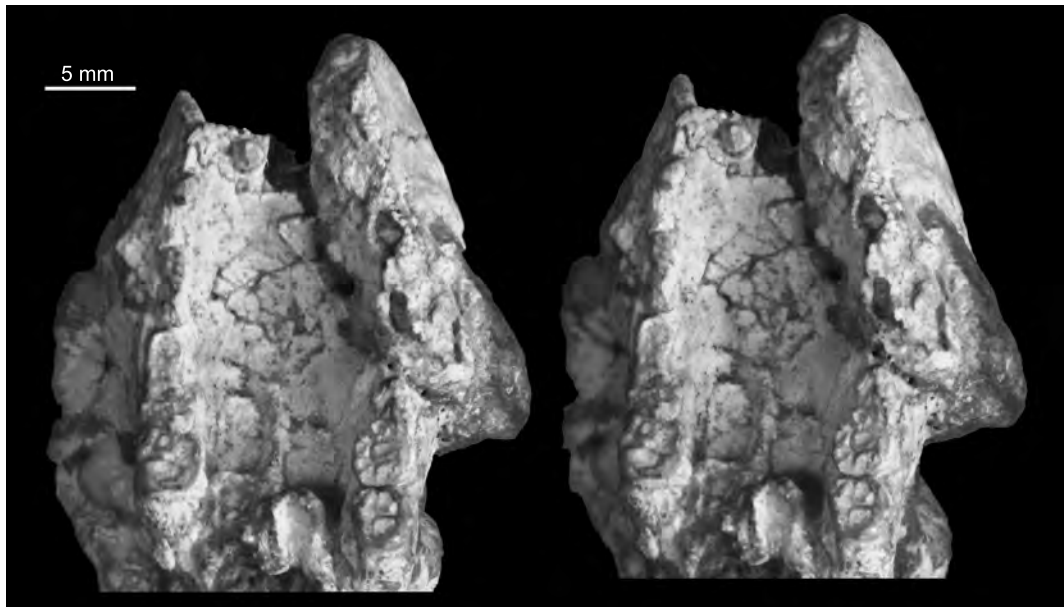Fig. 15. *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 142. Stereophotograph of the skull in dorsal view (**A**) and explanatory drawing (**B**). Dotted pattern represents matrix; parallel lines represent damaged surfaces.

fig. 32), or sole by these two bones, without the jugal. In *Mangasbaatar*, due to the posterior location of the orbit, the zygomatic arch is very short and throughout its length forms the ventral edge of the relatively small orbitotemporal fossa, characteristic of LCMM (Fig. 22). In other LCMM, a very small jugal has been described as occupying the medial surface of the arch (Hopson *et al.* 1989; Wible and Rougier 2000), but preser-
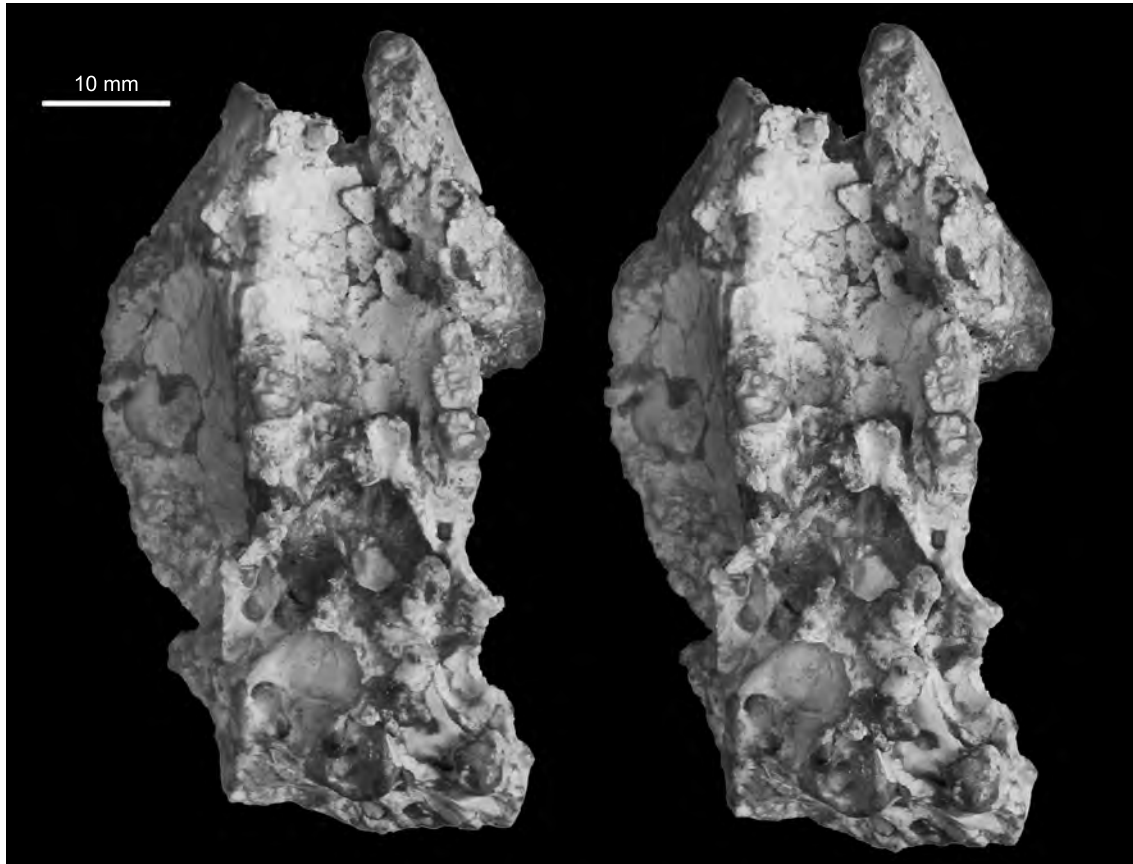
Fig. 16. *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 142. Stereophotograph of the skull in ventral view.

Fig. 17. *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 142. Stereograph of the palatal region in ventral view.

vation in PSS-MAE 141 and 142 is not sufficient to confirm or deny the presence of this element. The contact of the squamosal with the maxilla occurs through a relatively long and oblique suture seen on the left side of PSS-MAE 141 that reaches anteriorly to the level of the anterior edge of the orbit. The shape of the anterior portion of the zygomatic process is very conspicuous and characteristic of *Mangasbaatar* and *Catopsbaatar* (*Tombaatar* unknown); unlike other LCMM the squamosal achieves its maximum dorsoventral development at the posterior end, achieving a greater height than the lowest part of the zygomatic process.
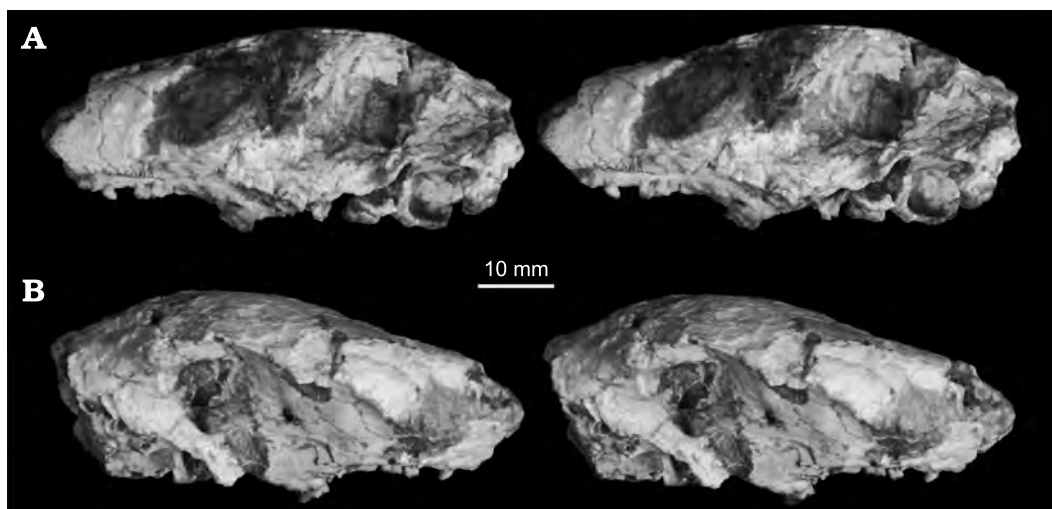
Fig. 18. *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 142. Stereophotographs of the skull in lateral view from the right (**A**) and left (**B**) sides.

Most of the lateral surface of the very short zygomatic process of the squamosal is occupied by a concave surface limited dorsally by a blunt ridge. This is the intermediate zygomatic ridge, which might marginally extend into the maxillary's contribution to the zygomatic arch. Behind the intermediate zygomatic ridge, the squamosal becomes narrower and more robust, forming a neck connecting the glenoid with the braincase. The glenoid is best seen in ventral view (Figs 3, 9, 10, 20, 21) and is teardrop-shaped with its broader portion oriented posteriorly. There is no post-glenoid ridge, but a broad crest continuous with the lower edge of the zygomatic arch marks the lateral extent of the glenoid. The articular surface is mostly flat, with a shallow anterior concavity.

Behind the glenoid, the squamosal neck forms a flat area that ultimately becomes continuous with the epitympanic recess of the petrosal. The medial extension of the neck reaches the braincase, broadens slightly and becomes the squama of the squamosal. The squama overlies the petrosal and does not contribute directly to the braincase proper. The anterior extension of the squama is limited by its contact with the anterior lamina of the petrosal. The suture between these two elements is not very clear in any of these specimens, but it is best on the left side of PSS-MAE 141. The right squamosal of PSS-MAE 142 (Fig. 18) is completely lost, exposing its contact with the underlying petrosal. This specimen shows that the squamosal forms the lateral and dorsal walls of the ascending canal as described in *Kryptobaatar* and *Vincelestes* (Rougier *et al.* 1992; Wible and Rougier 2000). The squama of the squamosal also forms part of the ventrolateral portion of the lambdoidal crest overlying the mastoid exposure of the petrosal.

Pterygoid. — The area of the skull presumed to be formed by the pterygoids is preserved only in PSS-MAE 141 (Figs 3, 9, 10) but no sutures are visible in the specimen. This is not to say that sutures were not present, but fractures make recognition of them difficult. In order to describe these elements
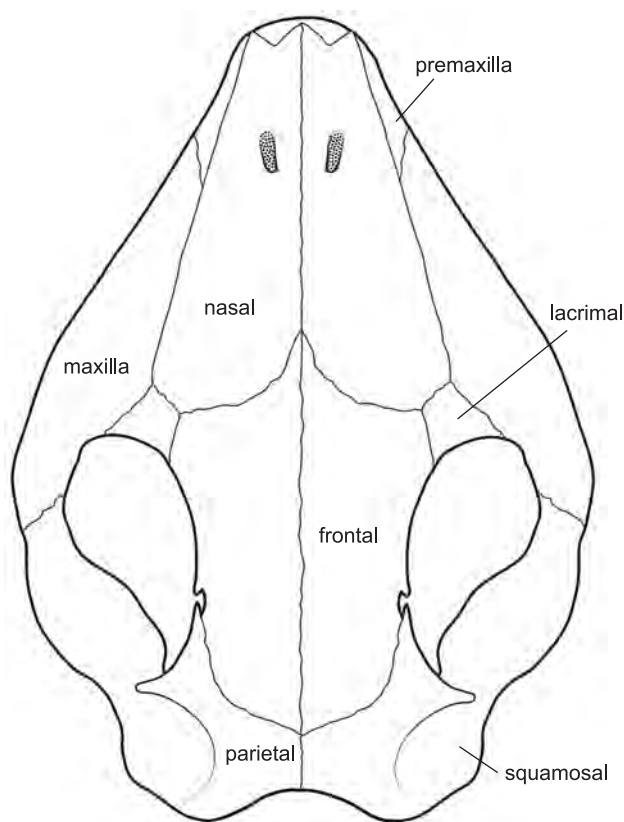
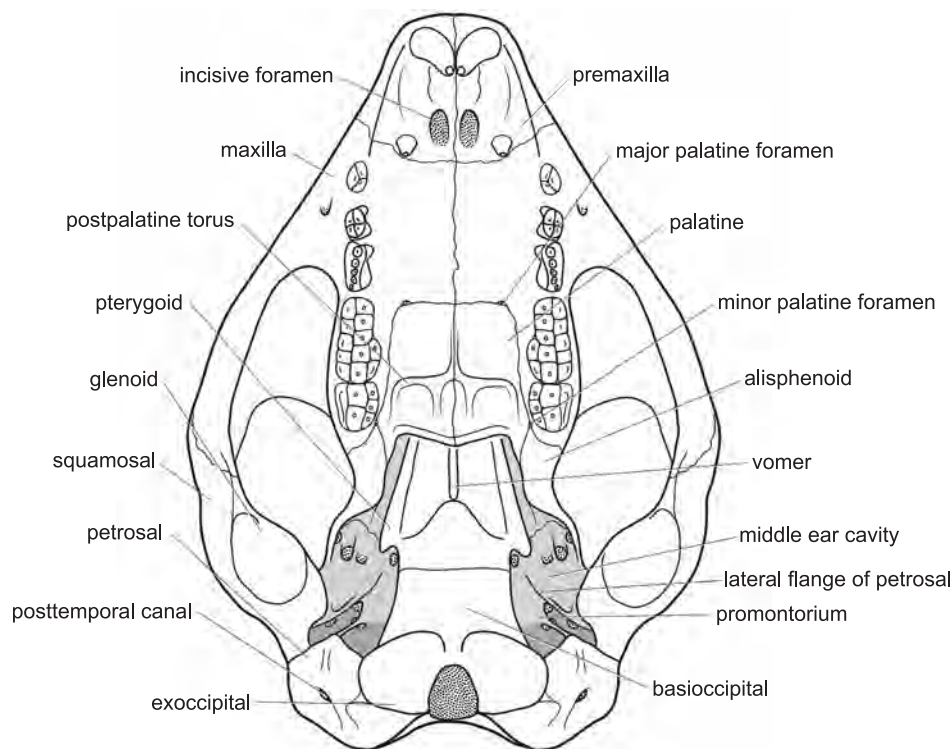Fig. 19. Reconstruction of the skull of *Mangasbaatar* in dorsal view.

Fig. 20. Reconstruction of the skull of *Mangasbaatar* in ventral view.

in *Mangasbaatar*, particular reference is given to the morphology present in other LCMM. Specifically, the pterygoids are interpreted as forming the two tall, parasagittal flanges present in the choanae following a similar pattern as seen in *Kryptobaatar* (Wible and Rougier 2000). There is a suture at the level of the posterior extent of the pterygoids connecting right and left elements. Behind this suture and between the flanges of the pterygoids there is a triangular element on the roof of the choanae interpreted as the basisphenoid. If this interpretation is correct the pterygoids would meet along the midline, in front of the vomer, and they would be separated by the latter along the posterior one-third of their length.

The pterygoid flanges are tall and subdivide the choanae into three passages: a broad median palatine groove, between right and left laminae, and two lateral palatine troughs, between the pterygoid lamina and the lateral walls of the choanae formed by the alisphenoid. In other multituberculates, like *Chulsanbaatar*, *Nemegtbaatar* (Kielan-Jaworowska 1971; Gambaryan and Kielan-Jaworowska 1995) and *Kryptobaatar* (Wible and Rougier 2000) the medial passage is partially subdivided in two by the mid-line vomers and therefore a total of four channels are present. The full anterior extent of the pterygoid laminae cannot be traced into the choanae because the left one is incomplete and the right one is obscured by matrix. The lamina ends posteriorly in a short, rounded process separated from the main portion of the lamina by a shallow notch. This notch and process are likely to be homologous to the hamular process, serving as a "pulley" for the *m. tensor veli palatini*, a muscle originated from the primitive pterygoid musculature of non-mammalian cynodonts (Barghusen 1986).

In the lateral palatine troughs, which are between the pterygoid laminae and the walls of the choanae, the pterygoid forms most, or all, of the roof and medial walls of the enormously excavated lateral connection of the nasopharynx and the middle ear; this space serves as an equivalent of the eustachian tube of extant mammals. The exact contribution of the pterygoids to this region, however, cannot be fully determined.

Sphenoid. — The sphenoid is at least partially preserved in both specimens and lacks a full complement of sutures delimiting its individual components, namely the presphenoid, alisphenoid, orbitosphenoid, and basisphenoid (Figs 3, 16). The individual names will be used here in reference to the identified sutures and to standard anatomical areas formed by these components in other mammals for which the embryological origin of the individual elements is known or presumed.

The alisphenoid has contributions to the palate, choanae, mesocranial region, and middle ear cavity (Figs 20, 22). The three-dimensional arrangement of the alisphenoid is complex so that this element is exposed in
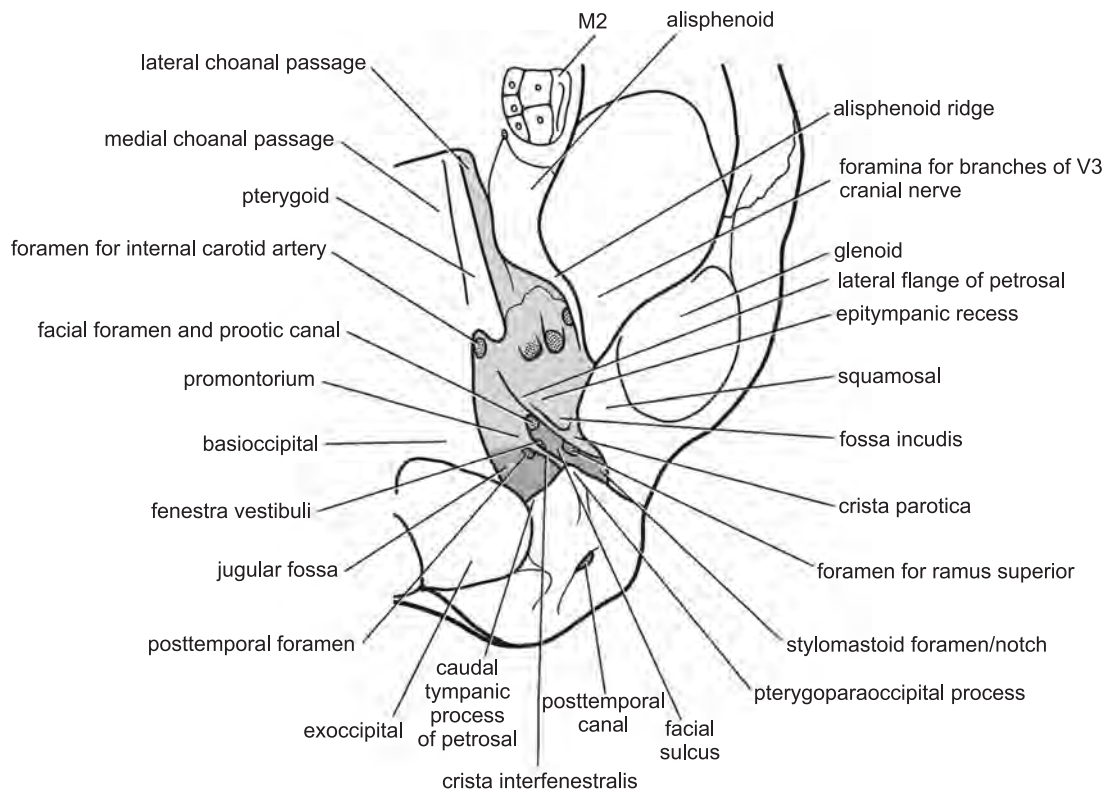
Fig. 21. Reconstruction of the basicranium of *Mangasbaatar* in ventral view.

ventral and lateral views, in addition to a sizeable portion around the sphenorbital recess that is not accessible in any of these views.

The alisphenoid is the portion of the sphenoid forming the lateral wall of the braincase in most mammals. In multituberculates, the alisphenoid is small (Kielan-Jaworowska 1971; Kermack and Kielan-Jaworowska 1971; Kielan-Jaworowska *et al.* 1986; Wible and Rougier 2000), probably reduced from a primitive condition in which it was large (Hopson and Rougier 1993; Rougier and Wible 2006). This reduced alisphenoid in multituberculates forms a small portion of the anteroventral area of the lateral wall of the cavum epiptericum (Kermack and Kielan-Jaworowska 1971). In *Mangasbaatar*, the alisphenoid, as recognized here, is also small and its braincase contribution is limited to the area surrounding the cavum epiptericum. The alisphenoid, however, has a long anterior process that reaches the back of the palate (Figs 5, 16, 17). The alisphenoid contacts the palatine, maxilla, pterygoid, and petrosal, and it becomes confluent with the basisphenoidal and orbitosphenoidal portions of the sphenoid. In ventral view, the most prominent feature of the alisphenoid is its anterior process that extends to the hard palate. A little slip of the alisphenoid forms part of the minor palatine foramen and wedges its way between the maxillary and palatine contributions to the rim of the foramen (Fig. 21). The anterior process of the alisphenoid has been described as having a Möbius strip shape (Wible and Rougier 2000), resembling the shape of a twisted ribbon. The alisphenoid of *Mangasbaatar* presents the same basic shape and, because of this "twisting" of the anterior process, the anterior, ventrally oriented surface becomes laterally oriented towards the back. This anterior portion of the alisphenoid is concave contacting anteriorly the maxilla. The medial limit of the alisphenoid in this area is formed by a ridge running along the edge of the choanae and its posterior limit is a tall and sharp crest that also bounds the middle ear cavity, this is the alisphenoid ridge (Fig. 21). This concave anterior surface is likely to provide the attachment for the medial pterygoid musculature. The alisphenoid is also likely to contribute to the formation of the lateral choanal passage or trough and contact the pterygoid in doing so. However, preservation in both specimens is deficient in this area and the morphology of the lateral wall of the choanae is, to some degree, uncertain.

Behind (distal to) the alisphenoid ridge in the alisphenoid is the middle ear contribution of the alisphenoid. The alisphenoid forms approximately one-fourth of the epitympanic recess. The alisphenoid portion of the epitympanic recess is restricted to the anterior pole of this cavity, forming the very prominent anterior and lateral walls of the recess. A thin, narrow process projects back medial to the petrosal contribution to the

epitympanic recess to almost reach the tip of the promontorium. Preservation on PSS-MAE 141 is not very satisfactory in this region; it is clearer to follow the morphology in PSS-MAE 142 (Figs 17, 20, 21). In the epitympanic recess, there are two large foramina for branches of V_3. The most anterior of these foramina is very near the serrated alisphenoid-petrosal suture, but the foramen is formed solely by the petrosal.

In lateral view, the alisphenoid is limited posteriorly by the tall ridge that marked the posterior edge of the Möbius strip in ventral view. The alisphenoid in this view (lateral) is the continuation of the alisphenoid surface immediately behind the palate in ventral view. The lateral aspect of the alisphenoid is best shown on the left side of PSS-MAE 142 (Fig. 18) and the right side of PSS-MAE 141 (Fig. 8). This surface is concave dorsally and anteriorly, extending toward the sphenorbital recess medial to the anterior lamina. This surface of the alisphenoid is broader anteriorly and tapers posteriorly. There is a small foramen anteriorly directed in the anterior lamina-alisphenoid suture or in its proximity depending on the specimen. Similar variation has been reported for *Kryptobaatar* (Wible and Rougier 2000). The foramen is lodged in a deep recess and, leading anteriorly from it, there is a deep groove. Given the orientation and position of the foramen, it is likely that this structure conveyed the buccal branch of the trigeminal nerve (V) and it is thus identified here (Figs 18, 22) as the foramen buccinatorium, which also occurs among other multituberculates (Kielan-Jaworowska *et al.* 1986; Hurum 1998b; Wible and Rougier 2000). Posteromedially from the foramen buccinatorium, the alisphenoid occupies the floor of the sphenoidal recess. Laterally, it contacts the tall petrosal wall that guards the lateral extension of the sphenoidal recess. Sutures between the anterior lamina of the petrosal and the alisphenoid in this area are not apparent.

The orbitosphenoid portion of the sphenoid is a laminar process that forms the medial wall of the orbito-temporal fossa connecting the skull base with the elements forming the skull roof and the rear of the nasal cavity (Figs 7, 8, 18, 22). The orbitosphenoid contacts the frontal dorsally and anteriorly, the maxilla anteriorly, the anterior lamina posteriorly, and is continuous with the rest of the sphenoid posteromedially. The orbitosphenoid has extensive contact with the frontal, and together these bones form the ethmoidal foramen in the anterodorsal aspect of the temporal area. The dorsal suture with the frontal is shown in the right side of PSS-MAE 141. It is a smooth line running obliquely from the vicinity of the anterior opening of the orbi-totemporal canal to the ethmoidal foramen (Fig. 22). The contact between frontal and orbitosphenoid under the ethmoidal foramen, as already mentioned, is less clear. With the exception of the left side of PSS-MAE 141, most of the orbitosphenoid spanning from the sphenoidal recess to the ethmoidal foramen is missing in both specimens. The left side of the skull PSS-MAE 141, however, is crushed and the suture pattern cannot be made out.

The orbitosphenoid abuts the medial aspect of the anterior lamina and forms the medial edge of the sphenorbital fissure. In PSS-MAE 142 the skull is deformed so that the fissure and its contents can be clearly seen, through the artificially enlarged fissure. The sphenorbital fissure is a large, oval-shaped foramen leading anteriorly and cannot be seen in lateral view, due to the lateral extension of the anterior lamina and alisphenoid, broken portions of these bones alow partial views of the fissure in PSS-MAE 141 and 142 (Figs 7, 8, 18) The sphenorbital fissure transmits the contents of the cavum epitericum into the orbit including V_1, V_2 branches and the nerves to the eye muscles (II, IV, VI). Directly medial to the edge of the sphenor-bital fissure, and slightly above its midpoint, there is a small foramen piercing the orbitosphenoid. This foramen is interpreted here as transmitting the oculomotor nerve (III). The multituberculates *Chulsanbaatar*, *Nemegtbaatar*, *Kryptobaatar*, and *Sloanbaatar* Kielan-Jaworowska, 1970 have been identified as having a separate foramen for cranial nerve III (Hurum 1998b; Rougier *et al.* 1997; Wible and Rougier 2000). Medial to the oculomotor foramen, slightly above its level, in the deepest part of the orbit, there is a circular foramen in both specimens PSS-MAE 141 and 142: the optic foramen. A broad, shallow sulcus extends anterodor-sally from the optic foramen, grooving the external surface of the orbitosphenoid. The portion of the orbito-sphenoid directly in front of and ventral to the optic foramen is the jugum sphenoidale (Wible and Rougier 2000), which, in multituberculates, is relatively narrow and proportionally tall. This is also the condition in *Mangasbaatar*. Anteroventral to the optic foramen, there is another foramen of relatively large size in both specimens that penetrates the substance of the sphenoid. This corresponds to the transverse canal identified in *Kryptobaatar* (Wible and Rougier 2000). The size of the transverse canal in *Mangasbaatar* is substantial and it grooves, slightly, the floor of the sphenorbital recess.

The orbitosphenoid appears to have been convex externally and would have essentially provided support (ventrolateral) for the frontal lobes of the brain. The orbitosphenoid contacts the anterior lamina immediately under the anterior opening of the orbitotemporal canal. The suture between these two elements is best shown
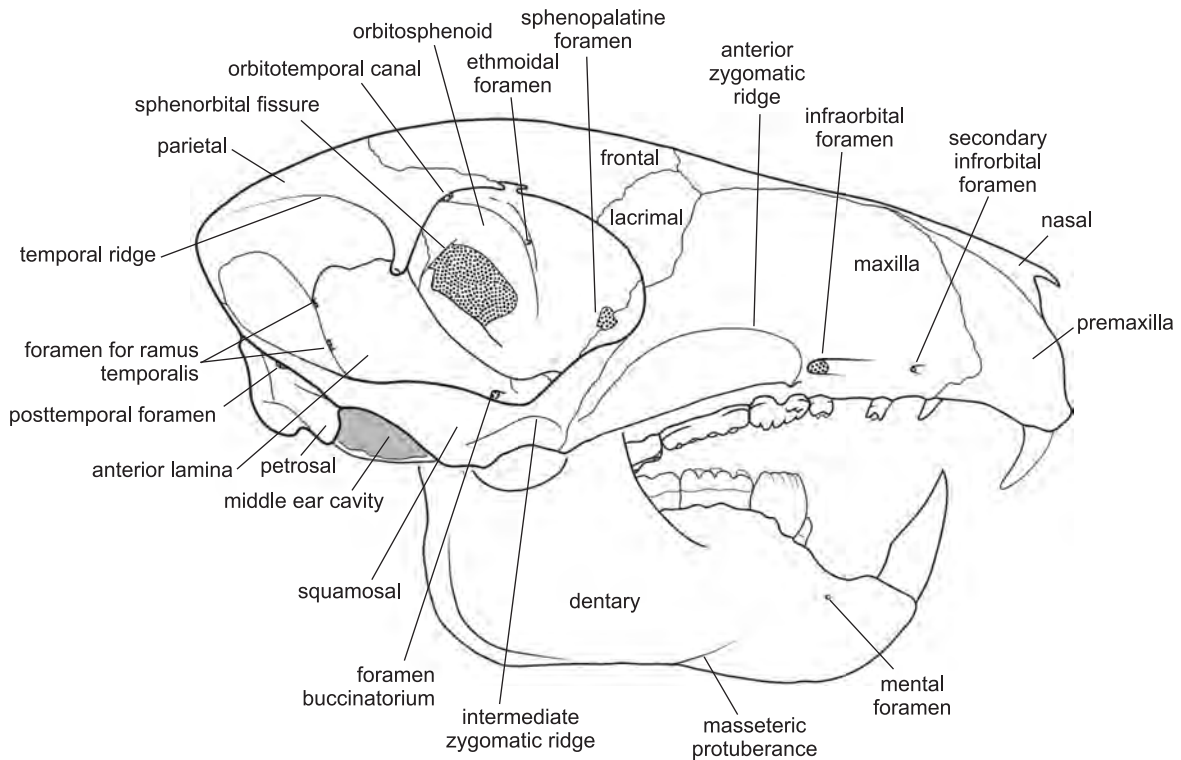
Fig. 22. Reconstruction of the skull and mandible of *Mangasbaatar* in lateral view. The mandible is in occlusion with the skull in expected life position.

on the right side of PSS-MAE 141. This suture is heavily interdigitated and runs almost vertically down towards the sphenorbital recess, but the ventral portion of the suture is not recognizable.

The presphenoid, if present in *Mangasbaatar*, is not recognizable in the specimens currently available. What remains of the sphenoid can be vaguely identified as part of the basisphenoid. It has a relatively small exposure in ventral view and a more substantial one in the area of the sphenorbital recess. The ventral exposure contacts the pterygoids, petrosals, and basioccipital. The orbital exposure is in contact with the alisphenoid and the anterior lamina, and possibly the maxilla.

The ventrally exposed basisphenoid is subtriangular with a smooth surface and lacks any evidence of carotid foramina (Figs 3, 16, 20). The basisphenoid, as part of the mosaic formed by the pterygoids, alisphenoid, and petrosal, is involved in the formation of the posteromedial wall of the lateral palatine trough. Concomitantly, these elements shape the enormously excavated posterior expansion of the lateral palatine trough, but their individual contributions are unclear.

Petrosal. — The petrosal, or parts thereof, are preserved in both specimens (Figs 3, 9, 10, 16, 24, 25). When viewed aneriorly, it is obvious that both skulls have been somewhat deformed from left to right. This makes observation of the left portion of the ear region, in particular, problematic but helps to expose the right sides very satisfactorily. In addition, the right squamosal and part of the petrosal are missing in PSS-MAE 141 and 142, helping observation (Figs 24, 25).

In therian mammals, the petrosal can be divided into two main portions: the pars cochlearis, housing the organs of hearing; and the pars canalicularis, housing the organs of equilibrium and balance. Breakage through the petrosal exposes some of these components of the inner ear in both skulls. A third element, the anterior lamina, is described here jointly with the petrosal. Among living mammals, monotremes are the only group presenting this structure (Kermack and Kielan-Jaworowska 1971; Griffiths 1978; Zeller 1989). In monotremes, the anterior lamina results from the ossification of the lamina obturans, which fuses at various stages of development with the endochondral petrosal (Presley and Steel 1976; Griffiths 1978; Presley 1981; Kemp 1983; Kuhn and Zeller 1987a, b; Zeller 1989; Hopson and Rougier 1993). Although the presence of an anterior lamina has been widely documented among basal mammaliaforms, thus far no sutural distinction between the anterior lamina and the petrosal proper has been identified. In multituberculates, these ossifications seem to be continuous. However, without developmental evidence, it cannot be excluded that the
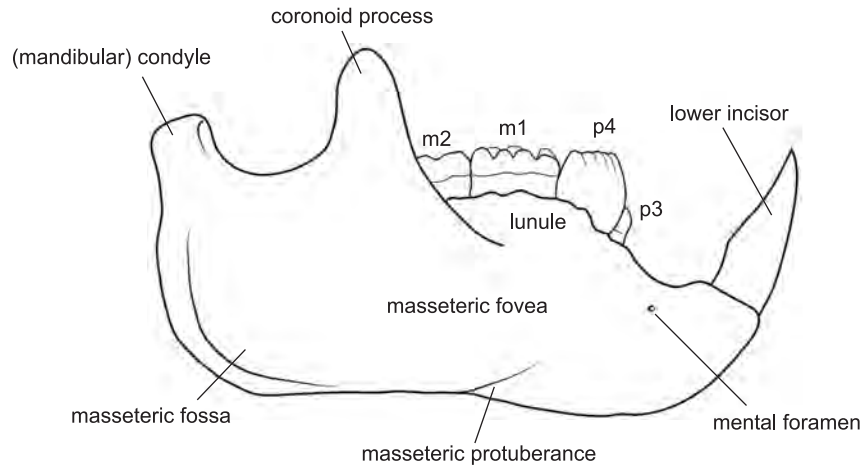
Fig. 23. Reconstruction of the jaw (lateral view) of *Mangasbaatar.*

anterior lamina and the petrosal were separate ossifications embryonically, but fused in adult. Nor is there evidence to reject a developmental fusion of the two. Nonetheless, considering the evidence afforded by monotremes, it is most parsimonious to assume a similar fundamental pattern in multituberculate mammals. As the petrosal proper and the anterior lamina cannot be strictly differentiated, and in order to be consistent with treatment of this area by other authors, the anterior lamina will be described as part of the petrosal (see Rougier and Wible 2006 for a review).

In lateral view (Figs 7, 18, 22), the petrosal contacts the basisphenoid anteriorly and medially, the frontal anteriorly, the parietal dorsally, and the squamosal posteriorly and laterally. In occipital view, the petrosal contacts the exoccipital and the supraoccipital medially, while contacting the squamosal dorsally. In ventral view (Figs 3, 9, 10, 16, 21), the petrosal contacts the exoccipital in the middle ear recess, basioccipital medially, basisphenoid, alisphenoid, and pterygoids anteriorly, and squamosal laterally.

None of the specimens show the endocranial surface of the petrosal and, therefore, its description will be limited to three views: lateral, ventral, and occipital. In ventral view, the most distinctive feature is the enormously excavated middle ear cavity. This cavity has an approximate volume of 4 mm^3 (average of four measurements of the left ear region of PSS-MAE 141, other ear regions are too damaged to provide reliable estimates). The middle ear cavity is formed mostly by the petrosal with sizeable contributions from the alisphenoid, basioccipital, and exoccipital. The limits of the middle ear cavity are defined by tall crests that approach each other ventrally and form a partial, but fairly extensive, floor for this cavity. Deeply recessed in this middle ear space, and occupying an approximate central position in it, is an elongated and ventrally bulging prominence, the promontorium. Several crests at the front and back of the promontorium connect it with other structures of the middle ear. Nevertheless, the main axis and bulging of the promontorium reflect the morphology of the finger-like cochlea, which is partially exposed on the right side of PSS-MAE 141. The three-dimensional arrangements of these crests connecting the promontorium to other structures are best preserved in PSS-MAE 142 (Figs 24, 25) because the specimen has sustained less damage to this area. The anterior pole of the promontorium forms a sharp crest that extends ventrally to form an extremely long and robust process, which, on its medial side, is continuous with the middle ear cavity and, on its lateral side, is grooved and is in communication with the epitympanic recess. This very peculiar process in *Mangasbaatar* is produced by elaboration of the rostral tympanic process of the petrosal (RTPP), which is present in other multituberculates such as *Kryptobaatar* (Wible and Rougier 2000). However, its extreme dorsoventral elongation results from a ventral projection of the basioccipital and anterior portions of the petrosal in order to accommodate a grossly enlarged middle ear cavity. The recess of the promontorium and medial margins of the epitympanic recess might also be factors in enlarging the middle ear space and in determining the unusual morphology of the middle ear of *Mangasbaatar.*

The groove on the RTPP opens ventrally at the likely junction of the pterygoids, basioccipital, and petrosal. This notch would accommodate the internal carotid artery (ICA). The ICA leaves no other traces of its presence on the skull base, but it was dorsoventrally oriented and tightly pressed to the lateral wall of the RTPP (Fig. 24). The broad ICA groove bifurcates at the level of the promontorium, sending a branch posteriorly and a larger one anteriorly. The larger branch excavates a recess in the bony floor of the epitympanic
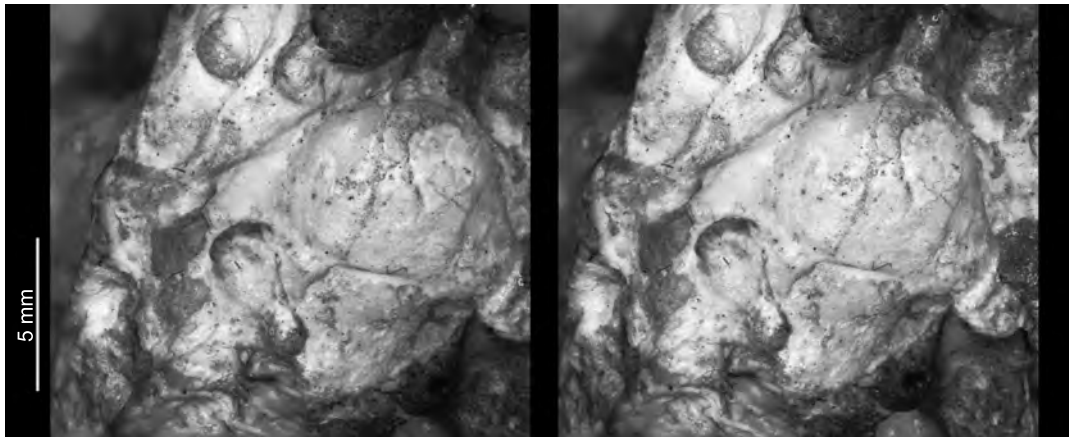
Fig. 24. *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 142. Stereophotograph of the middle ear region of the right side in ventral view.

recess. This recess leads to a canal located between the medial edge of the epitympanic recess and the crest marking the dorsal-most extent of the RTPP (Figs 24, 25). The opening of this canal is the carotid foramen (internal carotid foramen), well shown in the right side of PSS-MAE 141 and 142. A small fragment of bone is in the ICA foramen in PSS-MAE 142, obstructing the view of the ICA canal further into the bone. The ICA foramen is formed solely by the petrosal, but a slender posterior process of the alisphenoid, already mentioned, reaches its proximity (this is best shown on the right side of PSS-MAE 141). The condition in *Mangasbaatar* is different than that presumed to be primitive for members of Djadochtatheriidae, such as *Kryptobaatar*, where the posterior opening of the carotid canal is jointly formed by the petrosal and the alisphenoid before reaching the deeper-lying basisphenoid (Wible and Rougier 2000). Kielan-Jaworowska *et al.* (2005, p. 499) illustrated the carotid foramen in *Catopsbaatar* as exposed ventrally and in a very different position than in *Kryptobaatar* and *Mangasbaatar*; however, in their description they mention that the "carotid foramina have not been preserved" (Kielan-Jaworowska *et al.* 2005, p. 500). The posterior extension of the deep lateral palatine trough extends posteriorly to the edge of the petrosal formed by the RTPP and the carotid foramen.

The posteriorly directed groove originating from the ICA corresponds to the stapedial artery (Figs 24, 25). This extremely rostral position for the stapedial artery is unusual for mammals in general (Wible 1987) but is actually the condition present in all LCMM for which this area is known. This is also probably the case in most other cimolodont multituberculates given that is also present in *Lambdopsalis* (Miao 1988), but basal paulchoffatiids appear to retain the generalized mammalian condition (Hahn 1998). The groove for the stapedial artery is proportionally small and runs along the lateral aspect of the promontorium and ventral to the level of the epitympanic recess. The stapedial groove is shallow in all of the specimens and runs along the ventral edge of the fenestra vestibuli. In the vicinity of the fenestra vestibuli the direction of the groove is ambiguous when considering whether the stapes was columelliform or bicrurated. After traversing the fenestra vestibuli, or running in its vicinity, the stapedial artery is directed toward the common canal for the ramus superior and the prootic sinus.

At the posterior end of the promontorium, there are two fenestrae, one of them laterally positioned (the already mentioned fenestra vestibuli) and the other one medially positioned (the perilymphatic foramen) (Figs 9, 10, 16, 21, 24, 25). The fenestra vestibuli can be observed only on PSS-MAE 142 because those of 141 are obscured. The fenestra vestibuli is subcircular and is hardly recessed, if at all, in a fossula fenestra vestibuli. The stapedial ratio (Segall 1970) is 1.3 (average of right and left side of PSS-MAE 142). The fenestra vestibuli is separated from the perilymphatic foramen by a narrow, posteriorly trending bony ridge, the crista interfenestralis (Wible *et al.* 1995; Rougier *et al.* 1996a, b). The crista projects ventral to the body of the promontorium and marks the ventral-most extension of the petrosal. The back of the promontorium and the crista interfenestralis are damaged on the right side of both specimens. The crista, well-preserved on the left side of PSS-MAE 142 (Fig. 25), remains very tall behind the promontorium and partially subdivides the middle ear cavity into two areas: the first area, lateral to the promontorium, is formed mostly by the epitympanic recess. The second, more medial area, is developed around the jugular foramen and the portion of the middle ear created by contributions of the exoccipital, basioccipital, and petrosal.
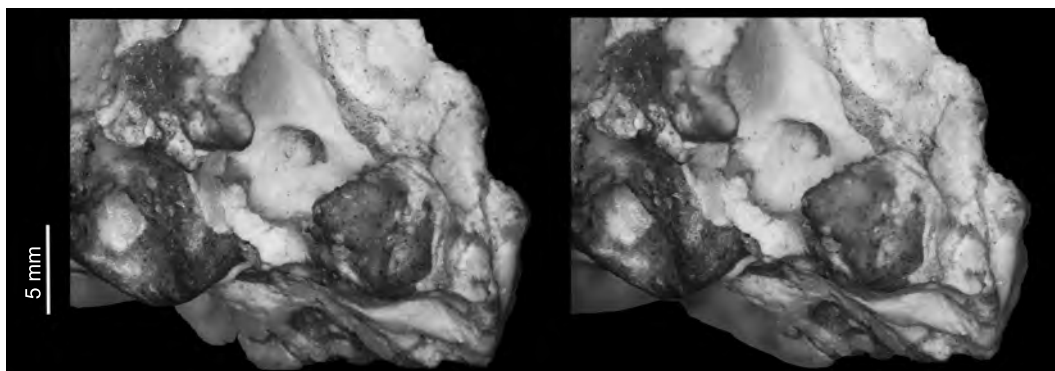
Fig. 25. *Mangasbaatar udanii* gen. et sp. n., PSS-MAE 142. Stereophotograph of the middle ear region of the left side in ventral view.

The medial portion of the middle ear cavity is further subdivided into two realms, an anterior and a posterior one, by a low crest that extends posteromedially from the edge of the perilymphatic foramen. The posterior portion includes the perilymphatic foramen, the jugular foramen, and the exoccipital contribution to the middle ear space. The perilymphatic foramen is lodged in a deeply-excavated recessus scalae tympani. The edges of the perilymphatic foramen are best seen on the right side of PSS-MAE 142 (Fig. 24) and appear to be sharp and particularly well developed on the medial aspect of the foramen. The perilymphatic foramen is oriented posteromedially in its direction with respect to the jugular foramen. The large recessus scalae tympani has its major axis oriented in the same direction. The recessus itself extends to the edge of the jugular foramen. On the right side of PSS-MAE 142, the anterodorsal border of the recessus scalae tympani is marked by a small crest that extends from the vicinity of the perilymphatic foramen to the jugular foramen.

A second crest, in conjunction to the before-mentioned crest, determines a deep groove identified here to have contained the perilymphatic duct. This groove, the perilymphatic sulcus, is almost transformed into a canal by the closely approaching crests mentioned above. It is unsettling, however, to notice that on the left side of the same specimen (PSS-MAE 142), there are no traces of the perilymphatic sulcus, and instead, a poorly developed bulge in the petrosal runs in a similar direction to the groove. The conspicuous absence of the groove on the left side suggests that the perilymphatic duct has been fully enclosed in bone and transformed into a cochlear aqueduct. It is possible that the open groove on the right side is an artifact; the edges of the crests show some breakage, though other portions seem natural. The left side of PSS-MAE 141 (the only side observable for this feature) agrees with the left side of PSS-MAE 142 in showing no traces of a perilymphatic groove. In monotremes the development of the aqueductus cochleae (or lack thereof) differs between *Ornithorhynchus* Blumenbach, 1800 and *Tachyglossus* Illiger, 1811, as shown by the collection of monotremes housed at the American Museum of Natural History (AMNH 252512, AMNH 200255, AMNH 157072). The platypus retains a perilymphatic duct mostly open to the middle ear space throughout life (Zeller 1989), but the echidna closes it later in development. *Zaglossus* Gill, 1877 has, in general, an even more complete enclosure of the perilymphatic duct than the echidna. It is possible that a similar situation happened in *Mangasbaatar*, but the fact that its development seems to be different on left and right sides of the same specimen is problematic. Technically, one side of *Mangasbaatar* should be labelled perilymphatic foramen and the other fenestra cochleae, but this would be confusing; we choose to label associated structures as via the primitive term reflecting the wider presence of this primitive morphology in other multituberculates and the possibility that part of the perylimphatic duct expanded into the middle ear cavity (see below).

The area of the middle ear cavity developed between the perilymphatic groove, the jugular foramen, the hypoglossal foramen, and the crests subdividing the medial portion of the middle ear cavity is slightly concave and essentially featureless. The petrosal forms at least half of the jugular foramen, which is equal in size to the fenestra vestibuli. The presence of a large jugular bulb in *Mangasbaatar* is evidenced by the large depression surrounding the jugular foramen and its endocranial enlargement. A portion of the middle ear, anterior to the crest that subdivides the medial portion of the middle ear cavity, forms the bulk of the middle ear volume and determines a concave median surface for the petrosal by excavating all the elements forming the middle ear roof. The RTPP forms the anterolateral limit of this space.

The petrosal extends laterally and posteriorly from the promontorium to form what can be roughly described as an L-shaped platform (Figs 20, 21, 24, 25). The long arm of the "L" is formed by the epitympanic

recess, and the short one is formed mostly by the caudal tympanic process of the petrosal (CTPP). The epitympanic recess extends from its contact with the alisphenoid anteriorly to the level of the fenestra vestibuli posteriorly. The posteriormost portion of the epitympanic recess is lost from the right side of both specimens and is distorted/incomplete on the left side of both of them. The epitympanic recess is a strongly concave surface that projects ventrally, especially at its anterior pole as it continues into the alisphenoid. Its lateral limits are marked by the ventral edge of the anterior lamina and its medial boundary is formed by a low crest that runs posteromedially and that approaches the promontorium quite closely, especially at the level of the fenestra vestibule (Fig. 24). This posterior portion of the epitympanic recess is formed by the medial folding of the free edge of the lateral flange that contacts the promontoriun, a feature present in all the LCMM and other multituberculate groups (Presley *et al.* 1996; Wible and Rougier 2000; Kielan-Jaworowska *et al.* 2005). Foramina are present in the petrosal contribution to the epitympanic recess (Figs 24, 25). The most anterior one, already mentioned in connection with the alisphenoid, is oval, anteroventrally directed, and placed approximately along the midline of the epitympanic recess. A second, much smaller foramen, seen only on the right side of PSS-MAE 142, is near the lateral edge of the epitympanic recess and is also anteroventrally directed; this foramen is omitted in the reconstruction of the ear region because it is considered an individual variation. A third foramen, of very large size, is centrally positioned in the epitympanic recess, roughly at the level of the internal carotid sulcus. Leading anteroventrally from this foramen, there is a broad, deep sulcus that nearly extends to the anteroventral limits of the epitympanic recess. The three aforementioned foramina of the epitympanic recess likely transmitted branches of the mandibular division of the trigeminal nerve (V_3). The first two foramina are in turn associated with a third foramen that perforates the anterior lamina of the petrosal in lateral view. The three of them can be considered the foramen masticatorium, with two branches directed ventrally and one ventrolaterally.

The big foramen occupying a central position in the epitympanic recess is the foramen ovale inferium (Figs 20, 21). In other multituberculates (Kielan-Jaworowska 1970, 1971; Kermack and Kielan-Jaworowska 1971; Kielan-Jaworowska *et al.* 1986; Hurum 1988b; Wible and Rougier 2000) and in some rodents (Hill 1935; Wahlert 1974, 1985) the mandibular division of the trigeminal nerve is also divided into numerous foramina. Variations in the number, pattern, and size of these foramina seem to be very frequent (Wible and Rougier 2000), but in PSS-MAE 141 and 142 the morphology in this area is consistent. Behind the foramen ovale inferior, the epitympanic recess is walled laterally by the ventral extension of the anterior lamina and at least partially by the squamosal. This region is best preserved in PSS-MAE 141. The medial limit of the epitympanic recess becomes confluent, in this area, with a low crest: the crista parotica, which increases in size posteriorly.

Lateral to the crista parotica, there is a small portion continuous with the epitympanic recess (the space dorsal to the incus and malleus articulation) that is deeper than the surrounding area and it is here identified as the fossa incudis (Fig. 21), for the short crus of the incus. On the left side of PSS-MAE 141, there is a fragment of a small bone, most likely a middle ear ossicle, lying in the fossa incudis. Unfortunately, it is not possible to exactly identify the element. The fossa incudis is fully continuous anteriorly with the epitympanic recess and its posterior limit is formed by the squamosal and the petrosal jointly.

The crest marking the medial limit of the epitympanic recess is connected in the anterior two-thirds of its length to the promontorium. The anterior-most portion of this connection is occupied by the groove for the internal carotid artery. The posterior portion of this connection is almost flat and is notched, only slightly, by the groove for the stapedial artery. The posterior one-third of the crest marking the medial edge of the epitympanic recess is free: the rostral continuation of the crista parotica. At the level of the posterior margin of the fenestra vestibuli there is a small process arising from the medial aspect of the crista parotica, which is ventromedially directed, the tympanohyal. Behind the tympanohyal, there is a shallow notch, the stylomastoid notch, or stylomastoid foramen, which corresponds to the exit of the hyomandibular branch of the facial nerve (CN VII) from the tympanic cavity.

A series of structures occupies the space between the epitympanic recess and the fenestra vestibuli. Posterior to the bony shelf, already described as connecting the epitympanic recess, the petrosal, and the promontorium, there is a deep recess that excavates the lateral surface of the promontorium. This recess marks the likely site of attachment of the *m. tensor tympani* and is identified here as the tensor tympani fossa. The tensor tympani fossa in *Mangasbaatar* seems to be proportionally small in relation to the size of the middle ear as compared with *Kryptobaatar* (Wible and Rougier 2000; Fig. 26).

In other LCMM, the facial nerve opening into the middle ear and the prootic canal opening into the middle ear are found behind the tensor tympani fossa. This area is preserved on the left side of PSS-MAE 141 and
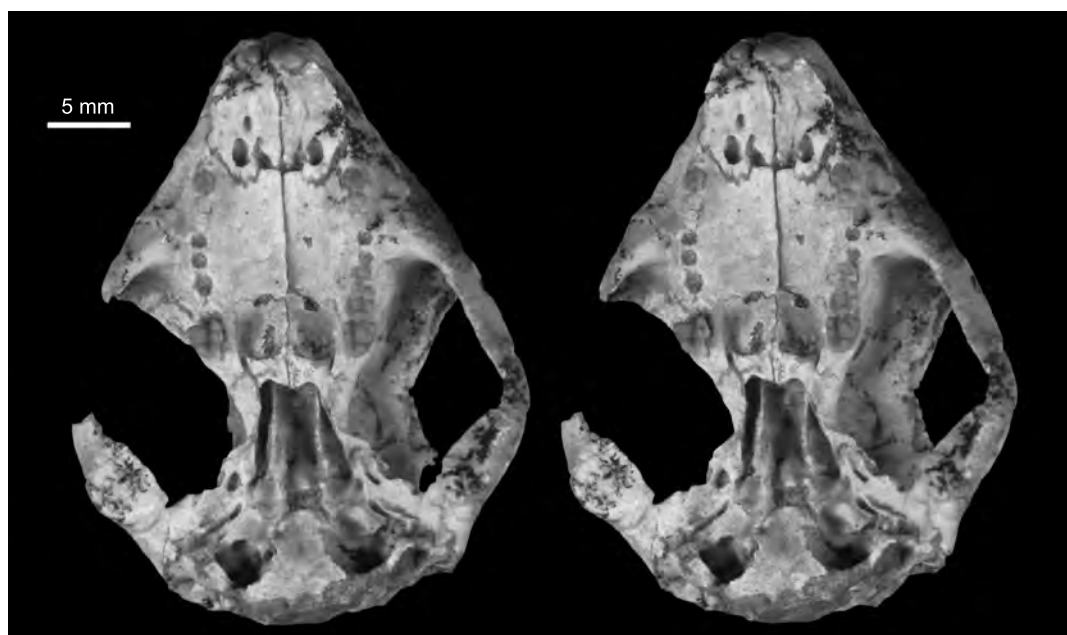
Fig. 26. Unpublished specimen of *Kryptobaatar*, field number PSS-MAE 631 from the Late Cretaceous of Mongolia. Stereo-photograph of the skull in ventral view.

142. Unfortunately, preparation of this area is not possible due to the distortion of the skull and the deeply recessed position of these openings. Presence of these structures, namely the prootic canal and the tympanic opening of the facial nerve (Fig. 21), is evidenced on the broken right side of PSS-MAE 141. In this specimen, directly rostral to the vestibular structures and lateral to the promontorium, there are two canals shown in section through the lateral flange/anterior lamina. The most medial of these corresponds to the facial foramen, and the more lateral canal corresponds to the prootic canal. The prootic canal can be traced posterodorsally to the vicinity of the subarcuate fossa on the internal surface of the petrosal in PSS-MAE 141. A broad facial groove extends posterolaterally, parallel to the promontorium and directed towards the stylomastoid notch. This groove is jointly limited by the squamosal and petrosal (Fig. 21). The stylomastoid notch occupies a deeply recessed space between the root of the squamosal, the tympanohyal, and the tall paraoccipital process of the petrosal. Medial to the stylomastoid notch, at the base of the prominent crista interfenestralis, there is an oval depression: the stapedial fossa. This fossa, subequal in size to the fenestra vestibuli, served as an attachment point for the *m. stapedius* and is hidden in posteroventral view by the prominent paraoccipital process.

The paraoccipital process (Figs 9, 10, 21), in occipital view, is subtriangular with a broad, round apex. A sharp crest extends anteroventrally from the tip of the paraoccipital process and connects this process with the back of the promontorium. The crest on the paraoccipital process is continuous with the crista interfenestralis of the promontorium.This rather large, anteromedially trending crest, partially subdivides the rear of the middle ear cavity and results in the absence of a continuous post-promontorial tympanic sinus. The crista interfenestralis-paraoccipital process crest fully separates the structures of the lateral trough from those in the area of the perilymphatic foramen and jugular foramen.

The crista interfenestralis, the edge of the perilymphatic foramen, and the back of the middle ear cavity separate a small portion of the tympanic cavity around the jugular foramen. This is the jugular fossa of other multituberculates (Kielan-Jaworowska *et al.* 1986; Wible and Rougier 2000). The jugular fossa in *Mangasbaatar* represents another out-pocketing of the massive middle ear cavity, more specifically a portion of the post-promontorial tympanic sinus. The jugular fossa (Figs 16, 21) is dominated by the round ventral bulging of the common ampulla of the posterior and lateral semicircular canals. This structure is very similar to that of *Kryptobaatar* (Wible and Rougier 2000; Fig. 30). The ampullar prominence determines two deep pits in the roof of the middle ear cavity: a lateral and a medial pit. The lateral pit is walled off medially by the crista interfenestralis and posteriorly by the posterior wall of the middle ear cavity. The medial pit is closely associated with the perilymphatic foramen and shows a very well delimited oval depression immediately posterior to the perilymphatic foramen. This area is similar to the recessus scalae tympani described in monotremes (Zeller 1989). The excavation of this pocket is not as prominent in PSS-MAE 142 as it is in

PSS-MAE 141. Determining the occupant of this space is problematic. The resemblance of this area with the recessus scala tympani could suggest that an expansion of the perilymphatic duct would occupy this area, but it was previously noted that the perilymphatic duct is enclosed in an aqueductus cochleae throughout much of its length. The lateral opening of this aqueduct is on the medial edge of the perilymphatic foramen and continuous with rim of the foramen. It is possible that the perilymphatic duct expanded out of the perilymphatic foramen in a sac filled with perilymph occupying this recess, which is essentially the condition found in monotremes. Alternatively, in eutherians the secondary tympanic membrane closes the fenestra cochleae (the partial homologue of the perilymphatic foramen) and there is no expansion of the perilymphatic system into the middle ear cavity. Under this model the recess in *Mangasbaatar* would be empty and part of the middle ear cavity, a post-promontorial tympanic sinus. The rest of the jugular fossa is gently concave around the jugular foramen.

From the paraoccipital process there is another crest in the petrosal that extends medially; this is the CTPP, which extends to its contact with the exoccipital immediately lateral to the occipital condyles. The CTPP extends anteroventrally and contributes, along with other elements of the braincase, to the walls and partial floor of the middle ear cavity.

In lateral view (Figs 7, 22), the anterior lamina is the dominant component of the petrosal and, in an undistorted specimen, would probably completely hide the pars canalicularis and the pars cochlearis of the petrosal. The anterior lamina contacts the parietal dorsally through a fairly horizontal suture, which extends rostrally up to the anterior opening of the orbitotemporal canal under the root of the postorbital process. The anterior lamina forms the posteroventral edge of this foramen. Following approximately the direction of the anterior lamina-parietal suture, there is an endocranial groove interpreted here as a space for the orbitotemporal system. The major occupant would be the orbitotemporal artery (Kielan-Jaworowska *et al.* 1986; Rougier *et al.* 1992; Wible and Rougier 2000), likely accompanied by a vein. The orbitotemporal artery was fed posteriorly through a fairly vertical dorsal ascending canal. This canal runs between the anterior lamina and the squamosal and is shown by the right side of PSS-MAE 142 (Fig. 18). In the specimen, the overlying squamosal is missing, affording a direct view of the inside of the ascending canal. When complete, the canal would have been perforated by a few foramina that would distribute its contents to the temporal area. The foramina would be occupied by temporal rami feeding the temporal musculature (Rougier *et al.* 1992; Wible and Gaudin 2004).

The ascending canal contacts two other grooves: a larger posterodorsal one and a somewhat smaller anteroventral one. The posterodorsal canal opens on the occiput through the posttemporal canal and likely transmitted the arteria diploëtica magna and a companion vein (Kielan-Jaworowska *et al.* 1986; Rougier *et al.* 1992). The anteroventral canal is filled with matrix in PSS-MAE 142 and represents the ventral ascending canal, likely transmitting a fairly horizontal portion of the ramus superior of the stapedial artery. This canal, horizontally directed, runs through the thickened ventral edge of the anterior lamina: the lateral flange. The ventral extent of the lateral flange is mostly complete on the left side of PSS-MAE 141; it should be noted that this ventral extent is lateral to the edge of the lateral flange that, as in most multituberculates, contacts the promontorium medially. The ventral projection of the lateral flange extends anteriorly along the lateral edge of the epitympanic recess as a gently concave lamina. At its most anteroventral extent, near the suture with the alisphenoid, there is a foramen that faces ventrolaterally: the lateral opening of the foramen masticatorium, which has already been mentioned. On the left side of PSS-MAE 141, there is a small foramen on the lower third of the anterior lamina, corresponding to the supraglenoid foramen of *Kryptobaatar* (Wible and Rougier 2000) and other LCMM.

The anterior margin of the anterior lamina has a long anteroventrally trending ridge that forms the lateral wall of the sphenorbital fissure. The very long anteroventrally-extending portion of the anterior lamina is one of the most conspicuous features distinguishing *Mangasbaatar* from other LCMM. The extension of the anterior lamina is coupled with the general enlargement of the middle ear cavity through the ventral projection of the elements involved in its formation. The dorsal portion of the anterior edge of the anterior lamina is moderately concave and faces forward as in other LCMM. In *Mangasbaatar*, this surface is proportionally more dorsally located. The reorganization of this area is mostly due to the very large opening of the sphenorbital fissure, which occupies the floor of the orbitotemporal region. The size and proportions of this area are very well shown by PSS-MAE 142 and at least partially confirmed by the right side of PSS-MAE 141.

In occipital view, the petrosal is exposed between the squamosal, exoccipital, and supraoccipital. The mastoid exposure of the petrosal supports, dorsolaterally, the base of the lambdoidal crest. Along the dor-

solateral edge of the petrosal, there is a fairly prominent posttemporal foramen, partially obliterated by crushing in PSS-MAE 141. This anteroventrally directed foramen is formed solely by the petrosal. A broad groove extends ventrally from the posttemporal canal, continuing into the mastoid exposure of the paraoccipital process. The posttemporal foramen is also slightly notched dorsally, suggesting that a large occipital artery ran in close contact with the occiput and continued dorsally to supply the nuchal musculature. The area of the mastoid exposure of the petrosal medial to the posttemporal canal is slightly concave and forms a shallow depression on the side of the occipital condyles. This shallow depression probably accommodated the transverse processes of the atlas during skull movements.

Basioccipital. — The basioccipital is preserved in both specimens, although only the one in PSS-MAE 142 is incomplete. The basioccipital forms most of the basicranial axis (Figs 3, 9, 10); it is in contact anteriorly with the basisphenoid, laterally with the petrosals, and posteriorly with the exoccipital. It is also possible that a small portion of the pterygoids contacts the anterolateral corner of the basioccipital. In ventral view the basioccipital shows a deep odontoid notch, as described earlier, and a narrow median exposure that is flanked by the exoccipital. In front of the exoccipital, the basioccipital expands laterally, contributing to the floor of the middle ear cavity through a thin lamina (Figs 2, 9). Further rostrally, the basioccipital contribution to the floor is in contact with a similar lamina of the petrosal. At the rostral end of the basioccipital there is a transverse suture, mentioned earlier in the description of the pterygoid, that separates the basioccipital from the basisphenoid and probably the pterygoids. The contribution of the basioccipital to the floor of the middle ear is laminar and ventrally convex, similar to the processes of other bones delimiting the middle ear cavity.

In the middle ear cavity, the basioccipital is deeply excavated medially so that this bone forms not only a substantial part of the floor of the middle ear cavity, but also the medial wall and part of the roof. The medial excavation of the basioccipital results in a bone that is very thin, so much so that it can be transilluminated from the opposite middle ear space. This very close approximation of right and left middle ear cavities to the midline is ventral to the braincase proper because, as mentioned above, only a thin, tall crest of the basioccipital separates right and left cavities (see Fig. 27 for a comparative example). The suture with the petrosal runs deeply in the roof of the middle ear, obliquely from the jugular foramen towards the anteromedial pole of the middle ear recess. The basioccipital, the petrosal, and possibly the exoccipital, jointly form the jugular foramen. The aperture is of a relatively small size with respect to the overall size of the skull.

Exoccipital. — The exoccipital is incomplete in both specimens. The left side of PSS-MAE 141 is the best preserved (Figs 9, 10). The exoccipital contacts the basioccipital anteriorly, the supraoccipital dorsally, and the petrosal laterally and dorsally in the occiput. The exoccipital forms the occipital condyles, most of the foramen magnum, and the posteromedial wall of the middle ear cavity. The sutures on the occiput are clear and both specimens are very similar regarding position and extent.

Only part of the left condyle is preserved in PSS-MAE 141. What is preserved resembles the condyles present in other LCMM. The condyles are not very prominent, are moderately convex, and have a small lateral extension. The articular surface extends over the bony floor of the middle ear cavity. Right and left exoccipitals are separated ventrally along the midline by a wedge of the basioccipital bearing the odontoid notch. The exoccipital forms most of the lateral edge and floor of the foramen magnum and right and left are separated ventrally, as mentioned before, by the basiocciptal and dorsally by the supraoccipital. The contribution of the exoccipital to the occiput is limited to the area immediately surrounding the foramen magnum. This lamina is flat and slopes slightly forward, away from the foramen magnum. The suture with the petrosal runs obliquely, from slightly above the level of the foramen magnum downwards to the medial side of the paraoccipital process in the middle ear cavity.

Mangasbaatar has an extremely well-developed and expansive middle ear cavity formed jointly by the squamosal, petrosal, basioccipital, alisphenoid, and exoccipital. The exoccipital forms the posteromedial aspect of this cavity, providing a thin floor that extends anterolaterally. This floor is incomplete in both specimens. From what remains of the left side of PSS-MAE 141, it is clear that this floor almost completely enclosed the middle ear. The contribution of the exoccipital to the internal surface of the middle ear can be evaluated only on the right side of PSS-MAE 141. The exoccipital is deeply excavated medially forming a small infundibulum separated anteriorly from the main middle ear cavity by a sharp crest.

In the posteroventral corner of both sides of PSS-MAE 142, a single hypoglossal foramen can be recognized. The area surrounding this foramen is damaged on both sides, so it is unclear if *Mangasbaatar* had only one hypoglossal foramen or more. A second foramen, piercing the substance of the exoccipital, can be seen
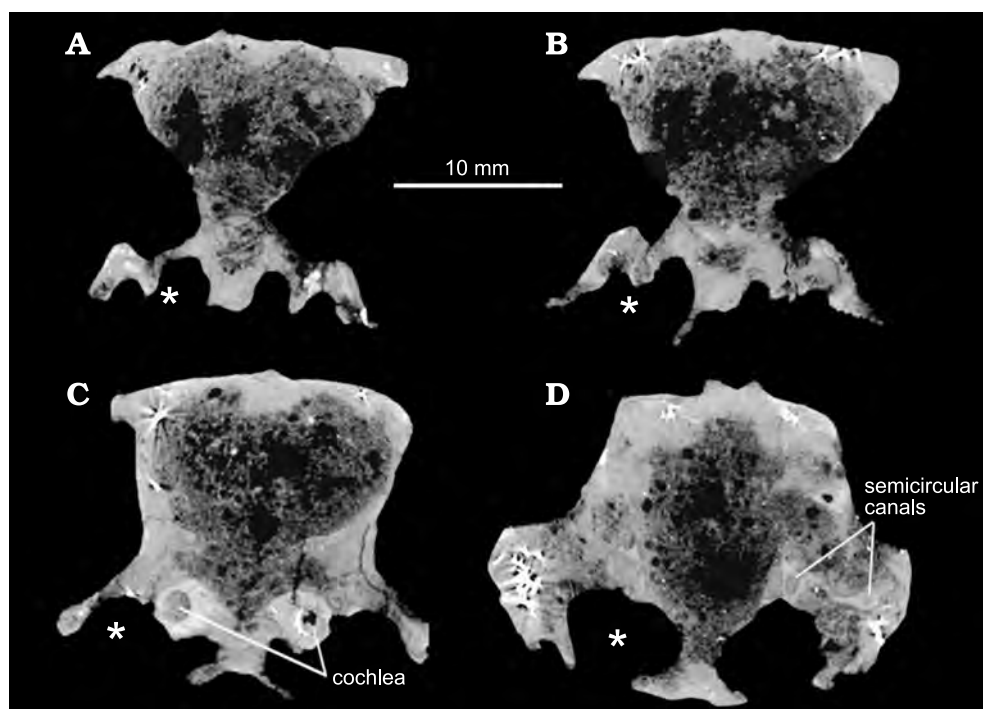
Fig. 27. CT cross sections through the mesocranium and ear region of a *Tombaatar* sp. skull from Ukhaa Tolgod, Mongolia, PSS-MAE 630. The * represents the middle ear cavity and its connection to the choanal passage.

on the right side of the exoccipital and part of the same foramen is preserved on the left side. The left exoccipital is more eroded than the right so that the above-mentioned foramen can be seen to be continuous with a cylindrical endocast of the left side. These foramina were inside a condylar area of the exoccipital and can be interpreted to be part of a condylar canal. The endocranial structure leading to the left condylar canal is congruent with similar endocasts described for *Kryptobaatar* (Wible and Rougier 2000). The relatively large size of these endocasts and the proportionally small size of the jugular foramen imply that most of the blood from the cranial venous system was drained in *Mangasbaatar* through the foramen magnum instead of the jugular foramen, a condition congruent with that reconstructed for other multituberculates (Kielan-Jaworowska *et al.* 1986; Rougier *et al.* 1992). The basioccipital-exoccipital suture in the middle ear region cannot be discerned in any of the specimens so the lateral extent of the bone cannot be ascertained with any certainty. However, it is likely that the relatively large hypoglossal foramen, present on the posteromedial corner of the middle ear cavity, is completely enclosed in the exoccipital (shown by the right side of PSS-MAE 141).

Supraoccipital. — The supraoccipital is a flat bone positioned sagittally on the occiput dorsal to the foramen magnum and is vertical, or inclined slightly forward. The supraoccipital is at least partially preserved in both of the specimens and its boundaries indicated by relatively clear sutures. This element contacts the parietals dorsally, the petrosals parasagittally and the exoccipitals ventrolaterally. A small portion of the supraoccipital forms the dorsal-most portion of the foramen magnum. In PSS-MAE 142 there are remnants of a small midline crest, which increases in size dorsally. The supraoccipital provides support to the lambdoidal crest but does not directly contribute to it and it is therefore limited to the occipital aspect of the skull.

Mandible (Figs 11–13, 23). — Fragments of both right and left lower jaws are preserved in both specimens. Those of PSS-MAE 142 were found dissociated among the numerous fragments that resulted from erosion of the skeleton. The jaws of PSS-MAE 141 were still articulated to the skull when found. The right jaw was almost completely eroded away, leaving only the tip of i1, p4–m2, and the apex of the coronoid process in articulation. An impression of the body of the jaw was present so that the shape and curvature of the area of the dentary surrounding i1 could be observed. Preparation of the specimen removed all of these remnants of the right jaw and destroyed the natural mold of the dentary. However, the specimen was molded before preparation and the relative positions of the elements are preserved in a rubber cast of the original. The left lower jaw is largely preserved (Figs 11, 12) but is missing the symphysis, most of the incisor, and the back of the jaw. This description is based on this jaw and is supplemented with details from PSS-MAE 142.

The jaw of *Mangasbaatar* is heavy and deep under the molars with a very steep diastema and i1 alveolus. The i1 is very high and almost reaches the level of the molars. The space between i1 and p3 is relatively short. The symphysis is very robust, as shown by the fragments of PSS-MAE 142. The bottom part of the body of the jaw is missing in both specimens, but can be observed in the cast of PSS-MAE 141. The external surface of the jaw is marked by a series of depressions. The first depression is ventral to the p4–m1 embrasure and has the masseteric fovea preserved as a gentle concavity. Between the masseteric fovea and p4, the alveolar ridge is slightly concave and continues along the chipped teeth to end directly medial to the coronoid process. The anterior portion of this depression under p4 is the lunule (Gambaryan and Kielan-Jaworowska 1995), which is not very well developed in *Mangasbaatar* (Fig. 23). The more substantial depression extending back is the temporal groove. As previously mentioned, the bottom of the jaw is not well preserved in the specimens and the masseteric crest cannot be fully recognized in any of them, but isolated fragments suggest the presence of the masseteric protuberance (Kielan-Jaworowska *et al.* 2005). The masseteric fossa, however, is slightly concave and not very large, restricted to the base of the coronoid process, and probably expanding towards the back of the jaw. The coronoid process in *Mangasbaatar* is high, narrow, and forms a sharp angle with the molariform occlusal plane (78º). The tall coronoid process resembles that described in *Catopsbaatar* (Kielan-Jaworowska 1974; Gambaryan and Kielan-Jaworowska 1995; Kielan-Jaworowska *et al.* 2005).

Only the dorsal-most portion of the condylar process is preserved in the left lower jaw of PSS-MAE 141. Fortunately, most of the condylar articular surface remains intact (Fig. 13). The condyle is perched in a broad neck and is separated from the coronoid process by a wide notch that places the condyle above the occlusal plane of the molars. An isolated left condyle is also preserved in PSS-MAE 142. The articular surface is tear-drop-shaped with the broad end directed anteriorly. The articular surface continues back along the posterior edge of the jaw for a short distance beyond the broader portions of the condyle, indicating the potential for a large range of jaw opening. The medial view of the jaw shows a deep pterygoid fossa that extends anteriorly up to the level of the m2. The pterygoid fossa is bordered anteriorly by the remnants of the pterygoid ridge, which is only partially preserved. At the anterior pole of the pterygoid fossa, there is a large foramen that is directed anteriorly into the substance of the dentary: this is the mandibular foramen or canal. All of the features of the medial view of the jaw described by Gambaryan and Kielan-Jaworowska (1995) cannot be described in these specimens.

Dentition (Figs 5, 6, 11–14). — *Mangasbaatar* is clearly a member of Djadochtatherioidea (Rougier *et al.* 1997; Kielan-Jaworowska and Hurum 1997, 2001) and, as seen in all members of this group, the lower dentition is reduced to one incisor, two premolars, and two molars. The upper dentition is reduced, like *Tombaatar* and *Catopsbaatar*, to two incisors, three premolars, and two molars. Therefore, the dental formula for *Mangasbaatar* is I2/1, C0/0, P3/2, M2/2 (Figs 6, 14)

PSS-MAE 141, the type, is a younger individual than PSS-MAE 142. The crown morphology of PSS-MAE 141 is very well preserved and most of the cusps are intact. PSS-MAE 142, on the other hand, shows extensive wear, which has reduced the cusps to their truncated bases. On the left side of PSS-MAE 141, there is a small element in the diastema between P1 and P3. This element is a tooth or parts thereof that might be incompletely preserved, but it seems more likely to be part of a deciduous tooth (likely a DP3) which is retained at this ontogenetic stage. The relevant area on the right side of PSS-MAE 141 is damaged, so the presence or absence of this element cannot be corroborated. There is, however, a fragment of a tooth in a position that approximately corresponds to the element mentioned above, but the damage to the area is so extensive that a positive identification is not warranted. PSS-MAE 141 is a young adult, but the older adult, PSS-MAE 142, shows no trace of this element between P1 and P3.

Upper dentition (Figs 5, 6, 16, 20). — The two incisors in LCMM are homologous to the I2 and I3 of the full complement of three incisors present among basal multitubercualtes such as of paulchoffatiids (Clemens 1963; Hahn 1969; Kielan-Jaworowska *et al.* 2004), we therefore refer to the teeth present in *Mangasbaatar* as I2–I3. The upper dentition is fairly well-preserved in PSS-MAE 141, although most of the I2s are missing, the left I3 and right P4 are damaged, and the right P1–P3 are missing. On the skull PSS-MAE 142, only part of the right and left I2 are preserved. Both of the I3, as well as the right P1 and P4, are damaged. The left P1–P4 and the right M1 are also missing.

Incisors: The upper I2 is a big, strong tooth that is sharply curved, and occupies most of the premaxilla. The tooth is strongly compressed mediolaterally with a thick layer of enamel covering its lateral aspect, wrapping around the dorsal aspect of the tooth to extend into the medial face (restricted enamel). The medial

extension of the enamel is limited to a small dorsal band that occupies less than a third of the medial height of the tooth. Right and left I2 were medially directed and probably contacted each other in the midline. This, however, cannot be seen in the specimens because of imperfect preservation.

The left I3s of both skulls seem to be complete and show heavy wear on their occlusal facets. The I3 in *Mangasbaatar* is a cylindrical tooth that is slightly curved posteriorly, occupying a position close to the midline on the palate (Figs 3, 16). The I3 projects ventrally as a long freestanding tooth that culminates into a flat subhorizontal wear facet. The wear of the I3 crowns is enough to obscure the original crown morphology of this element. It is, therefore, uncertain if the I3 had one or more cusps (a primitive condition). The wear on the I3 is so extensive that the boundary between the crown and the root is obliterated. The wear has also exposed, in the center of the cylinder, a small area showing the cementum surrounded by dentin. This condition is well developed in PSS-MAE 141, but in PSS-MAE 142 the wear on the I3 crown does not reach the cementum.

Premolars: PSS-MAE 141 bears a well-preserved left P1 which shows little wear. The P1 is biradiculated, short, and has a short crown that culminates in three conical cusps. The cusp formula is 1-2. The cusps are arranged in a closed triangle. The roots are unequal, the anterior root being larger and sloping backwards, a feature quite common among LCMM, likely associated with the palinal masticatory movements (Wall and Krause 1992; Gambaryan and Kielan-Jaworowska 1995).

The P2 seems to be absent in *Mangasbaatar*. No traces of it remain on both sides of PSS-MAE 142 (Fig. 16). The alveolar bone in this area is well preserved, showing a smooth, short diastema between P1 and P3. On PSS-MAE 141, however, the left side shows the remnant of a tooth between P1 and P3. As preserved, this remnant is little more than a rootlet. It is likely that this is a transitory remnant of a deciduous premolar, likely DP3. The right side of the same specimen is not preserved well enough to be certain of the presence or absence of a P2. Under this interpretation, *Mangasbaatar* shares the absence of a P2 in the adults with *Tombaatar* and *Catopsbaatar*. All these large LCMM represent a closely related group (Kielan-Jaworowska and Hurum 1997; Rougier *et al.* 1997). Kielan-Jaworowska *et al.* (2005) described that, in old *Catopsbaatar* specimens, P1 and P3 disappear without leaving traces of their respective alveoli. This does not seem to be the case in *Mangasbaatar* as attested by the relatively old PSS-MAE 142 that still preserves P1 and P3.

The P3 is a small subrectangular tooth in occlusal outline, with two roots that slant posteriorly. The crown is separated by a strong neck from the roots and bears four conical cusps. The cusp formula is 2-2. The four cusps of the P3 occupy the corners of a rectangle with a small posterior broadening of the crown behind the two posterior cusps. The posterobuccal and the two lingual cusps are subequal in height, but the anterobuccal is substantially shorter than the other three. The three larger cusps suggest a triangular pattern similar to that present in the P1.

The P4s are missing or badly broken in PSS-MAE 142 and the right side of PSS-MAE 141. The left side of the latter, though, has this element preserved almost completely (Fig. 5). The P4 is a large, strong premolar supported by two roots. The cusp formula on the P4 is 1-5-1?. The lingual row is damaged or worn down on both sides of PSS-MAE 141 and it is likely that only one cusp was present; however, it would be possible to have a very small cusp anteriorly positioned relative to the main one. The buccal cusp is small and conical, showing no wear on PSS-MAE 141. The middle row has five cusps that increase in size posteriorly from the first to the fourth, forming a continuous ridge. The fifth cusp is separated by a deep embrasure from the rear slope of the prominent fourth cusp. The buccal row, as in other multituberculates, is more dorsally placed than the middle and lingual rows in the P4. The lingual row is likely formed by a single cusp and forms a medially bulging projection that, in essence, represents the abraded base of that large cusp. The wear that obliterated the lingual cusp extends a flat surface to the lingual slopes of the cusps forming the middle row. The buccal bulge formed by the buccal row is offset by the medial bulge of the lingual row, resulting in a slightly oval crown view for the P4. In *Mangasbaatar*, as is common among multituberculates, the direction of the middle row is oblique, aligned anteriorly with the lingual row of the P3 but aligned posteriorly with the buccal line of the M1.

Molars: The M1 is well preserved in both sides of PSS-MAE 141 (Figs 4, 5), but is worn down or broken in PSS-MAE 142. There are three rows of cusps on this molar with a cusp formula of 5-5-3. As is common in other LCMM, the buccal and middle rows extend through the length of the tooth, but the lingual row is incomplete and has only posterior cusps (posterolingual cusps). In *Mangasbaatar*, the incomplete lingual row of the tooth reaches anteriorly to the level of the apex of the third cusp of the middle row, or to the embrasure between the second and third buccal cusps. The elongated M1 is supported by two roots. The anterior root is buccolingually compressed and the posterior root, which supports the back half of the tooth, is massive and cylindrical.

The cusps have subrectangular to hexagonal bases (Fig. 6) and probably culminated in conical apices when unworn. At present, the M1 in PSS-MAE 141 shows small crater-like depressions centrally positioned on each cusp of the middle row, reflecting wear through the enamel and exposing the softer dentin. PSS-MAE 142 shows that in older individuals the molars lose almost all relief in their crowns and that the "craters" seen in PSS-MAE 141 expand to occupy the whole crown. The only remnants of the original cusp pattern are in PSS-MAE 142, seen in the eroded bases of the cusps. The buccal row that is formed by five subequal cusps shows strong wear facets in all of the lingual slopes. The individual cusps of the buccal row are separated by valleys that become shallower posteriorly; therefore, the first buccal cusp, which is somewhat removed from the anterior margin of the molar, is also separated from the rest of the cusps by the deepest valley. The valley between the second and third cusps of the buccal row is relatively shallow and the bases of these two cusps are partially merged together, a condition that is also present in *Tombaatar* and other LCMM (Rougier *et al.* 1997). The fifth buccal cusp is small and poorly separated from the fourth. A blunt ridge extends posterolingually from its apex towards the last cusp in the middle row, thus closing the trough between the buccal row and other rows. The middle row has five cusps that increase in size progressively toward the back. The cusps in the middle row are positioned at the level of the valleys between the cusps in the buccal row. The imbrication between the cusp bases of the buccal and middle row results in a strongly angular trough between the buccal and middle row. The lingual row has three poorly differentiated posterior cusps, of which the middle is the highest. The bases of these cusps are not as well-developed as those of the first two rows and they develop a fairly uniform, straight slope that is continuous from the most mesial cusp to the most distal one. Wear facets are developed only on the buccal slope of these cusps.

Both M2s are preserved in both specimens, but those of PSS-MAE 142 are very heavily worn. The M2 is a pear-shaped tooth supported by two roots, a large anterior one and a smaller posterior one that slopes backwards. This position of the roots of the M2 make the occlusal surface of the last molar face anteroventrally, giving the dental arcade a slightly concave outline in lateral view, that is characteristic of multituberculates (Wall and Krause 1992). The cusp formula of the M2 is ridge-2-3. The two cusps in the middle row are larger than the rest in the molar and continue the posterior increase in size of the middle row of the M1. The bases of these cusps are not polygonal as in the M1. The lingual row is much more prominent in the M2 than the M1, forming a fairly sharp ridge that is separated from the middle row by a broad valley. The middle cusp of the three is the largest and has heavy wear as shown by the left molar of PSS-MAE 142. The cusps on the lingual row are very poorly differentiated from one another. The buccal row is very short and does not extend throughout the length of the tooth. It reaches, posteriorly, the middle of the cusp space of the posterior cusp of the middle row. The row lacks distinct cusps and forms a broad, low, shallow crest aligned with the buccal row of the M1.

Lower dentition (Figs 11–14, 23). — The best lower dentition is that of the specimen PSS-MAE 141, which is complete (with the exception of the i1). In PSS-MAE 142, only part of the right dentition is still in place in a small fragment of the dentary. The left is represented only by isolated broken crowns of the i1, m1, and m2.

The first lower incisor is a strong tooth, buccolingually compressed with a partial covering of enamel that, as in the I1, covers only the external and a small portion of the lingual surface of the tooth. As in all large LCMM, the i1 are very large teeth with an anterior-posterior length subequal to the m1 length, the largest cheek tooth.

As in all LCMM, *Mangasbaatar* shows only two premolars, conventionally called p3 and p4. The p3 is, in *Mangasbaatar* and other LCMM, a very small element, essentially "peg"-like in front of the towering p4. The p3 in *Mangasbaatar* has only one anteriorly curved root. This root follows the concave contour of the mandibular diastema between i1 and the p3. There is a clear distinction between the crown and root, indicated by a conspicuous neck. The crown is essentially a more bulbous, enamel-clad continuation of the root that culminates in a single blunt cusp. The apex of the p3 is at roughly the level of the neck between the roots and the crown of the p4. The anterior margin of the p4 overhangs the minute p3 so that the anterior edge of the p4 is continuous anteroventrally with the mesial edge of the p3. The p3 is well preserved in both the left jaw of PSS-MAE 141 and the right jaw of 142.

The p4 is well preserved in both jaws of PSS-MAE 141, but missing on the left of 142. The p4 in all cimolodont multituberculates is blade-like with a serrated margin. This is also the condition in *Mangasbaatar*. The p4 in *Mangasbaatar* is a peculiar trapezoidal shape with a nearly straight mesial edge and a fairly horizontal occlusal surface. A similar condition is seen in *Catopsbaatar* and in *Tombaatar* (unpublished

specimens). The premolar is supported by three roots, two large and stout located mesially and distally and a small one between the two, a condition also known in other LCMM including *Kryptobaatar* (Kielan-Jaworowska 1971). The cusp formula in the premolar is ridge-5. The labial ridge is substantial, forming a broad platform on the posterior one-third of the tooth, approximately the area supported by the back root. This ridge becomes broader and stronger posteriorly, reaching the occlusal plane of the buccal row of the m1 at its posterior extent. The cusps in the central row are very blunt and form a weakly-serrated edge that reaches the level of the occlusal plane of the lingual row of cusps of the m1.

The first molars (m1) are present bilaterally in both specimens. The best preserved are those in PSS-MAE 141. The m1 is the largest of the lower cheek teeth, has a cusp formula 4-3, and is supported by two massive cylindrical roots. The crown of the m1 is very low and the cusps of the buccal and lingual rows have different heights (the buccal cusps are lower than the lingual cusps). This difference in height may be exaggerated by differential wear. As is common in other LCMM, the cusps of the buccal and lingual rows occupy alternate positions, with the lingual cusps placed between two successive buccal cusps. The cusps on the buccal side have subhexagonal bases but those on the lingual side are less so. All the cusps in the m1 were, in the unworn state, conical.

The m2 is well preserved and lodged in the dentaries, or fragments thereof, with the exception of the left m2 of PSS-MAE 142 that was found isolated. The m2 is a relatively small tooth with only two cusps in the labial and lingual rows. Therefore, its cusp formula is 2-2. The crown outline is subrectangular and cusps in both rows are subequal in height. The two rows of cusps are further apart than in the m1 and, the cusps of different rows do not alternate with each other so that the first cusp of the lingual row is at the same level as the first cusp of the buccal row. The four cusps occupy the corners of the subrectangular m2, determining a broad basin between them. The left m2 of PSS-MAE 142 was found isolated and it had sustained substantial damage; however, the buccal row is almost complete and shows that the posterior buccal cusp is, in this tooth, subdivided into subequal cusps, a condition not clearly seen on the right m2 of the same specimen or those of PSS-MAE 141. The m2 is supported by one root. This root is approximately of the same diameter as the crown and is deeply constricted apically, but is not divided.

DISCUSSION

CLADISTIC ANALYSIS

Few published phylogenetic analyses include LCMM among a wider sample of multituberculates, most notably Simmons (1993), Rougier *et al.* (1997), and Kielan-Jaworowska and Hurum (1997, 2001). Following Rougier *et al.* (1997) and Kielan-Jaworowska and Hurum (1997), this study recognizes Djadochtatherioidea as a monophyletic group of Late Cretaceous multituberculates and based on shared diagnostic features (see diagnosis), the new taxon is included in a modified simple matrix compiled by Kielan-Jaworowska and Hurum (1997) for other LCMM, some of which are found in the same, or similarly-aged, sediments. The wider problem of the position of Djadochtatherioidea within Allotheria is not the main purpose of this study and Kielan-Jaworowska and Hurum (2001); Kielan-Jaworowska *et al.* (2004), Yuan *et al.* (2013), and Bi *et al.* (2014) provide a framework for the higher-level relationships of Djadochtatherioidea. The matrix scores 45 characters across 17 taxa. The resultant data were analyzed using implicit enumeration via Asado version 1.7, which uses TNT as its base searching algorithm. The analysis recovered one most parsimonious tree of 101 steps (CI: 0.64 and RI: 0.68) that concurs in its structure with that of Kielan-Jaworowska and Hurum (2001) and recovers Djadochtatherioidea as a distinctive taxonomic unit, among which the large-sized multituberculates including *Djadochtatherium*, *Catopsbaatar*, *Tombaatar*, and *Mangasbaatar*, are terminal taxa (Fig. 28). These very distinctive mulituberculates reduce the blade-like lower p4, have very robust jaws, and dorsoventrally shallow skulls with small temporal areas, but preserve, overall, the typical cimolodontan morphology for the upper and lower molars. *Kryptobaatar* is a more generalized LCMM and, as a point of comparison, can be interpreted as pleisomorphic within LCMM with regards to the more derived characters seen in *Mangasbaatar* (Figs 29, 30). Namely, among those, is the development of a very prominent jugular fossa and middle ear cavity, which develops to an unparalleled degree in *Mangasbaatar* and *Tombaatar*.

The topology of the tree does not identify any clear geographical or stratigraphic pattern. Udan Sayr, where the specimens of *Mangasbaatar* are from, has traditionally been considered of likely affinities with Barun Goyot from the western Gobi (Kurzanov 1992; Szalay and Trofimov 1996). It should be noted, however, that the closest relative of *Mangasbaatar* appears to be *Tombaatar* from Ukhaa Tolgod, a locality that is likely to be a Djadochta near-equivalent (Loope *et al.* 1998; Dingus *et al.* 2008). Obviously, the faunas from Ukhaa Tolgod, Barun Goyot, and Udan Sayr are all very similar, though, lacking any clearly datable horizons, the relative temporal resolution is somewhat poor (but see Makovicky 2008).

Four taxa can be considered as large LCMM: they are *Djadochtatherium*, *Tombaatar*, *Mangasbaatar*, and *Catopsbaatar* (Figs 29–31). The first two are poorly known, mostly based on palate and jaws, while *Catopsbaatar* and *Mangasbaatar* are represented by better-preserved specimens. A skull of *Djadochtatherium* has been utilized in discussing cranial evolution of the large-sized Late Cretaceous Mongolian multituberculates (Kielan-Jaworowska and Hurum 2001) based on photographs published in reports (sent by Mahito Watabe to Zofia Kielan-Jaworowska in 1996) and popular articles (Webster 1996). However, the specimen has never been thoroughly studied and it is uncertain if it actually is *Djadochtatherium*. As such, there are limited opportunities for comparisons

Fig. 28. Phylogenetic tree showing interrelationships between multituberculates. Green branches indicate Djadochtatherioidea. Red branches indicate Djadochtatheriidae.

with those bona fide *Djadochtatherium* specimens recovered by the American expeditions (Simpson 1925) and deposited in the AMNH (Rougier *et al.* 1997). It follows that most of what is known about the cranial morphology of these multituberculates is based on *Catopsbaatar* and now these two specimens of *Mangasbaatar*. *Catopsbaatar* has been the focus of a detailed revision by Kielan-Jaworowska *et al.* (2005), where a detailed description is provided of the known specimens. All of them, however, have a missing or poorly preserved basicranium. *Mangasbaatar*, on the other hand, has a relatively complete ear region preserved, with some deformation, in two specimens. It is presently uncertain if the extreme development of sinuses and cavities in the ear region of *Mangasbaatar* is characteristic of all four of these large LCMM. However, in unpublished specimens of *Tombaatar* (PSS-MAE 630; Fig. 27), the ear region is also greatly excavated but differs substantially in detail from that of *Mangasbaatar*. In conjunction with the fact that, in *Kryptobaatar* there is already a substantial excavation of the middle ear region (Fig. 30), and particularly of the area surrounding the jugular fossa (Wible and Rougier 2000, figs 13, 19, 20), it seems likely that at least some degree of middle ear expansion was present in all of these large-sized LCMM. The specimen of cf. *Tombaatar* published by Ladevèze *et al.* (2010) is not illustrated to determine if the middle ear cavity is similarly expanded, but their fig. 1 seems to suggest that this is indeed the case. The enlargement of the middle ear cavity would therefore be a synapomorphy of this group that is further elaborated and taken to an extreme among the large forms.

Status of Djadochtatheriidae. — The results of our analysis are consistent with recent LCMM phylogenies and discusssions (Rougier *et al.* 1997; Kielan-Jaworowska and Hurum 1997, 2001; Kielan-Jaworowska *et al.* 2005) that assign *Kryptobaatar, Djadochtatherium*, *Catopsbaatar*, and *Tombaatar* to the monophyletic
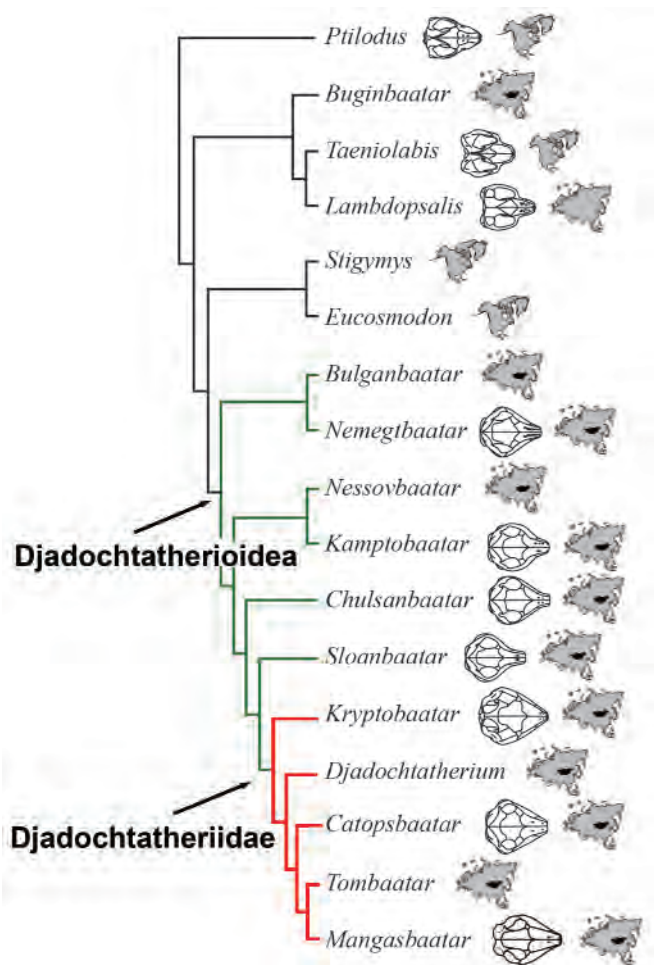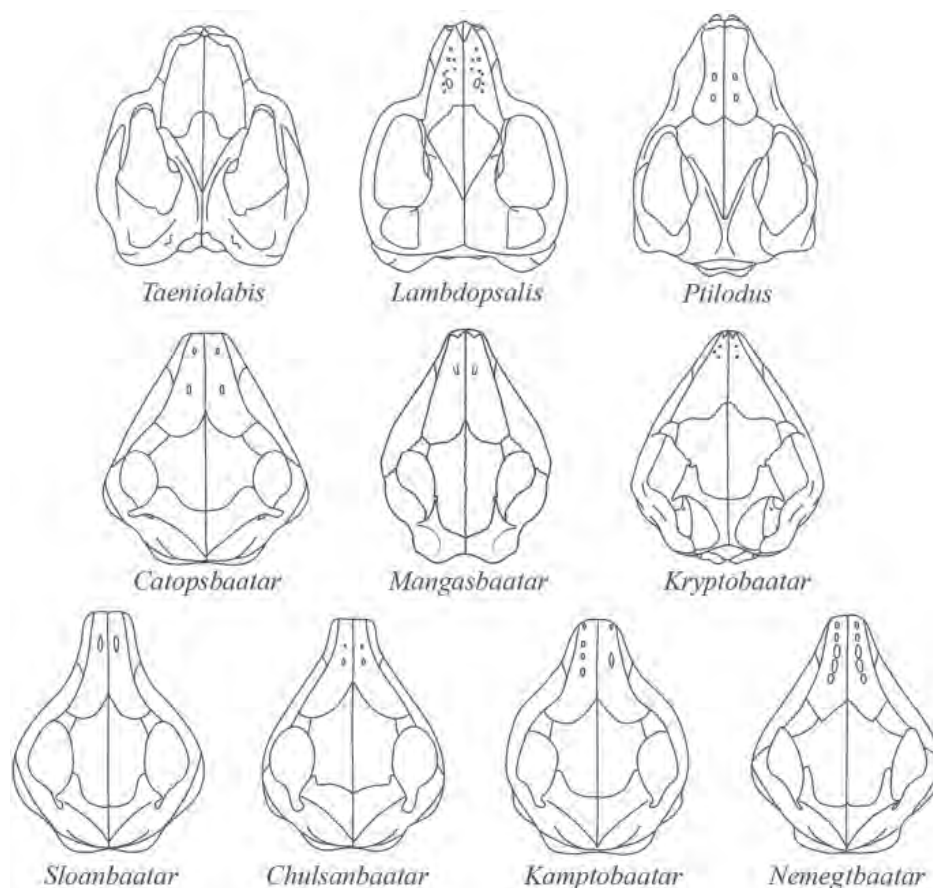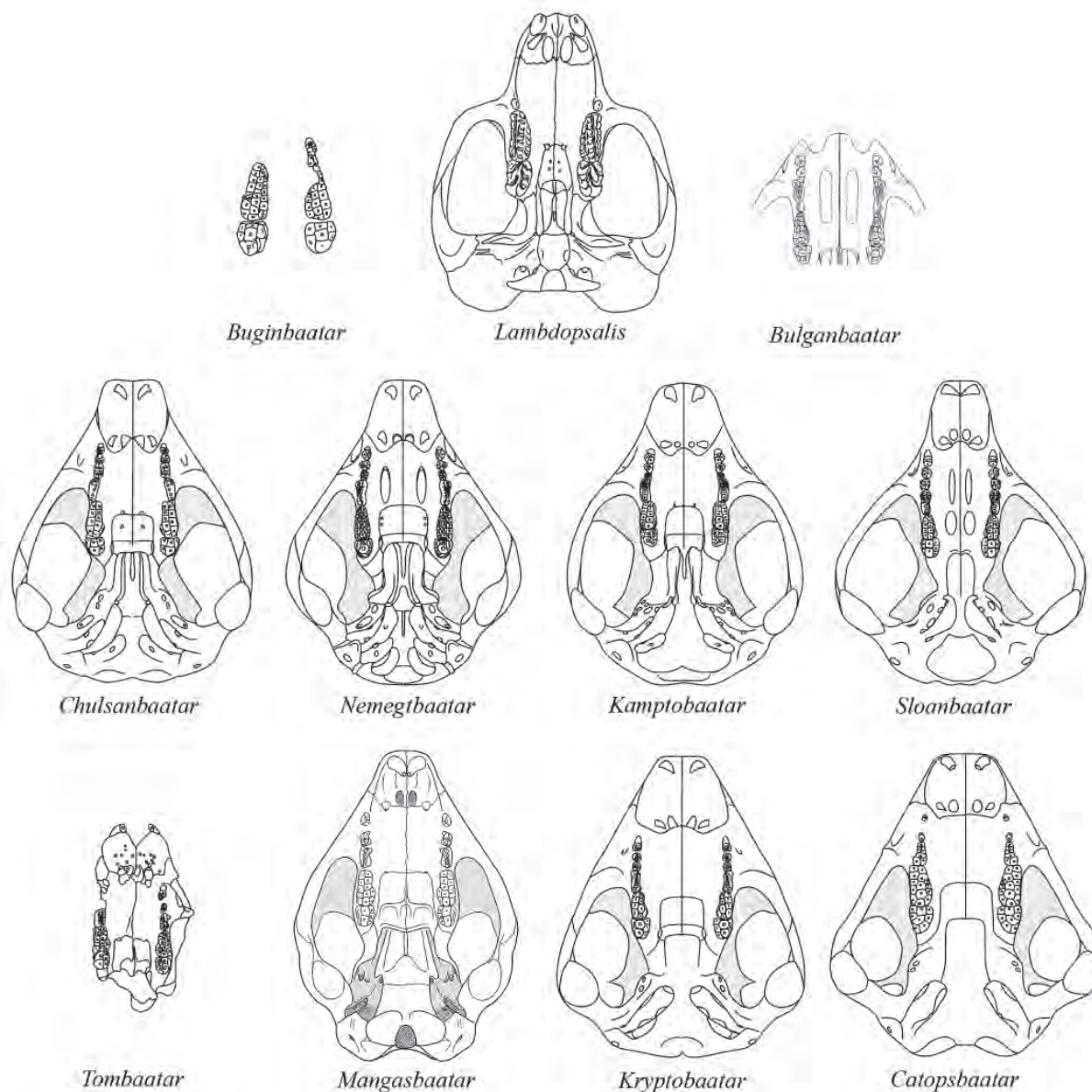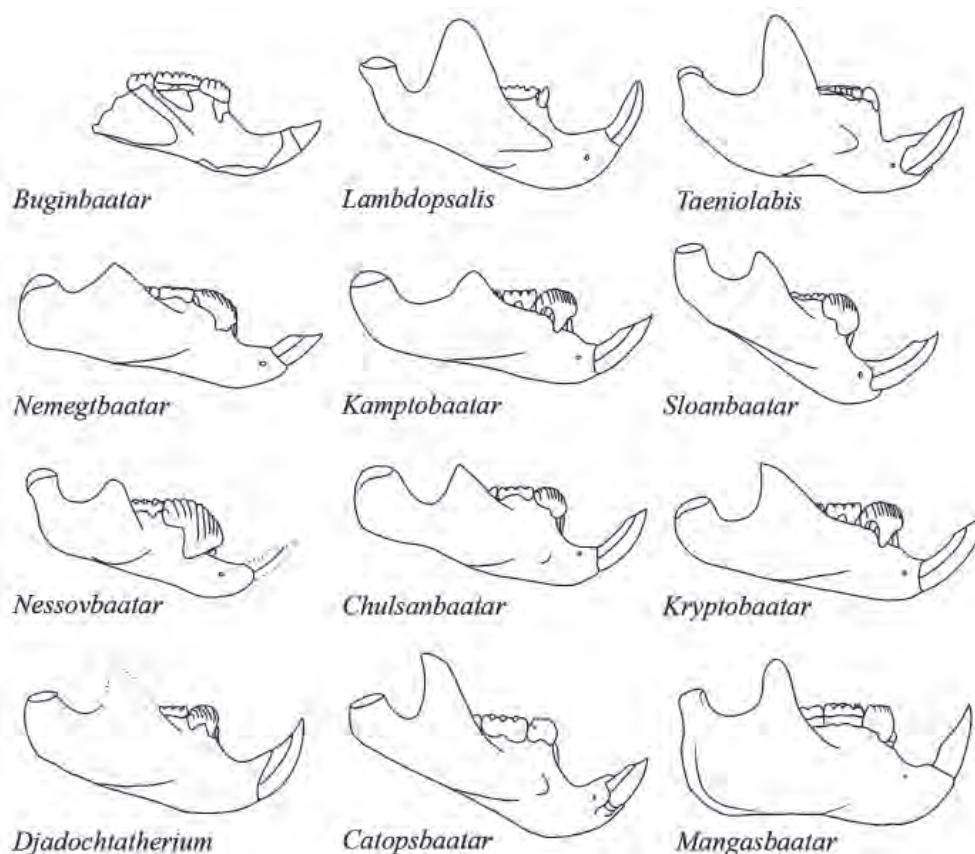
Fig. 29. Multituberculate skull reconstuctions in dorsal view, rendered to be approximately the same length. Drawing is modified from Kielan-Jaworowska *et al.* (2004) to include *Mangasbaatar*.

clade Djadochtatheriidae. This family of LCMM is recognized by cranial characters, differing from the remaining members of Djadochtatherioidea (Figs 29–31) in having a subtrapezoidal snout in dorsal view that is confluent with the zygomatic arches, an irregular, non-oval anterior part of the promontorium, in addition to the snout extending for more than 50% of the skull length (Kielan-Jaworowska *et al.* 1997). Given the anatomical evidence provided by the two skulls in this study and the resulting cladogram, *Mangasbaatar* is here referred to Djadochtatheriidae. Ultimately, this contribution adds yet another Mongolian taxon represented by well-preserved skull material, that provides details that can potentially serve as a reference for the derived multituberculate morphology characteristic of the large-sized LCMM.

Kryptobaatar is perhaps the best known LCMM (Kielan-Jaworowska 1971; Wible and Rougier 2000), with hundreds of skulls known from Ukhaa Tolgod, Mongolia (Dashzeveg *et al.* 1995; Wible and Rougier 2000). There are, however, discrepancies regarding its relationships within Djadochtatheriidae, mostly due to differences in the characters used in the phylogenetic analyses; Kielan-Jaworowska *et al.* (1997) placed *Kryptobaatar* within Djadochtatheriidae in contrast with a cladistic analysis by Rougier *et al.* (1997), which placed *Kryptobaatar* between *Chulsanbaatar* and *Bulganbaatar* Kielan-Jaworowska, 1974. Kielan-Jaworowska reasoned that the character for the subtrapezoidal snout, which is unique for Djadochtatheriidae within all of Mammalia, likely evolved only once, which places *Kryptobaatar* as a sister group to *Djadochtatherium, Tombaatar* and *Catopsbaatar*; however, *Kryptobaatar* is similar in size to the smaller and more generalized LCMM. Given the matrix employed, it is not surprising that *Kryptobaatar* is here recoverd as a related form to the LCMM multituberculates.

COMPARISONS WITH OTHER LCMM

Premaxilla. — In ventral view the premaxilla has thickenings between the alveoli for I2 and I3, a feature which is present in several other forms such as *Tombaatar*, *Nemegtbaatar*, *Kryptobaatar*, and

Fig. 30. Multituberculate skull reconstuctions in ventral view, rendered to be approximately the same length. Drawing is modified from Kielan-Jaworowska *et al.* (2004) to include *Mangasbaatar*.

Chulsanbaatar, but not present in *Kamptobaatar* Kielan-Jaworowska, 1970 (Kielan-Jaworowska *et al.* 1986; Wible and Rougier 2000; Rougier *et al.* 1997).

As is the condition for nearly all multituberculates described to date, there is no internarial bar or septomaxilla present in *Mangasbaatar*. The internarial bar was noted by Miao (1988) in two specimens of *Lambdopsalis*, though this finding is controversial as both of these bars were of differing size between specimens. Regardless, the feature has no taxonomic utility, as *Lambdopsalis* is the only known multituberculate to express this condition. The condition is currently unknown in *Haramiyavia* Jenkins *et al.*, 1997, *Arboroharamiyavia* Zheng *et al.*, 2013, and *Megaconus* Zhou *et al.*, 2013 and is absent in other primitive forms, only making an appearance within basal mammaliaformes such as *Morganucodon* Kühne, 1949 (Kermack *et al.* 1981), *Haldanodon* Kühne *et* Krusat, 1972 (Lillegraven and Krusat 1991), and possibly *Docodon* Marsh, 1881 (Rougier *et al.* 2015). *Vintana sertichi* Krause *et al.*, 2014 shows an elevated internarial process of the premaxilla that, however, does not reach the nasals.

Hahn and Hahn (1994) described and illustrated a septomaxilla in *Pseudobolodon krebsi* Hahn, 1977, a paulchoffatiid from the Jurassic of Portugal; this putative septomaxilla was wedge-like and located posterior to the premaxilla, between the nasal and the maxilla. Wible *et al.* (1990) argue that the septomaxilla in

Fig. 31. Multituberculate mandible reconstructions in lateral view, rendered to be approximately the same length. Drawing is modified from Kielan-Jaworowska *et al.* (2004) to include *Mangasbaatar.*

Pseudobolodon was an artifact, an interpretation followed by Kielan-Jaworowska *et al.* (2004) in their revision of the morphological diversity of multituberculates. One of us had the opportunity to study the specimen and we agree with Wible's *et al.* (1990) interpretation; as far as we are aware there is no reliable record of a septomaxilla in any multituberculate including the LCMM. The premaxilla is hypertrophied in early multituberculates probably related to the large size of the incisors, a feature present with variable development in all multituberculates.

Maxilla. — The sub-trapezoidal shape of the skull is due, in part, to the lateral bulging of the maxilla. This bulging is, as indicated by CT scans (Kielan-Jaworowska and Hurum 1997, 2001; Rougier *et al.* 1997; Kik 2002; Kielan-Jaworowska *et al.* 2004, 2005), an accommodation for an enlarged maxillary sinus. Such a large development of the maxillary sinuses is found uniquely within some members of Djadochtatherioidea, namely *Kryptobaatar*, *Djadochtatherium*, *Catopsbaatar*, and *Tombaatar* (Kielan-Jaworowska and Hurum 1997; Rougier *et al.* 1997; Wible and Rougier 2000; Kielan-Jaworowska *et al.* 2005) and results in a distinctive trapezoidal snout. Other LCMM, ptilodontoids, and taeniolabidoids such as *Lambdopsalis* and *Taenolabis,* exhibit an arcuate snout which forms a sharp angle with the zygomatic arches at their point of contact (Miao 1988; Kielan-Jaworowska and Hurum 1997) and represents the generalized mammalian condition.

Like *Catopsbaatar* (Kielan-Jaworowska *et at.* 2002, 2005)*,* there appears to be a secondary infraorbital foramen present in *Mangasbaatar,* though the utility of this feature in cladistics has been questioned by Miao (1988) and others, as it may be variable within a species. Nevertheless, multiple rostral exits for the infraorbital canal is a basal mammaliaform feature present in morganucodontids (Kermack *et al.* 1981), basal multitubeculates (Hahn 1985), some dryolestoids, and *Vincelestes* Bonaparte, 1986 (Rougier *et al.* 1992; Rougier 1993) in addition to monotremes (Kuhn 1971; Zeller 1989).

Palatine. — The bones that contribute to the formation of the "orbital mosaic" are best known in *Kryptobaatar* and *Lambdopsalis*, in which the palatine has no contribution and the maxilla forms the anterior part of the orbital roof. Like these two taxa, *Mangasbaatar* also lacks an exposure of the palatine

within the orbital fossa. Miao (1988) speculated that the lack of the palatine within the orbit may be a synapomorphy for multituberculates, which is supported by *Lambdopsalis*, *Kryptobaatar*, and *Mangasbaatar*. Interpretations of the orbital fossa of *Nemegtbaatar* by Hurum (1994, 1998a) and illustrations of *Ectypodus* Matthew *et* Granger, 1921 (Sloan 1979, fig. 1) noted a palatine exposure within the orbital area that would, if interpreted correctly, suggest that the feature is polymorphic within LCMM. In contrast, Wible and Rougier (2000), though unable to examine some of the reported specimens of *Nemegtbaatar*, examined *Ectypodus* (YPM-PU 14724) and did not identify the sutures suggesting the presence of this exposure, confirming that the same area in *Kryptobaatar* is formed of maxilla. It appears likely that in LCMM the palatine is excluded from the orbital mosaic or it is at least very small.

Djadochtatheriid multituberculates routinely share a uniquely developed postpalatine torus, most strongly developed in *Mangasbaatar*. The presence, absence, and relative size of this feature has been scored for several multituberculates including *Kryptobaatar* (Wible and Rougier 2000), *Tombaatar* (Rougier *et al.* 1997), *Catopsbaatar* (Kielan-Jaworowska *et al.* 2005), *Lambdopsalis* (Miao 1988), and a variety of therian such as *Zalambdalestes* Gregory *et* Simpson, 1926 and metatherians (Rougier *et al.* 1998). The postpalatine torus in *Tombaatar* is strongly developed; however, when compared with that in *Mangasbaatar*, the central ridge on the torus lacks the shallow recess that the torus of *Mangasbaatar* exhibits. The torus in *Kryptobaatar* is weaker than in either one of the large multitubeculates, *Tombaatar* and *Mangasbaatar*, and shares with *Tombaatar* the lacks of a central recess. In 2005, a specimen of *Catopsbaatar*, ZPAL MgM-I/80, was published in which the torus was completely preserved but weakly developed. Nevertheless, some degree of postpalatine torus development is consistently present among large Mongolian multituberculates.

Though the exact role of the postpalatine torus in extinct and extant mammals remains ambiguous, the degree of development within djadochtatheriids to the exclusion of other multituberculates suggests that it may represent, at least, a useful phylogenetic character. In extant mammals, such as the aardvark or the hedgehog, this bony feature is located at the attachment for the tensor veli palatini muscle (Barghusen 1986), which tenses the soft palate. It is unclear what benefit a more robust process of this sort confers, as modern taxa that share it do not establish a clear pattern among diet, body size, and the morphology of the torus.

Pterygoid. — The mesocranium, the portion of the skull between the hard palate and the anterior pole of the promontorium, is dramatically altered in early mammals from the primitive condition present in non-mammaliaform cynodonts like brasilodontids and probainognathians (Martinelli and Rougier 2007; Kielan-Jaworowska *et al.* 2004).

In multituberculates the pterygoids are rarely separated by sutures from the surrounding elements but they have been consistently identified as the main element forming the bulk of the lateral wall of the median or medial choanal passage, the number of choanal passages depending on the presence of a mid-line crest (Kielan-Jaworowska 1971; Kielan-Jaworowska *et al.* 1986; Miao 1988; Wible and Rougier 2000). In *Mangasbaatar* a strong median ridge is missing and therefore there are only three choanal passages: one in the midline interpreted as the nasopharyngeal passage and bounded laterally by the pterygoids, and two lateral ones developed between pterygoids and alisphenoid, interpreted as for the eustachian tube and the pharyngotympanic connection. Barghusen (1986) recognized the complex nature of the mesocranium in non-mammalian cynodonts and called the ridges medial to the transverse process of the pterygoid present in *Thrinaxodon* Seeley, 1894 and relatives pterygopalatine ridges. He also recognized these ridges in *Kamptobaatar* (Barghusen 1986, fig. 6) and by extension in other LCMM with similar palatal morphology. This nomenclature and identification has been followed since by most researchers working in multituberculates until quite recently (*i.e.*, Wible and Rougier 2000; Kielan-Jaworowska *et al.* 2005). Implicit in Barghusen identifications is the fact that the hamulus (or lateral pterygoid process) is not homologous with the pterygopalatine ridges and that both structures are separated. However, Kielan-Jaworowska (1971 and subsequent papers) and Wible and Rougier (2000) recognized a hamular process in the distal portions of the pterygopalatine ridges, but doubted its homology with the therian hamulus. In *Mangasbaatar* and other LCMM the hamulus develops in the pterygoid wall separating the lateral from the medial choanal passages (medial and lateral pterygopalatine troughs of Wible and Rougier 2000). The lateral passage is bounded laterally by the forward extension of the alisphenoid and it is presumably, at least in the degree of development, a derived feature of multituberculates. It would follow that the hamulus in multituberculates and the transverse process of the pterygoid of non-mammalian cynodonts can be homologized. Therefore, the pterygopalatine ridges of *Thrinaxodon* and similar forms would not be homologous with the "pterygopala-

tine ridges" of multituberculates. Despite concerns on the position and relationships of the multituberculate hamulus (Kielan-Jaworowska 1971; Wible and Rougier 2000), we believe its homology with the therian hamulus is the most likely assumption.

Nasal. — PSS-MAE 142 retains the posteriormost portion of the right nasal, which reveals that the frontals project as a wedge in between the suture between the nasals posteriorly, a primitive character present in nearly all Mesozoic mammals, save for perhaps *Catopsbaatar*, though it is likely that this is due to poor preservation of the sutural pattern in this form (Kielan-Jaworowska *et al.* 2005). Unlike some of the small LCMM, *Nemegtbaatar* for example (Kielan-Jaworowska *et al.* 1986), that show a multitude of nasal foramina, *Mangasbaatar* and relatives seem to have a few large-sized foramina.

Lacrimal. — The lacrimal of the LCMM is characteristic; it is present as a large, roughly rectangular bone visible on the dorsal surface of the skull, separating the frontal from the maxilla (Kielan-Jaworowska and Hurum 1997). Wible and Rougier (2000) were unable to identify with certainty the presence of a lacrimal in the specimens of *Sloanbaatar*, *Catopsbaatar*, or *Bulganbaatar* stored in Warsaw, though other specimens of *Catopsbaatar* show the character clearly. A sizable lacrimal is a primitive feature in multituberculates, present in paulchoffatiids and LCMM, though the extent of the orbital exposure of this bone was uncertain in other taxa. *Lambdopsalis* (Miao 1988) lacks the lacrimal completely and *Taeniolabis* must have lacked a facial exposure of the bone if it were present as claimed by Kielan-Jaworowska and and Hurum (1997). *Mangasbaatar* fits the condition described for other LCMM, displaying a large, subrectangular lacrimal that separates the frontal from the maxilla on the dorsal surface of the skull. In *Mangasbaatar*, the lacrimal contributes to the formation of an orbital pocket, as in *Kryptobaatar*, which has a small orbital process (Wible and Rougier 2000).

Frontal. — The ethmoidal foramen in *Mangasbaatar* is formed by both the frontal and orbitoshpenoid and likely distributed the ethmoidal nerve and artery. Though the presence of this foramen was questioned by Simmons (1993) in both *Ectypodus* and *Ptilodus* Cope, 1881, a more recent analysis by Wible and Rougier (2000) refuted this claim, holding that the foramen is present, not only in *Kryptobaatar* but in all multituberculates including *Ptilodus* and *Ectypodus*, as well as in most or all living mammals.

Parietal. — The postorbital process is common among mammalian skulls (Novacek 1986), and its morphology, whether long, short, or composed of frontal, parietal or both has been a point of interest in distinguishing relationships within multituberculates. Miao (1988) held that the postorbital process seen in multituberculates is not homologous to that seen in other mammals because the parietal position of the postorbital process does not delimit the back of the orbit. This claim has, however, been refuted numerous times (see Wible and Rougier 2000). Among multituberculates the postorbital process is positioned more posteriorly over the orbit than in other therians and among LCMM this feature is entirely formed by the parietal (Gambaryan and Kielan-Jaworowska 1995). In *Tombaatar*, *Catopsbaatar*, *Mangasbaatatar*, and *Djadochtatherium*, the postorbital process is comprised entirely by the parietal and, contrary to the condition in *Chulsanbaatar*, *Kamptobaatar*, and *Nemegtbaatar* (Kielan-Jaworowska and Hurum 1997), is very long (Kielan-Jaworowska and Hurum 1997; Wible and Rougier 2000; Kielan Jaworowska *et al.* 2005) and is best seen on the left side of PSS-MAE 141.

Squamosal. — The exposed region on the right side of PSS-MAW-141 reveals the contact between the squamosal and the petrosal, showing that the squamosal forms the lateral and dorsal walls of the ascending canal. This has been previously described in *Kryptobaatar* and *Vincelestes* (Rougier *et al.* 1992; Wible and Rougier 2000) and it is a primitive component of the basal mammaliaform circulatory pattern (Wible 1983, 1986, 1987; Rougier *et al.* 1992; Wible and Hopson 1993; Rougier and Wible 2006).

Petrosal. — The perilymphatic duct is primitively exposed in the middle ear cavity, and such is the condition regarded as primitive among monotremes, despite the partially enclosed perilymphatic duct of the echidnas (Rougier and Wible 1996). Most therians enclose the duct via a process, the processus recessus (Goodrich 1930; de Beer 1937), which is a derived feature present also among other mammals closely related to marsupials and placentals, like *Vincelestes* and dryolestoids (Rougier *et al.* 1992; Luo *et al.* 2012). It is notable that the perilymphatic grooves differ on the left and right of PSS-MAE 142, presenting a hurdle in the comparison of these specimens. The left side of PSS-MAE 141 has no evidence of a groove, agreeing with the condition on the right side of PSS-MAE 142, suggesting that, in *Mangasbaatar*, the groove is covered by

bone forming an enclosed duct. Despite some variability in this particular feature, the jugular fossa between the two is highly similar. Multituberculates, though, have shown some variability in the perilymphatic duct's enclosure by bone. Several isolated petrosals, likely belonging to taeniolabidoids collected from the Late Cretaceous of North America, displayed a condition wherein the perilymphatic duct was not fully bounded by bone, but rather by two bony lappets bordering the groove without making contact with one another (Rougier and Wible 2006).

Some multituberculates share certain features with monotremes such as a large anterior lamina of the petrosal, and, like adult monotremes, in *Mangasbaatar* no clear suture can be seen between the anterior lamina and the petrosal. Given the developmental origin of this feature within monotremes (Presley and Steel 1976; Kemp 1983), however, it is parsimonius to assume that a similar origin accounts for the feature within multituberculates. The anterior lamina of the petrosal is lacking in *Lambdopsalis* but present in *Mangasbaatar* and other LCMM, further distinguishing Djadochtatherioidea from *Lambdopsalis* (Miao 1988; Kielan-Jaworowska *et al.* 2004) and potentially other taeniolabidoids.

On the ventral view it becomes apparent that the region surrounding the braincase is significantly dorsally depressed posterior to the palatine, which produces several exaggerated features such as an enlarged rostral tympanic process of the petrosal. In *Mangasbaatar* the RTPP is significantly larger in proportion with the rest of the skull when compared with *Kryptobaatar,* likely owing to the deeply excavated ear region. Within this area, a concave space formed between the RTPP and the basioccipital is composed of both the petrosal and the basioccipital in *Mangasbaatar* as in *Kryptobaatar* (Wible and Rougier 2000). The two bones both contribute to this cavity; however, in *Mangasbaatar,* the bordering basioccipital bone which forms the cavity's medial wall has a greater height dorso-ventrally and the contribution of this bone to the aforementioned cavity is nearly vertical in its entirety. This space is further subdivided by crests expanding into the middle ear cavity from the petrosal and the basioccipital; these extensions do not fully divide the region in compartments, but determine specific areas within the cavernous middle ear.

Middle ear (petrosal, basioccipital and exoccipital). — Due to the acquisition of several derived features, particularly in the ear region, *Mangasbaatar* appears as a highly specialized member of Djadochtatherioidea, closely related to *Tombaatar* and *Catopsbaatar.* Observations of *Kryoptobaatar,* currently the most thoroughly-documented multituberculate, and related members establish a trend among derived members of this group to enlarge the middle ear space. This region in *Mangasbaatar* is unique among other LCMM in the depth created by a dorsal excavation of the basicranium, measured at approximately 4 mm^3. It is difficult to compare this specimen to related taxa due to lack of consistent preservation of the region; however, it is clear that this cavity is proportionally larger than that of *Kryptobaatar* or *Catopsbaatar,* and similar to *Tombaatar* (Fig. 27).

In *Mangasbaatar*, all of the surrounding elements of the ear region project ventrally and help to encompass a very large space. The membranous component of the middle ear cavity likely extended ventrally from the edges of those cavities, and it was certainly of sizable proportions. But if compared with other LCMM, the proportion of the cavity delimited by bone is much larger in *Mangasbaatar* than in any of the other previously described multituberculates from the region. In *Kryptobaatar*, the same elements — exoccipital, basioccipital, basisphenoid, squamosal, and petrosal — also project ventrally and form distinct pockets, but these are not as prominent. The circumscribing of the middle ear region by bony projections in *Mangasbaatar* results in a relatively extensive bony encasing of the middle ear region, analogous to the auditory bulla present in many lineages of therians (Klaauw 1931; MacPhee 1981; Novacek 1977, 1986). A similar "sinking" of the petrosal into the braincase can been seen in some borhyenoid marsupials (de Muizon *et al.* 1997), and the surrounding elements also provide a partial enclosure of the middle ear cavity; in these marsupials, as in multituberculates, most of the middle ear space was enclosed ventrally by a membrane in the absence of a fully developed bulla.

The functional significance of an expanded middle ear region is not straightforward to ascertain. The mammalian middle ear is an impedance transformer that matches the impedance between air-transmitted sound and the perilymphatic fluid in the inner ear (Webster and Webster 1984). Among most of living therian mammals, the middle ear cavity is surrounded by a rigid osseous bulla composed by a variety of bony elements that include the ectotympanic as the main support for the tympanic membrane. The ectotympanic can contribute to the enclosure of the middle ear by forming a substantial portion of the bulla, but depending on the group, a variety of neomorphic elements or other bones from the basicranium can participate in the formation of the bulla. The specific composition of the bulla has traditionally been a source of systematic and phylogenetic data (Novacek and Wyss 1986). The combination of elements, shapes, sizes, and presence

of internal division by septae, etc., of the ear region determine an optimal frequency for a given array of morphologies; this is the natural frequency of a middle ear (Fleischer 1978; Mason 2015, 2016a). This frequency increases with stiffness of both membrane-ear ossicles and tympanic cavity, but decreases with a greater mass of the membrane (functionally including the ossicular chain) and a larger air volume (Dallos 1973; Fleischer 1978; Mason 2006, 2013, 2015, 2016a, b). However, the primitive condition for mammals is the absence of a bulla, and most of the tympanic cavity is surrounded by a membrane that has, on its lateral aspect, a ring formed by the ectotympanic that supports the tympanic membrane. Such a middle ear is susceptible to deformation by chewing and jaw movements that deform the middle ear space and alter its auditory tuning; additionally, a membrane-encased middle ear region is more susceptible to interference of the low frequency sounds (Tonndorf *et al.* 1966; Mason 2015, 2016b). This primitive mammalian ear is present among monotremes and basal marsupials (Klaauw 1931; Simpson 1938; Griffiths 1978; Ashwell 2013). Similarly, in *Mangasbaatar* the middle ear cavity is surrounded only partially by bone and most of its ventral surface must have been enclosed by membrane; given the osteological morphology, most likely multituberculates lacked the stiffness of the middle ear enclosure as, for example, in desert dwelling rodents with large middle ear spaces enclosed by a bulla (Webster 1966; Fleischer 1973; Mason 2006, 2013, 2015, 2016a). Nevertheless, many of these recent mammals with large middle ear spaces (Mason 2004, 2013) live in arid environments or spend a substantial portion of their lives underground; the environmental conditions in Ukhaa Tolgod and most of the Late Cretaceous Mongolian sites seem to indicate that the environment was dominated by sands and some degree of periodical or seasonal aridity (Loope *et al.* 1998; Dingus *et al.* 2008). Dry air rapidly dissipates high frequency sound (Huang *et al.* 2002), therefore it would be expected some reliance on low frequency sound by the LCMM. In this context, an enlarged, more rigidly enclosed middle ear region would be consistent with an optimization for the perception of low frequency sound by increasing the non-pliable surfaces surrounding the middle ear.

Talpids (moles) and golden moles share a medially sunken middle ear cavity which forms an open connection between the two middle ears through an opening in the basicranium, which allows for pressure-difference localization in the low frequency range (Mason 2013). Though such an adaptation is common among non-mammalian tetrapods, it is rare among mammals, which typically have these two cavities separated by bone and soft tissue. Among the talpids and golden moles the expansion of the middle ear cavity is done by recession of the basicranium bordering the medial wall of the middle ear cavity, while other mammals typically expand their middle ear cavities via ventral expansion of the bulla (Mason 2013). If the volume of the middle ear spaces of *Kryptobaatar* and *Mangasbaatar* are compared, it is clear that the increase is due mostly to the "sinking" of the petrosal and promontorial area into the braincase. Though there is no known open connection between the middle ear spaces of any multituberculate studied thus far, the medial expansion of the middle ear cavity is similar to what must have occurred in the ancestors of golden or talpid moles.

Furthermore, the tensor tympani fossa, which is formed via attachment of the *m. tensor tympani*, is relatively small in *Mangasbaatar* in comparison with the rest of the middle ear space. It can be inferred, by extension, that the *m. tensor tympani* was also relatively small. A similar morphology is noted in the marsupial mole *Notoryctes* Stirling, 1891 (Ladevèze *et al.* 2008), while the muscle is completely lost in adult golden moles (Mason 2003) and a variety of mammals with a fossorial life-style (Mason 2013). Indeed, the tensor tympani muscle has been lost, convergently, in at least 4 distantly-related groups: marsupial moles, spalacid mole-rats, golden moles and talpid moles, all of which occupy a subterranean habitat (Mason 2013). The stapedius muscle is also often missing in forms with enlarged middle ear cavities (Hinchcliffe and Pye 1969; Webster and Webster 1975; Heffner *et al.* 2001), however, no mammal is known to be missing both muscles, the tensor tympani and the stapedius muscle. The stapedius muscle increases stiffness of the middle ear ossicles and this in turn dampens transmission of low frequency sound. The presence or absence of a stapedius muscle cannot be unequivocally ascertained in *Mangasbaatar*; however, a stapedius fossa has been identified in multituberculates (Kielan-Jaworowska *et al.* 1986; Rougier *et al.* 1992, 1996a; Wible and Rougier 2000) and it appears likely that the muscle was present among LCMM. Meng (1992) described the stapes of *Lambdopsalis*; the element is well preserved, columelliform, and without a distinct stapedius process. It is therefore possible that in at least some multituberculates the stapedius muscle was much reduced or absent. A partial stapes of *Kryptobaatar* was described by Rougier *et al.* (1996a) as bicrurate, but the specimen is incomplete and no evidence of a stapedius process is preserved. It is clear that some degree of diversity existed among multituberculates and that the LCMM and *Lambdopsalis* are both radically different regarding their adaptation related to the ear region. Reports of middle ear bones by Hurum *et al.* (1995,

1996) in some LCMM are hampered by misidentification of calcite concretions as fragmentary ear ossicles and cannot be discussed further until the specimens are restudied.

Regardless of the functional similarities that may exist between the middle ears of LCMM and therians it is clear that the expansion of the middle ear cavity was acquired independently in both linages. Basal members of the therian lineage, like symmetrodonts, dryolestoids and *Vincelestes*, lack any particularly enlarged ear regions (Hughes *et al.* 2015; Ji *et al.* 2009; Rougier *et al.* 1992, 2003; Ruf *et al.* 2009).

Dentition. — The dental formula of both *Mangasbaatar* specimens (I2/1, C0/0, P3/2, M2/2) and their molar and premolar morphology clearly refer these multituberculates to Djadochtatherioidea, and further analysis of their skull morphology and petrosal anatomy refers them as terminal members of Djadochtatheriidae. Unlike *Tombaatar,* and similar to all other LCMM, the I3 is placed entirely within the premaxilla, whereas in *Tombaatar,* the I3 is in direct contact with the maxilla and premaxilla, lying within the suture between the two bones. Like *Tombaatar*, the biradiculated P1 has three, conical cusps and the P3 in turn has four conical cusps; all that remains between P1 and P3 is a short diastema which likely housed the remnants of the DP3 (Rougier *et al.* 1997). The best preserved P4 among these two specimens is highly similar to that in *Tombaatar,* differing in the relative heights of the cusps within the middle row. In *Tombaatar,* the middle cusp row in P4 contains five cusps, with the third in the row being the tallest of them all (Rougier *et al.* 1997), in contrast to *Mangasbaatar,* in which the 5 cusps of the middle row of P4 increase in size posteriorly. Aside from this difference, the overall morphology of this cusp row is highly similar to *Tombaatar* and other LCMM, aligned posteriorly with the buccal cusp row of M1 and anteriorly with the lingual cusp row of P3 (Rougier *et al.* 1997).

The M1 cusp formula in *Mangasbaatar* (5:5:2) differs from *Tombaatar* (4:5:2)*, Catopsbaatar* (5-6:5-6:4) and *Kryptobaatar* (4-5:4:3-5), while the M1 is not preserved in the type specimen of *Djadochtatherium* (Rougier *et al.* 1997; Kielan-Jaworowska and Hurum 1997; Kielan-Jaworowska *et al.* 2004; Kielan-Jaworowska *et al.* 2005). *Mangasbaatar* most closely resembles *Tombaatar* in this regard, though the molars are slightly larger within *Mangasbaatar*. Additionally, in occlusal view, the outer edge of the lingual cusp row in the M1 of *Tombaatar*, *Mangasbaatar*, and *Kryptobaatar* forms a bulge from the remaining body of the tooth. In *Catopsbaatar*, the outer edge of the M1 lingual cusp row is confluent with the remaining rows in the M1.

Though the type specimen of *Tombaatar* is lacking the posterior half of the cranium, preliminary observations of another, more complete specimen of *Tombaatar* show a high degree of similarity with *Mangasbaatar* (Fig. 27). Despite their similarities, both specimens of *Mangasbaatar* are slightly larger in comparison with *Tombaatar*. The M2 on *Tombaatar* are slightly smaller with respect to *Mangasbaatar*, and the skull length of PSS-MAE 141 (6.30 cm) is greater than that of the unpublished specimen of *Tombaatar* (5.91 cm). Though PSS-MAE 141 and PSS-MAE 142 are somewhat deformed, the palatal region and the dental arch of *Mangasbaatar* can be accurately observed and exhibit less curvature than in *Tombaatar*. The dentition of the large members of Djadochtatherioidea retains the same overall morphology of more generalized multituberculates like *Kryptobaatar*, where the M/m1 is of moderate size and the M/m2 remains small but distinctive, while the P4 is relatively small and uncomplicated. The p4, on the other hand, loses the blade-like aspect characteristic of most multituberculates and it is supported mesially by a peg-like p3. The trapezoidal outline of the p4 and the absence of a P2 are distinctive dental feature of the large LCMM.

CONCLUSIONS

The skull of *Mangasbaatar* is highly similar to the closely related *Tombaatar*, *Catopsbaatar*, *Kryptobaatar*, and *Djadochtatherium*. The suite of features, including the subtrapezoidal shape of the skull, the dentition, petrosal anatomy and other features, clearly allies *Mangasbaatar* with these other taxa. The morphology of the postpalatine torus, though unknown in function, is a highly conspicuous character among more derived members of LCMM and is most strongly developed in *Mangasbaatar* and *Tombaatar*. Based on the phylogenetic analysis adapted from Kielan-Jaworowska and Hurum (1997), and amended here, this study recovers *Mangasbaatar* among the djadochtatherian LCMM. Specifically, *Mangasbaatar* is a terminal member of the monophyletic clade Djadochtatherioidea and sister-group to *Tombaatar*.

The degree of excavation of the middle ear cavity in *Mangasbaatar*, in addition to the relatively small tensor tympani fossa, may suggest a fossorial or semi-fossorial habit for *Mangasbaatar*, as this is a pattern

seen among modern, fossorial, desert-dwelling rodents (Mason 2013). The ventral expansion of the bones enclosing this space may have functioned similarly to the bulla in modern mammals, forming a rigid base for the soft structures encasing the middle ear, increasing the rigidity of the cavity, and thus aiding in low frequency audition (Fleischer 1978; Mason 2013), adding to the wide variety of habitats and niches occupied by multituberculates.

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APPENDIX 1

Character list adapted from Kielan-Jaworowska and Hurum (1997), with the addition of character 44 for the postpalatine torus and the addition of *Mangasbaatar udanii* as a new taxon.

1. Enamel covering of lower incisor of uniform thickness (0), thicker on labial surface than on lingual surface (1), completely restricted to labial surface of tooth (2). ***Mangasbaatar* (2)**
2. p3 present (0), absent (1). ***Mangasbaatar* (0)**
3. p4 serration count 5 or less (0), 6–10 (1), more than 10 (2). ***Mangasbaatar* (0)**
4. p4 in lateral view rectangular (0), arcuate (1), trapezoidal (2), triangular (3). ***Mangasbaatar* (2)**
5. m1 cusp formula 4:3 (0), 4:4 (1), 5:4–5 (2), 7:4 or higher (3). ***Mangasbaatar* (0)**
6. Ratio of p4:m1 length less than 0.6 (0), 0.6–1.7 (1) above 1.7 (2). ***Mangasbaatar* (1)**
7. m2 cusp formula 2–2 (0), more (1). ***Mangasbaatar* (0)**
8. I2 bicuspid (0), single-cusped (1). ***Mangasbaatar* (?)**
9. I3 located on margin of palate (0), slightly shifted from the labial margin (1), in about the middle of the palatal part of the premaxilla (2). ***Mangasbaatar* (2)**
10. Upper premolars five (0), four (1), three (2) one (3). ***Mangasbaatar* (2)**
11. P3 double-rooted (0), single-rooted (1). ***Mangasbaatar* (0)**
12. P4 double-rooted (0), single-rooted (1). ***Mangasbaatar* (0)**
13. Length of upper premolar tooth row: molar tooth row more than 1.5 (0), 1.54.5 (1), 0.5–0.1 (2). ***Mangasbaatar* (1)**
14. P4 cusp formula 0–5:1–4:0–5 (0), 0–5:5–10:0–5 (1), 5–7:5–8:2–5 (2). ***Mangasbaatar* (1)**
15. M1 cusp formula 4–5:4–5:0–5 (0), 5–7:5–8:2–5 (1), 5–11:7–10:611 (2). ***Mangasbaatar* (0+1)**
16. M1 inner ridge length: length of M1 0.5 or less (0), more than 0.5 (1). ***Mangasbaatar* (0)**
17. Width of P4:M1 ratio more than 0.9 (0), 0.9–0.6 (1), 0.6–0.45 (2), 0.45–0.2 (3). ***Mangasbaatar* (2)**
18. M2 cusp formula 1:2:2 (0). 1:2:3 (1), more (2). ***Mangasbaatar* (0+1)**
19. Ridge between the palate and the lateral walls of the premaxilla absent (0), present (1). ***Mangasbaatar* (1)**
20. Shape of the snout in dorsal view: incurved in front of the zygomatic arches with anterior part directed posterolaterally (0), incurved with anterior part of zygomatic arches directed transversely (1), trapezoidal, not incurved in front of zygomatic arches (2). ***Mangasbaatar* (2)**
21. Number of pairs of vascular foramina on nasal: 1 (0), 2 (1), more (2). ***Mangasbaatar* (?)**
22. lnfraorbital foramen positioned dorsal to P1 (0), dorsal to P2 (1), dorsal to P3 or P3 (2). ***Mangasbaatar* (1)**
23. Base of zygomatic arch as marked by posterior edge directly dorsal to P4 (0), dorsal or posterior to P4/M1 embrasure (1). ***Mangasbaatar* (0)**
24. Postorbital process short (0), long (1). ***Mangasbaatar* (1)**
25. Snout length 49% or less of total skull length (0), 50% or more of skull length (1). ***Mangasbaatar* (0)**
26. Frontals pointed anteriorly and not deeply inserted between the nasals (0), pointed anteriorly and deeply inserted between the nasals (1), with subtransversal anterior margins (2). ***Mangasbaatar* (1)**
27. Frontal-parietal suture V-shaped (0), U-shaped (1). ***Mangasbaatar* (1)**
28. Contacts between nasal and parietal absent (0), present (1). ***Mangasbaatar* (0)**
29. Facial surface of lacrimal very small and arcuate (0), large, roughly rectangular (1). ***Mangasbaatar* (1)**
30. Thickening in palatal process of premaxilla absent (0), present (1). ***Mangasbaatar* (1)**
31. Incisive foramen situated within premaxilla (0), limited posteriorly by maxilla (1). ***Mangasbaatar* (1)**
32. Palatal vacuities absent (0), single (1), double (2). ***Mangasbaatar* (0)**
33. Foramen ovale inferium placed medial to foramen masticatorium (0), posterior to foramen masticatorium (1). ***Mangasbaatar* (0)**
34. Jugular fossa small and shallow (0), large and deep (1). ***Mangasbaatar* (1)**
35. Anterior part of the promontorium oval (0), irregular with incurvatures on both sides (1). ***Mangasbaatar* (1)**
36. Glenoid fossa (anterolateral to posteromedial) length: width ratio more than 1.7 (0), below 1.69 (1). ***Mangasbaatar* (1)**
37. Angle of coronoid process relative to tooth row steep, 45º or > 45º (0), low < 45º (1). ***Mangasbaatar* (0)**
38. Coronoid process parallel to the rest of the outer wall of the dentary (0), flared laterally (1). ***Mangasbaatar* (0)**
39. Posttemporal fossa large (0), reduced to a small foramen (1). ***Mangasbaatar* (0)**
40. Angle between the lower margin of the dentary and the occlusal level of the molars between 11–20º (0), above 20º (1). ***Mangasbaatar* (0)**
41. Mandibular condyle opposite or below the level of the molars (0), above the level of the molars (1). ***Mangasbaatar* (1)**
42. Width of the snout:skull length ratio below 0.3 (0), 0.3–0.39 (1), above 0.4 (2). ***Mangasbaatar* (2)**
43. Skull width:skull length ratio 0.79 and below (0), above 0.8 (1). ***Mangasbaatar* (1)**
44. Postpalatine torus absent or very faint (0), developed laterally and with a ventral projection from the palate, forming a distinctive bulge (1), strongly developed, forming a raised, ornate and sharply angled plate (2). ***Mangasbaatar* (2)**

APPENDIX 2

Scored character matrix, adapted from Kielan-Jaworowska and Hurum (1997) for 44 characters across 17 taxa including *Ptilodus*, *Stigymys*, *Taeniolabis, Eucosmodon*, *Lambdopsalis*, *Sloanbaatar*, *Buginbaatar*, *Kamptobaatar*, *Nemegtbaatar*, *Chulsanbaatar*, *Kryptobaatar*, *Djadochtatherium*, *Catopsbaatar*, *Tombaatar*, and *Mangasbaatar*. "A" denotes a multi-state (0+1).

Ptilodus	00212211010002210200120?00000011000100000100
Stigymys	21213210211011102??0?00??????111????10?0????
Taeniolabis	2103311103?120213201?2??020100?0????001?1110
Eucosmodon	21213210??10??10????????????????????1??00???
Lambdopsalis	2103201113?120213201221?02010010?11?0?101110
Sloanbaatar	10110101210011002110010001101102 0?0001011010
Buginbaatar	0101301????0?12132??????????????????0?0????
Nessovbaatar	?011021??????????????????????????????1?01??1
Bulganbaatar	???????1210011011010?10?????11?1????????????
Kamptobaatar	101101?1210011012110200001101110?10011001101
Nemegtbaatar	20112111210011111210210001101111010010000101
Chulsanbaatar	20110101210011002010100001101110110110000001
Kryptobaatar	20110111210011002112110011101110111110000021?
Djadochtatherium	20?101?121???0????12?1011110111?????00001???
Catopsbaatar	20021101220011112212121111101100?11100011211
Tombaatar	2??????122001100211211 0??1?01110??????????2
Mangasbaatar	2002010?220011A02A12?10101101110011100001212

RECONSIDERATION OF THE SYSTEMATIC POSITION OF THE MIDDLE JURASSIC MAMMALIAFORMS *ITATODON* AND *PARITATODON*

YUAN-QING WANG and CHUAN-KUI LI

Two Middle Jurassic mammaliaforms, *Itatodon* Lopatin *et* Averianov, 2005 and *Paritatodon* Martin *et* Averianov, 2010 have been considered to be members of the Docodonta. Detailed comparison of their dental morphologies with that of typical docodonts shows clearly the differences in cusp pattern and cusp-crest relationship of their lower molar crowns. In docodonts, four crests, originating from the apex of cusp a, extend respectively toward cusps b, g, c, and d, and meet the crests therefrom; all the major crests point to the center of cusps. In contrast, in *Itatodon* and *Paritatodon*, only two crests from cusp a extend to cusps g and c, and all the crests reconcile to the anterior or posterior cusp surface. Such differences suggest that the docodont molars function mainly by cutting and crushing, whereas those of *Itatodon* and *Paritatodon* have a clear shearing function. Both the morphological features and possible molar occlusal function of *Itatodon* and *Paritatodon* distinguish them from the typical docodonts and indicate their shuotheriid affinities. Moreover, the term "pseudotalonid" is used in describing the non-homologous dental features, representing different occlusal relationships, in Shuotheridia and Docodonta. It should thus better be restricted in the description of lower dentition of Shuotheridia, as proposed by the original study.

Key words: *Itatodon*, *Paritatodon*, Middle Jurassic, pseudotalonid, Docodonta, Shuotheridia.

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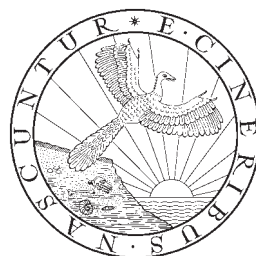
INTRODUCTION

Studies on Mesozoic mammals (*sensu* Kielan-Jaworowska *et al.* 2004) have achieved great progress since 2004, when Zofia Kielan-Jaworowska, Richard L. Cifelli, and Zhe-Xi Luo published their comprehensive review book entitled *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*. The progress has significantly expanded our knowledge of Mesozoic mammals in various aspects, such as taxonomy, phylogeny, biogeography, and biochronology, etc. Meanwhile, the systematic position of some taxa and the usage of a few concepts need to be clarified. Here we present a reconsideration of taxonomic status of two genera, *Itatodon* Lopatin *et* Averianov, 2005 and *Paritatodon* Martin *et* Averianov, 2010, and a discussion on the usage of the term "pseudotalonid", a concept proposed by Chow and Rich (1982) and reviewed by Rich and Vickers-Rich (2010).

Itatodon is a monotypic genus of Middle Jurassic mammaliaformes. It was originally proposed, with type species *I. tatarinovi*, by Lopatin and Averianov (2005) on the basis of an isolated right lower molar from the upper part of the Itat Formation of Krasnoyarsk Territory in West Siberia, Russia. Additional specimens referred to the species include another right lower molar (Averianov and Lopatin 2006) and a left dentary fragment with a premolar, the first lower molar, and the alveoli for three premolars and m2 (Averianov *et al.* 2010) from the same quarry. The genus was first considered as a member of the family Tegotheriidae in Docodonta (Averianov and Lopatin 2006; Lopatin and Averianov 2005), which was followed by Martin and Averianov (2010), but it was excluded from the Tegotheriidae later (Averianov *et al.* 2010; Hu *et al.* 2007; Luo and Martin 2007). Even so, its docodont affinity has not been questioned since the first report of *Itatodon* in 2005.

Sigogneau-Russell (1998) referred two lower molars from the Middle Jurassic Forest Marble Formation of Kirtlington, Oxfordshire, England to the shuotheriid genus *Shuotherium* and named a new species *S. kermacki*. However, when they reported the fossil mammals from the Middle Jurassic (Callovian) Balabansai Formation in northern Fergana Depression, Kyrgyzstan, Martin and Averianov (2010, p. 859) considered that the holotype of *S. kermacki* is similar to a lower molar of the docodont *Itatodon tatarinovi* Lopatin *et* Averianov, 2005. They proposed a new genus *Paritatodon* for the holotype of *S. kermacki* and referred a left ultimate lower molar to *Paritatodon* sp. However, detailed comparison of dental morphology reveals some differences between *Itatodon* and other docodonts, and requires a reconsideration of the systematic position of *Itatodon* and *Paritatodon*.

Institutional abbreviations. — CqMNH, Chongqing Museum of Natural History, Chongqing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; PM TGU, Paleontological Museum of Tomsk State University, Tomsk, Russia; ZIN, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

DIAGNOSTIC MOLAR FEATURES OF DOCODONTA

Docodonta is a mammalian group, uncontestably ranging from the Middle Jurassic to Early Cretaceous (Kielan-Jaworowska *et al.* 2004). Docodonts are characterized by distinctive molars with a complex cusp and crest pattern. The terminology and homology of the molar structures, especially the cusps, have been contro-

versial for many years (*e.g.*, Butler 1939, 1988, 1997; Jenkins 1969; Krusat 1980; Patterson 1956; Sigogneau-Russell 2003; Sigogneau-Russell and Godefroit 1997). Most later researchers generally followed the framework of docodont molar homology established by Butler (1997), with their own modification (*e.g.*, Averianov *et al.* 2010; Hu *et al.* 2007; Ji *et al.* 2006; Lopatin *et al.* 2009; Luo *et al.* 2015; Luo and Martin 2007; Martin and Averianov 2010; Martin *et al.* 2010; Maschenko *et al.* 2002; Meng *et al.* 2015; Pfretzschner *et al.* 2005; Rougier *et al.* 2015). For the sake of convenience in discussion, the terminology of docodont molar cusps and crests is labeled on a diagrammatic illustration (Fig. 1). We largely accepted Butler's (1997) terminology with one exception in designation of the distal lingual cusp (cusp f of Butler 1997) as cusp dd following Hu *et al.* (2007). Using Butler's terminology in the present study does not mean we agree with his homologous designation for all cusps in a docodont molar. The homology of docodont cusps with other mammals will not be discussed here because it is beyond the scope of the paper and we would like to simply focus on the dental morphology of related forms.

The complex cusp and crest pattern of docodont molars is unique in mammaliaforms. On the upper molars of docodonts, the crests A-X and C-Y connect the labial cusps A and C to the lingual cusps X and Y, respectively. The pattern is even more complicated on the lower molars, where nearly all cusps are connected by crests to the nearby cusps. Unlike in other mammals, where the crests or ridges connect the cusps by reconciling with either anterior or posterior surface of cusps, the crests on docodont molars run toward the

Fig. 1. Diagram showing the terminology of docodont upper (**A**, based on *Docodon*) and lower (**B**, based on *Borealestes*) molars (modified from Luo and Martin 2007). Arrow on the upper molar indicates the mid-constriction between the labial and lingual parts. Single letters represent cusps, and two letters with hyphen represent crest linking cusps. Both the anterior basin (ab) and posterior basin (pb) are used following the definition of Hu *et al.* (2007).
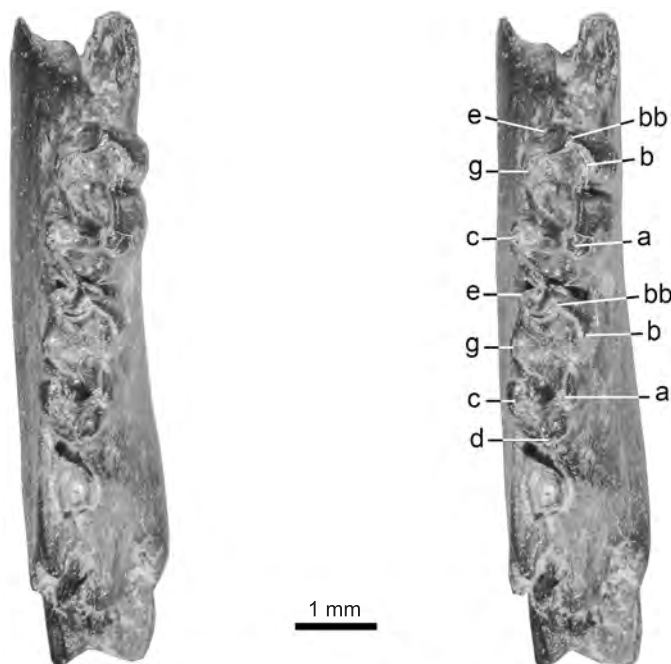
Fig. 2. Dorsal view (stereopair) of a right dentary fragment of *Hutegotherium yaomingi* (PIN 5087/8) from the Middle Jurassic Itat Formation (Bathonian) of West Siberia, Russia (fossil images courtesy of A.O. Averianov).

middle of cusps. Most notably on the lower molars, four crests, originating from the top of cusp a, form respectively a part of the crests a-b, a-g, a-c, and a-d, with concave areas in between except for crests a-b and a-d. In most docodont genera, three crests connect cusp b to other cusps: a (a-b), g (b-g), and e (b-e). The exceptions are absence of crest b-g in *Tegotherium*, *Sibirotherium*, and *Hutegotherium* (Lopatin *et al.* 2009; Martin *et al.* 2010; Maschenko *et al.* 2002; Tatarinov 1994). However, the function of crest b-g may be substituted by crest bb-g connecting cusp g to cusp bb (a neomorphic cusp) (Fig. 2).

DENTAL FEATURES OF *ITATODON* AND *PARITATODON*

The dental features of *Itatodon* were only known from the two isolated right lower molars and a left dentary fragment with a premolar and the first molar (Averianov *et al.* 2010). With the description of the left dentary fragment (PIN 5087/7), Averianov *et al.* (2010) revised the diagnosis of the type and only species, *I. tatarinovi* (Fig. 3), and hence of the genus as follows:

Fig. 3. Occlusal view (stereopairs) of right lower molars of *Itatodon tatarinovi* Lopatin *et* Averianov, 2005 from the Middle Jurassic Itat Formation (Bathonian) of West Siberia, Russia (fossil images courtesy of A.O. Averianov). **A**. Holotype PIN 5087/2. **B**. PM TGU 200/3-BR-7. Cusps labeled with quotation marks means that they occupy the same topographic position but may not be homologous with the respective cusps in docodont molars.

"*Itatodon* is unique among docodontans in having cusp b reduced to the cingular cusp, crests a-g and a-b diverging at the base of cusp a, no pseudotalonid basin on the first lower molariform tooth (absent also on the highly modified m1 of *Castorocauda*), and having the cingular cusp e incorporated into the wall of the pseudotalonid basin on the more posterior molariform teeth. Additionally, it differs from Docodontidae by having cusp b smaller than cusp c and well separated from cusp a, and a narrow mesiolingual cingulid; from Simpsonodontidae fam. nov. by presence of cusp e, a narrow mesiolingual cingulid, and lack of enamel folding; from Tegotheriidae by lack of cusp bb. Among docodontans *incertae familiae* it additionally differs from *Castorocauda* by the first lower non-sectorial molariform tooth, a large cusp g which is almost equal to cusp c, absence of crests b-g and a-d, presence of crest c-d, and the presence of cusp c on the lower molariform tooth; from *Castorocauda* and *Tashkumyrodon* by presence of a lingual cingulid and lack of the cusp dd and the crest c-dd" (Averianov *et al.* 2010, p. 124).

Of these diagnosing features, absence of crests "b"-"g" and a-"d" cannot only distinguish *Itatodon* (and *Paritatodon*) from *Castorocauda*, but the other docodonts as well, except *Tegotherium*, *Sibirotherium*, and *Hutegotherium*, which also lack crest b-g but have bb-g instead. Averianov *et al.* (2010) also stated that the pseudotalonid basin (= anterior basin) is absent on the first molar of *Itatodon* and *Castorocauda*. Unlike the other genera, however, the first two molars of *Castorocauda* are laterally compressed (Ji *et al.* 2006). It is possible that both teeth are highly specialized molars or could be alternately interpreted as premolars.

In addition to all the above-mentioned characters of *Itatodon*, a significant feature clearly distinguishing *Itatodon* from docodonts is that only two crests originate from the top of cusp a on *Itatodon* lower molars, extending to cusps "g" and "c" respectively. Both crests reconcile the anterior and/or posterior surface of the three cusps in *Itatodon*, which is similar to the cusp-crest connection pattern in the lower molars of obtuse-angled symmetrodonts (*e.g.*, *Tinodon*; see Crompton and Jenkins 1967; Simpson 1925) and, to a certain extent, of some cladotherians. This type of cusp-crest pattern suggests an occlusal relationship of the upper and lower molars different from that of docodonts, and can usually well perform a shearing function. No crest links cusp a and cusp "b", but a short crest from cusp "b" extends posterolingually to a point below the notch between cusp a and "g".

Martin and Averianov (2010) named *Paritatodon* for the holotype (a left lower molar) of *Shuotherium kermacki* Sigogneau-Russell, 1998 from the Middle Jurassic Forest Marble Formation (Bathonian) of England, but left the referred specimen (a broken right lower molar) as a shuotheriid. However, the comparable parts of both lower molars are not clearly different from each other according to the description and figures. They are probably from the same species. Martin *et al.* (2010, p. 859) considered that the holotype of

S. kermacki is extremely similar to a lower molar of *Itatodon tatarinovi* Lopatin *et* Averianov, 2005 from the Itat Formation at Berezovsk Quarry, Western Siberia, Russia. They also listed some morphological features that distinguish *Paritatodon* from *Itatodon*. In *Paritatodon*, the labial arms of crests a-c and a-g are almost longitudinal, whereas their lingual arms are more transverse, forming the angles between the labial and lingual arms approximating 90°. The labial cingulid is less pronounced than in *Itatodon* (Martin and Averianov 2010). Apparently, all the differences of *Itatodon* from docodonts are totally applicable to *Paritatodon*.

SHUOTHERIID AFFINITIES OF *ITATODON* AND *PARITATODON*

The above-mentioned morphological features of the lower molars of both *Itatodon* and *Paritatodon* not only separate them from true docodonts, but are similarities to those of *Shuotherium dongi* Chow and Rich, 1982 from the Late Jurassic Upper Shaximiao Formation, Sichuan, China. *S. dongi* is the type species of *Shuotherium*, the type genus of Shuotheriidae that is a peculiar mammalian group with pseudo-tribosphenic molar pattern (Chow and Rich 1982). The most striking dental feature of Shuotheriidae is a talonid-like structure (pseudotalonid) present anterior to trigonid; a point of contrast to tribosphenic mammals that have a talonid posterior to trigonid. When they reported *Shuotherium dongi*, Chow and Rich (1982) hypothesized that its upper molars possess a protocone-like lingual cusp (named pseudoprotocone) that occluded with the pseudotalonid of the lowers, and further proposed the pseudotribosphenic concept in describing such kind of occlusal pattern. After controversial discussion for many years (see Hopson 1995; Kermack *et al.* 1987; Tatarinov 1994), the validity of the pseudotribosphenic concept received support from referral to *Shuotherium* of some isolated triangular tricuspid upper molars from the same site as *S. dongi* and from the Middle Jurassic of England (Sigogneau-Russell 1998; Wang *et al.* 1998), and it was further confirmed by the discovery of *Pseudotribos robustus* with occluded upper and lower dentition from the Middle–Late Jurassic Daohugou biota of Inner Mongolia, China (Luo *et al.* 2007; see also Sullivan *et al.* 2014).

The morphology of shuotheriid lower molars was best documented by the type specimen of *Shuotherium dongi* (Fig. 4). The cusp a (protoconid) has two crests ex-
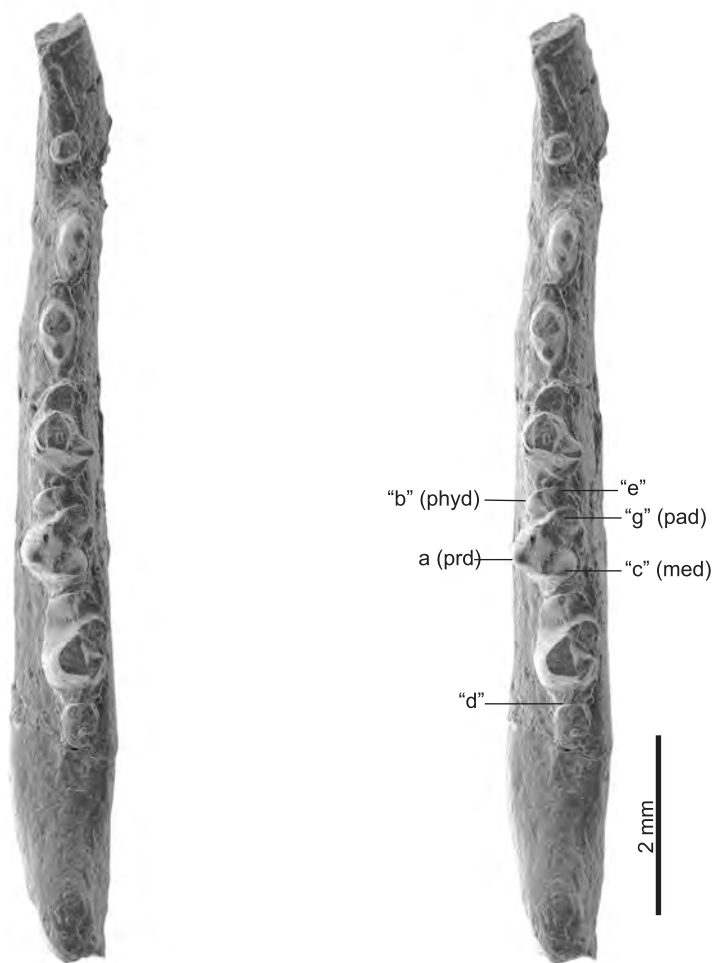
Fig. 4. Left dentary fragment in dorsal view (stereopair) of *Shuotherium dongi* Chow *et* Rich, 1982 (IVPP CV 6448, cast of the holotype, CqMNH V.729[1]) from the Late Jurassic Upper Shaximiao Formation (Oxfordian–Kimmeridgian) of Sichuan, China (modified from Chow and Rich 1984). Cusps labeled with quotation marks means that they occupy the same topographic position but may not be homologous with the cusp in docodont molars. The designation of cusps in pseudotribosphenic molars is given in parentheses. Abbreviations: hyd, hypoconid; med, metaconid; pad, paraconid; phyd, pseudo-hypoconid; prd, protoconid.

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[1] Chow and Rich (1982) originally used IVPP catalogue number V6448 for the holotype of *Shuotherium dongi*, but the specimen was recatalogued after it was returned to the Chongqing Museum of Natural History, Chongqing, China.

tending to cusp "g" (paraconid) and cusp "c" (metaconid) respectively. Both crests a-"g" and a-"c" reconcile with the anterior and/or posterior surface of three cusps, forming the shearing structure. Crests "b"-"g", a-"b" and a-"d" are absent. A distinct crest (pseudo-cristid obliqua), directed posterolingually from the cusp "b" (pseudo-hypoconid), terminates at the base of the prevallid, the notch between cusp a (protoconid) and "g" (paraconid). Similar to *Itatodon tatarinovi*, the first lower molar (m1) does not have the pseudotalonid (Chow and Rich 1982).

The dental features mentioned above are all shared by *Shuotherium* with *Itatodon* and *Paritatodon*, and clearly suggest a close relationship between *Shuotherium* and *Itatodon* plus *Paritatodon*. The major differences of *Itatodon* and *Paritatodon* from *Shuotherium* include more longitudinal labial arms and more transverse lingual arms of the crests a-"c" and a-"g", with wider angle between these arms. Such differences are also applicable in distinguishing *Itatodon* and *Paritatodon* from docodonts and do not support a relationship to docodonts.

Although they mentioned the possibility that the first lower molar of *Shuotherium dongi* may be the last premolar, Chow and Rich (1982) considered the dental formula of the lower cheek teeth as p3m4. Kielan-Jaworowska *et al.* (2002) argued that *Shuotherium dongi* has a dental formula of four (or more) premolars and three molars, on the basis of the differences of previous m1 from the other molars in lacking a pseudotalonid and having a wider opened trigonid, which Chow and Rich (1982) had noted. However, as Chow and Rich (1982: p. 132) stated, "the sharpest change in the form of adjacent post-canine teeth occurs between the simple, somewhat blade-like P_3 and the highly molariform M_1". Compared with trechnotherians, the lack of pseudotalonid and wider opened trigonid do not indicate the tooth is a premolar, and it is not necessary for the first molar to have a pseudotalonid (Averianov 2002). The absence of a pseudotalonod in the first lower molar of *Itatodon* and *Shuotherium* shows that it is a common characteristic of Shuotheridia.

Shuotheriids are known from the Middle to Late Jurassic of China and the Middle Jurassic of England (Chow and Rich 1982; Luo *et al.* 2007; Sigogneau-Russell 1998; Wang *et al.* 1998). Those two places are widely separated. The reallocation into the Shuotheriidae of *Itatodon* from West Siberia, Russia and *Paritatodon* from Kyrgyzstan greatly narrows the biogeographic gap of shuotheriids between England and China.

DEFINITION OF PSEUDOTALONID

When they described the peculiar *Shuotherium dongi*, Chow and Rich (1982) realized that the basin in front of the trigonid functioned in an analogous manner to the talonid posterior to the trigonid in therians with tribosphenic molar pattern. They thus named the basin pseudotalonid. They further proposed the pseudotribosphenic concept describing the occlusal pattern of the pseudoprotocone in the upper molars with the pseudotalonid in the lowers. It is clear that the term pseudotalonid was originally associated with the pseudotribosphenic occlusal pattern. Later studies on shuotheriids followed Chow and Rich's original definition of pseudotribosphenic and pseudotalonid (Luo *et al.* 2007; Sigogneau-Russell 1998; Wang *et al.* 1998), but the term pseudotalonid was extended in description of docodont lower molars.

Kermack *et al.* (1987) first applied the term pseudotalonid to the lower molars of docodonts when they reported *Simpsonodon* from the Forest Marble of Kirtlington Quarry in Oxfordshire, England. Subsequently, pseudotalonid was widely used in describing lower molars of docodonts, *e.g.*, *Tegotherium* (Martin *et al.* 2010; Tatarinov 1994), *Krusatodon* and *Borealestes* (Sigogneau-Russell 2003), *Tashkumyrodon* (Martin and Averianov 2004), *Dsungarodon* (Martin *et al.* 2010; Pfretzschner *et al.* 2005), *Castorocauda* (Ji *et al.* 2006), *Haldanodon* (Luo and Martin 2007), *Sibirotherium* (Lopatin *et al.* 2009), *Simpsonodon* (Averianov *et al.* 2010; Martin and Averianov 2010), *Hutegotherium* (Averianov *et al.* 2010), *Docofossor* (Luo *et al.* 2015), and *Agilodocodon* (Meng *et al.* 2015). At first, some researchers described the anterior part of docodont lower molars as pseudotalonid, mostly because they considered that *Shuotherium* is a docodont (*e.g.*, Kermack *et al.* 1987) or the described docodont taxon is closely related to *Shuotherium* (*e.g.*, Tatarinov 1994). Later use of pseudotalonid in docodonts mainly followed the previous work or kept the term for the purposes of simplicity (Sigogneau-Russell 2003, p. 363). Some researchers designated the anterior basin of docodont lower molars as the pseudotalonid in quotation marks or used the term in association with anterior basin (Ji *et al.* 2006; Martin and Averianov 2004; Maschenko *et al.* 2002; Pfretzschner *et al.* 2005), implying the uncertainty on homology of the pseudotalonid in *Shuotherium* to that in docodonts. In addition, the definition of

the docodont "pseudotalonid" varied in different papers as noted by Luo and Martin (2007) in a review paper on the dentition of docodonts.

Although some researchers argued or accepted that the docodont molars are capable of shearing and grinding (or crushing) function (*e.g.*, Butler 1988; Gingerich 1973; Hu *et al.* 2007; Jenkins 1969; Kermack *et al.* 1987; Kielan-Jaworowska *et al.* 2004; Luo and Martin 2007; Pfretzschner *et al.* 2005), the morphology of docodont molars is clearly different from that of tribosphenic molars of therian mammals, which have both shearing and grinding function. Compared to the occlusal patterns of the nontherian mammaliaforms, the tribosphenic pattern of therian mammals is most efficient in food processing. Its shearing function is performed by the precise occlusion of both paracrista-preprotocrista on the upper molars to protocristid on the lower molars and metacrista-postprotocrista on the uppers to paracristid on the lowers, whereas the occlusion of protocone within the talonid performs its grinding function. The cusp-crest pattern of docodont molars does not clearly indicate the presence of precise shearing occlusion similar to that in tribosphenic therians, which may suggest that the docodont molars may have had less shearing function. Given that potential for grinding function in the docodont *Haldanodon* molar is much less than in the tribosphenic molar (Brinkkötter *et al.* 2014), it is clear that the docodonts had much lower efficiency in food processing than therian mammals. Unlike the shuotheriid molars, the molars of docodonts probably did not function in a reversed manner analogous to tribosphenic molars. Therefore, to use pseudotalonid in describing the anterior basin of docodonts "seems improper for docodonts, where the homology of cusps involved is not established" (Sigogneau-Russell 2003, p. 363). For the sake of precise use of the term pseudotalonid, it is appropriate to return to its original definition, restricted in the shuotheriid lower molars as explicitly advocated by Rich and Vickers-Rich (2010). Meanwhile, "anterior basin" is a proper name in describing the anterior part of docodont lower molars, as used by some researchers (*e.g.*, Hu *et al.* 2007; Ji *et al.* 2006; Lopatin *et al.* 2009; Martin and Averianov 2004; Maschenko *et al.* 2002; Pfretzschner *et al.* 2005; Sigogneau-Russell 2003).

CONCLUSIONS

The topographic distribution of cusp and the crest pattern of molars are the basic features for the comparison of dental morphology in mammaliaforms, especially for those groups whose cusp homology has not been well established. Docodonts are clearly distinguished from other mammaliaforms in having a unique and complex cusp and crest pattern. Among the taxa previously referred to Docodonta, *Itatodon* and *Paritatodon* have a cusp and crest pattern that is significantly different from that of true docodonts and very similar to that of shuotheriids, to which we accordingly refer them. The attribution of *Itatodon* and *Paritatodon* to the Shuotheriidae extends the shuotheriid record to West Siberia and central Asia, narrowing the geographic gap between China and England.

The extended usage of pseudotalonid in the description of docodont lower molars has varied in different studies, without either a clear definition or conformation to the original definition. It is better to restrict the use of pseudotalonid to shuotheriids, and to instead use the term anterior basin in docodonts.

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THE LATE TRIASSIC AND EARLY JURASSIC FISSURE FAUNAS FROM BRISTOL AND SOUTH WALES: STRATIGRAPHY AND SETTING

DAVID I. WHITESIDE, CHRISTOPHER J. DUFFIN, PAMELA G. GILL, JOHN E.A. MARSHALL, and MICHAEL J. BENTON

The famous vertebrate-bearing fissures of the Bristol area in southwest England and in south Wales were traditionally referred to "upland" environmental settings, and assigned an overall time range of some 60 Myr; we reject both of these viewpoints. In terms of the environmental setting, based upon the evidence of palaeogeography, sediments, and fossils, we show that all the Triassic-aged fissures were near-coastal and embedded in karst formed on palaeo-islands in a subtropical archipelago. Further, the dates of these fissure fills in both regions do not span the Carnian to Rhaetian, as commonly supposed, but instead they are probably all Rhaetian. We update information on the Charles Moore Holwell "*Microlestes*" fissure assemblage and demonstrate that the marine fauna confirms a Rhaetian age. As proposed by previous authors, younger fissure fills around the St. Brides area of South Wales were also formed on an island, but during the Hettangian–Sinemurian. The youngest fissure deposit in the region is Pliensbachian. The age range of the fissures thus shrinks to c. 20 Myr, and the first episode of tetrapod fissure infilling shifts from the time of the Carnian "pluvial" episode, to the early Rhaetian, when western Europe was undergoing major rifting associated with the beginning of the opening of the North Atlantic, and when the Rhaetian sea flooded over landscapes that had long been purely terrestrial and arid. We recognise clear changes in the faunal composition of the terrestrial vertebrate biota from the early Rhaetian, dominated by reptile taxa, with some mammaliamorphs, that then declined rapidly in diversity before the Hettangian. This herpetofauna was followed by three faunal assemblages in the Early Jurassic of St. Brides which became increasingly diverse following the end-Triassic mass extinction; each had prominent mammaliamorphs as well as high numbers, but few species, of rhynchocephalians.

Key words: Rhaetian, Triassic, Bristol fissures, Jurassic, Hettangian, Sinemurian, reptiles, mammaliamorphs.

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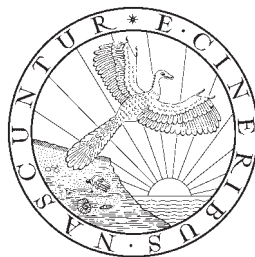
INTRODUCTION

The Late Triassic and Early Jurassic fissure fill deposits located on both sides of the Bristol Channel in southwest England and South Wales yield rich and unique vertebrate faunas (Robinson 1957; Kermack *et al.* 1973; Fraser 1994; Whiteside and Marshall 2008). The fissure fills, emplaced in Carboniferous Limestone, have produced many new vertebrate genera including fish, mammaliamorphs, and archosauromorph and lepidosauromorph reptiles. The tetrapods are of global importance as they span the end-Triassic mass extinction (ETE) and comprise well-preserved animals of small size that are not so commonly found in coeval deposits elsewhere. Two debated themes concerning the fissures are their ages and their environmental setting.

The earliest recorded find of Bristol fissure vertebrates was the small sauropodomorph dinosaur *Thecodontosaurus* Morris, 1843 from Durdham Down, Bristol (Riley and Stutchbury 1836, 1840), which was one of the first dinosaurs to be named (Benton *et al.* 2000). The geology and faunas of the fissures have been documented in reviews by Moore (1867, 1881), Robinson (1957), Savage (1993), and Benton and Spencer (1995). Other researchers have described specific fissure systems, including Windsor Hill (Kühne 1956), St. Brides Island quarries and additional South Wales localities (Kermack *et al.* 1973), Cromhall (Fraser and Walkden 1983; Walkden and Fraser 1993), and Tytherington (Whiteside 1983; Whiteside and Marshall 2008). The fissure faunas include some of the best known Mesozoic vertebrates that were first described from these localities and continue to be important in evolutionary studies and palaeogeography (Figs 1–3). The genera first described from the infills include mammaliaforms (*Morganucodon*, *Kuehneotherium*, *Microcleptes* [now *Thomasia*], *Bridetherium*, *Eozostrodon*, and *Paceyodon*), reptiles (*Thecodontosaurus*, *Clevosaurus*, *Gephyrosaurus*, *Planocephalosaurus*, *Diphydontosaurus*, *Sigmala*, *Pelecymala*, *Terrestrisuchus*, *Kuehneosaurus* [and *Kuehneosuchus*], *Tricuspisaurus*, *Variodens*, *Pantydraco*, *Agnosphitys*), and chondrichthyan fishes (*Duffinselache*, *Pseudocetorhinus*).

The dating of the fissures has been contentious: many authors have assumed that the fissures fills represent a long time range, perhaps as much as 60 Myr, spanning from the Carnian (*e.g.*, Simms and Ruffell 1990; Benton and Spencer 1995; Fraser and Sues 2010) to the Mid Jurassic (Savage 1977). Most authors have distinguished two age categories of vertebrate-bearing fissures of Bristol; the predominantly reptile-bearing "sauropsid" fissures and the mammal-bearing fissures (Robinson, 1957), also termed the "complex A" and "complex B" fissures respectively (Shubin and Sues 1991). Robinson (1957) interpreted the former as infilled underground water-courses that pre-dated the Rhaetian transgression and perhaps spanned the Late Triassic, from Carnian to Norian — though in a later paper, Robinson (1971) suggested that these fissures were more precisely upper Norian based on two sets of evidence. First, she perceived lithological similarities between the older fissure deposits and the red and green Norian mudstones in the local Blue Anchor Formation. Second, she projected from geological relationships that the nearby "Rhaetic" would have once capped the Emborough "sauropsid" fissure and thus post-dated the infill. Finding two *Kuehneotherium* teeth in the Emborough deposit, Fraser *et al.* (1985) used Robinson's age assignment to report the first "pre-Rhaetic" "therian" mammal. This dating of Emborough was contradicted by Whiteside and Marshall (1985, 2008) who deduced that the fissure infill post-dated the Rhaetian transgression. Kermack *et al.* (1973), Whiteside (1983), and Whiteside and Marshall (2008) also argued that any suggested lithological similarities with the Blue Anchor Formation were spurious; "the lithological evidence is useless" said Kermack *et al.* (1973), "except to warn against the red is Norian fallacy" said Evans and Kermack (1994). Indeed, Whiteside and Marshall (2008) depicted a red and green-banded rock interspersed with black laminae from fissure 2 at Tytherington that yielded Rhaetian palynomorphs. The younger, mammal-bearing fissures have generally been assigned a "Rhaeto-Liassic" age (Kermack *et al.* 1973; Evans and Kermack 1994) based on the palaeobotanical evidence of Harris (1957) and Lewarne and Pallot (1957), or on palaeogeography (Robinson 1971).

The environments represented by the fissure deposits have also been debated, and the traditional view, widely promulgated is that they represent a distinctive "upland" biota based on the small size of the tetrapod species, including dinosaurs, and their supposed occurrence in Mesozoic hilly limestone "caves" (Robinson 1957; Tarlo 1962; Halstead and Nicoll 1971; Halstead and Halstead 1981). However, this concept was challenged by Marshall and Whiteside (1980), Whiteside (1983), Whiteside and Robinson (1983), and Whiteside and Marshall (2008), who used palynological, fish and glauconitic clay evidence to demonstrate that the sauropsid fissures at Tytherington were formed and infilled in limestone islands set in a marginal marine location.
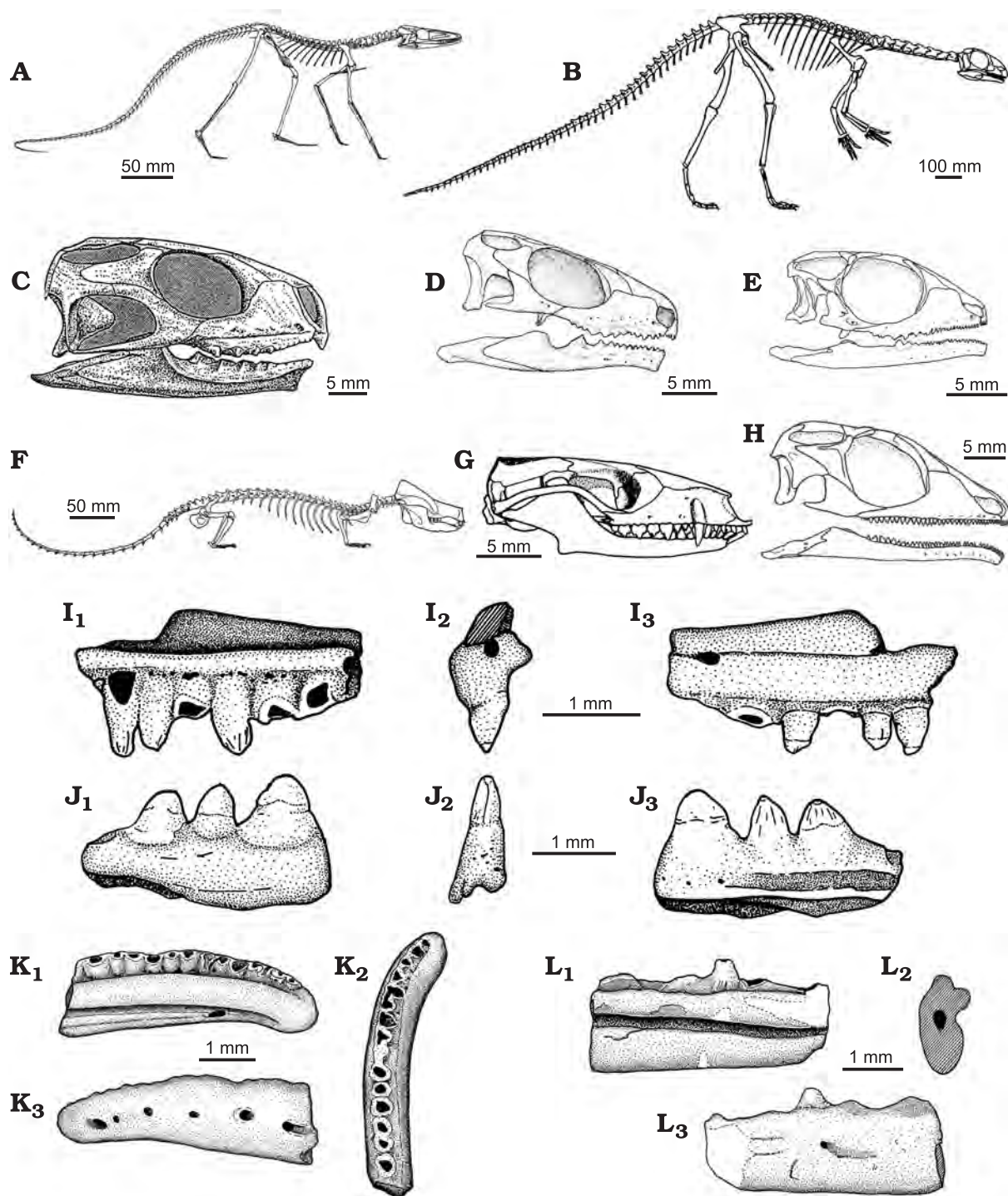
Fig. 1. Characteristic taxa found in the Triassic and Jurassic fissure faunas and new lepidosaur specimens from Holwell. **A–E**. Taxa typical of Rhaetian sauropsid fissures. **A**. *Terrestrisuchus* from Pant-y-ffynnon (from Crush 1984). **B**. *Thecodontosaurus* (based on *Pantydraco*) from Durdham Down (from Kermack 1984). **C**. *Clevosaurus hudsoni* from Cromhall, lateral view of skull and lower jaw (from Fraser 1994). **D**. *Planocephalosaurus* from Cromhall, lateral view of the skull and lower jaw (from Fraser 1982). **E**. *Diphydontosaurus* from Tytherington, lateral view of the skull and lower jaw (from Whiteside 1986). **F–H**. Taxa typical of St. Brides Early Jurassic fissures. **F**. *Oligokyphus* from Windsor Hill (from Kühne 1956). **G**. *Morganucodon*, lateral view of skull and lower jaw from a variety of St. Brides quarries (from Evans and Kermack 1994). **H**. *Gephyrosaurus*, lateral view of skull and lower jaw from Pontalun (from Evans 1980). **I–L**. Lepidosaur remains from Holwell (Moore Collection, BATGM). **I**. CD7, undetermined pleuracrodont rhynchocephalian maxilla fragment in medial (I_1), anterior (I_2), and lateral (I_3) views. **J**. C126, jaw fragment with posterior acrodont teeth of cf. *Diphydontosaurus* sp. in lateral (J_1), posterior (J_2), and medial (J_3) views. **K**. CD2, left dentary anterior fragment of ?*Diphydontosaurus* sp. in lateral (K_1), medial (K_2), and occlusal (K_3) views. **L**. CD6, left dentary fragment of *Diphydontosaurus* sp. in medial (L_1), cross-sectional (L_2), and lateral (L_3) views.
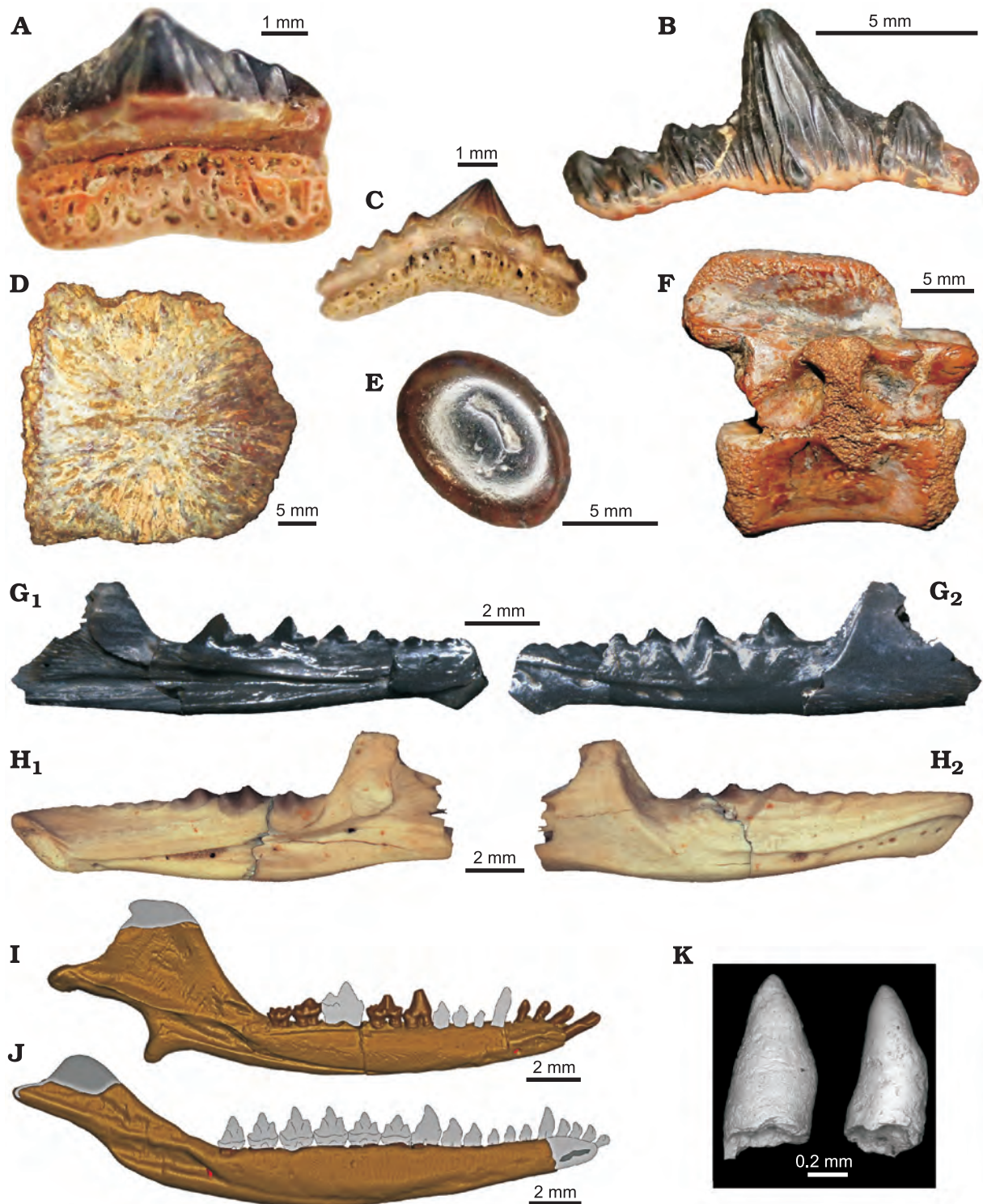
Fig. 2. Specimens from the Rhaetian and Early Jurassic fissures of the Bristol region and South Wales. **A–F**. Holwell sharks and aquatic reptiles from the Moore collection in BATGM. **A**. M64, tooth of *Lissodus minimus* in lingual view. **B**. M192, tooth of *Hybodus cloacinus* in labial view. **C**. M183, lateral tooth of *Synechodus rhaeticus* in lingual view. **D**. CD10, osteoderm of *Psephoderma alpinum* in surface view. **E**. M193, tooth of *Psephoderma alpinum* in occlusal view. **F**. C28, vertebra of *Pachystropheus rhaeticus* in lateral view. **G–J**. Tooth-bearing lower jaws. **G**. *Clevosaurus sectumsemper*, a reconstructed left dentary from Woodleaze quarry in medial (G_1) and lateral (G_2) views (after Klein *et al.* 2015). **H**. *Clevosaurus* aff. *sectumsemper*, a reconstructed right dentary from Fissure 2 at Tytherington in lateral (H_1) and medial (H_2) views (after Van den Berg *et al.* 2012). **I**. A reconstructed left lower jaw of *Morganucodon*, with paler areas missing (after Gill *et al.* 2014). **J**. A reconstructed left lower jaw of *Kuehneotherium*, with paler areas missing (after Gill *et al.* 2014). **K**. SEM image of two aff. *Gyrolepis* teeth (BRSMG CC 6087) from a Cromhall terrestrial fissure.
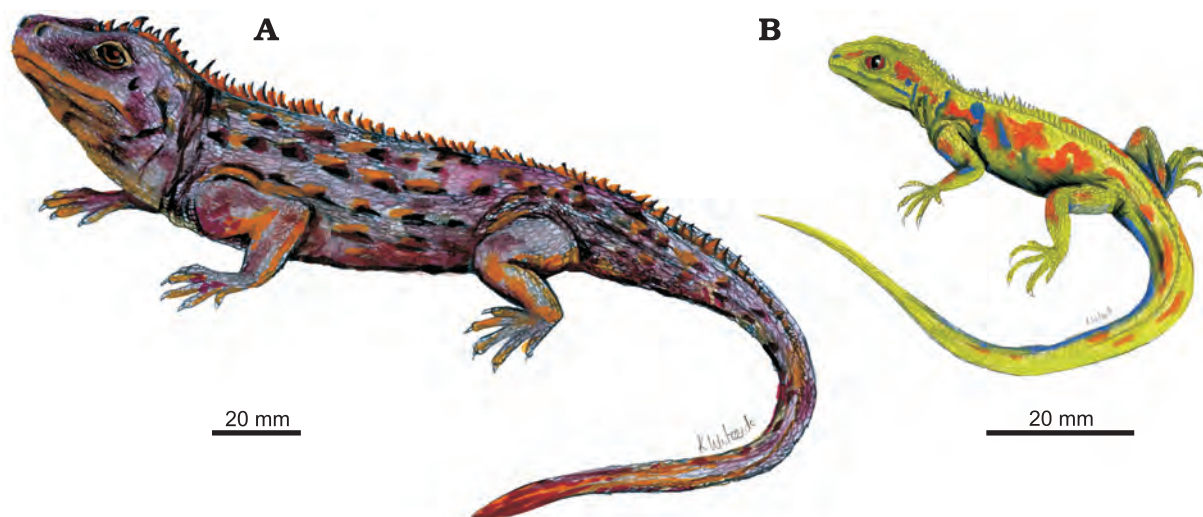
Fig. 3. Life reconstructions of *Clevosaurus hudsoni* and *Diphydontosaurus avonis*. **A**. *Clevosaurus hudsoni*, based on Fraser (1988a, 1994). **B**. *Diphydontosaurus avonis*, based on Whiteside (1983, 1986). Drawings by Katharine Whiteside.

In this review we provide our analysis, with new evidence, of the fauna, geology, dating and palaeo-environment of the suite of "sauropsid" and mammaliamorph-bearing fissures in South West Britain, the nature of their infill and their fossil content. As emphasised by Whiteside and Marshall (2008), there is no *prima facie* evidence that any of the "sauropsid fissure" infills in southwest Britain (and their contained tetrapods) date from pre-Penarth Group (Rhaetian) times. The age and environment of the principal mammaliaform-bearing fissures of Holwell and particularly St. Brides Island are re-considered based on faunal comparisons, geological relationships, and palynological findings. The dating and palaeoenvironment of the fissure fishes, reptiles and mammaliamorphs reveal a coherent picture of a vertebrate biota that inhabited the karst at or near the marine margins of small islands around the Triassic–Jurassic boundary.

Institutional abbreviations. — BATGM, Bath Geological Museum, UK (Bath Royal Literary and Scientific Institution); BGS, British Geological Survey, Nottingham, UK; BRSMG, Bristol City Museum, Geology Collection, UK; BRSUG, University of Bristol, Geology Collection, UK; NHMUK, Natural History Museum, London, UK; NMW, National Museum of Wales, Cardiff, UK.

Fig. 4. Late Triassic–Pliensbachian fissure localities in the Bristol area and in South Wales. A simplified Rhaeto-Liassic geography of the palaeo-archipelago. Light grey is the region of sauropsid fissures and dark grey that of the principal mammaliamorph localities. Note proximity of Emborough to dark area. Upper left inset is a close up of the quarries in the St. Brides area, from Evans and Kermack (1994), and lower left inset shows the position of the localities within the UK. Modified from Whiteside and Marshall (2008) and Klein *et al.* (2015).

THE LOCALITIES

The main sauropsid localities (Fig. 4) with a diverse fauna are situated in South Wales at Pant-y-ffynnon and Ruthin and also to the north of Bristol at Durdham Down, Tytherington, and Cromhall, the last of which has the most recorded genera. Other sauropsid sites are Woodleaze (near Tytherington), Emborough, and Batscombe, which are in the Mendip Hills to the east and south of Bristol. Twyn-yr-Odyn, near Cardiff, has only been recorded as yielding fishes (Howgate 1976), but is considered here as a sauropsid-type fissure locality from its palaeogeography and the fact that fishes from similar fissure fills have been found in Cromhall and Tytherington.

Mammaliamorph-bearing fissure fills are found in the neptunian dykes at Holwell and Windsor Hill in the Mendip Hills, but the main finds derive from the quarries of Ewenny, Pontalun (currently known as Lithalun) and Pant, north of St. Brides Major in South Wales (Fig. 4). All the fissures are found within the Carboniferous Limestone of the region, and their locations are given in Table 1.

GEOLOGY

The vertebrate-bearing fissures of the Bristol region and in South Wales are emplaced in Carboniferous Limestone of Early Carboniferous (Mississippian) age. The fissures follow vertical joints and fractures

Table 1. List of key fissure localities around Bristol, and in South Wales, with UK grid references. Information is from Fraser (1994) and current analysis.

	Locality	UK grid reference
Bristol region	Cromhall	ST 704 916
	Tytherington	ST 660 890
	Woodleaze	ST657 885
	Durdham Down	ST573 747
	Emborough	ST 623 505
	Batscombe	ST 460 550
	Windsor Hill	ST 615 452
	Holwell	ST 727 452
South Wales	Twyn-yr-Odyn	ST 116 738
	Pant-y-ffynnon	ST 046 743
	Ruthin	SS 975 796
St. Brides palaeo-island quarries	Cnap Twt	SS 911 753
	Duchy	SS 906 757
	Ewenny	SS 902 768
	Pontalun	SS 895 765
	Pant	SS 893 760

developed in the limestones, particularly of the Black Rock Limestone Subgroup and/or Gully Oolite Formation (*e.g.*, Cromhall, Tytherington, Pant-y-ffynnon, St. Brides quarries, Woodleaze and Windsor Hill). Other localities show fissures in the Clifton Down Limestone Formation, including Durdham Down (Foffa *et al.* 2014) and Holwell (Savage 1977), the Hunts Bay Oolite Group (*e.g.*, Ruthin), younger sections of the Pembroke Limestone Group (High Tor Limestone; western side of Pant and Pontalun quarries) and the Hotwells Limestone (now termed the Oxwich Head Limestone Formation), as at Emborough (Savage 1977). The nature of these different Carboniferous Limestone formations probably constrains the morphology of the fissures, and it may be that the types of caverns observed at Cromhall (Fig. 5A) and Tytherington, for example, reflect the material properties of the massive Black Rock Limestone.

Where documented, the fissure systems generally trend W-E or NW-SE, but few fissure systems have been observed as the quarry face is progressively worked. As an exception, Robinson (1957) depicted a fissure at Cromhall quarry with a N-S orientation. Whiteside and Marshall (2008, fig. 9) described the change in cross section of the NW-SE trending fissure 2 at Tytherington quarry, and they noted that other Tytherington reptile-bearing fissures were oriented W-E. Moore (1867) recorded the fissures at Holwell as trending W-E, and Savage and Waldman (1966) reported WNW-ESE directions for fissure fills left standing after quarrying. Savage (1977) also recorded the Windsor Hill fissure as trending W-E. Kermack *et al.* (1973) reported that the fissures in Duchy and St. Brides Pant 2 were W-E whilst PGG has observed that the fissures in Ewenny, St. Brides Pant 4 and 5, and Pontalun also lie W-E. The W-E and NW-SE trends of these fissures accord with the same trends of fractures reported by Wall and Jenkyns (2004) and Woodcock *et al.* (2014) for the main Late Triassic dilatational openings and infillings. Extension of the fractures and sediment fill probably continued until at "least the early Cretaceous" (Woodcock *et al.* 2014).

Some of the fissures, particularly those at Holwell and Windsor Hill, are regarded as neptunian dykes which are near-vertically sided, tectonically generated openings under a marine but near-shore environment and contain significant proportions of aquatic as well as terrestrial fauna.

Although there were clearly tectonic influences in the opening and widening of fractures in the Carboniferous Limestone, the host limestone often has matching bedding planes crossing the fissures, showing that there was no vertical movement on either side (see *e.g.*, Whiteside and Marshall 2008, fig. 8c). Many of the fissures have solutional features that were developed sub-aerially or in phreatic (below the water table) conditions below the limestone surface. Fluting or cusps have been recorded on the limestone walls of the fissures at Pant, Pontalun (Kermack *et al.* 1973), Cromhall (Walkden and Fraser 1993), and Tytherington (Whiteside 1983; Whiteside and Marshall 2008). Karstic features such as dolines, swallets or swallow holes have been described from Tytherington (Whiteside and Marshall 2008) and Emborough (Savage 1977), and a pipe that led to an infilled cavern can be seen in an old photograph of the Cromhall deposit (Fig. 5A). There is phreatic cavern development at Tytherington (Whiteside and Marshall 2008), Woodleaze (Klein *et al.* 2015), Pant-y-ffynnon and on St. Brides palaeo-island at Cnap Twt (Harris 1957), and Ewenny (Kermack *et al.* 1973).
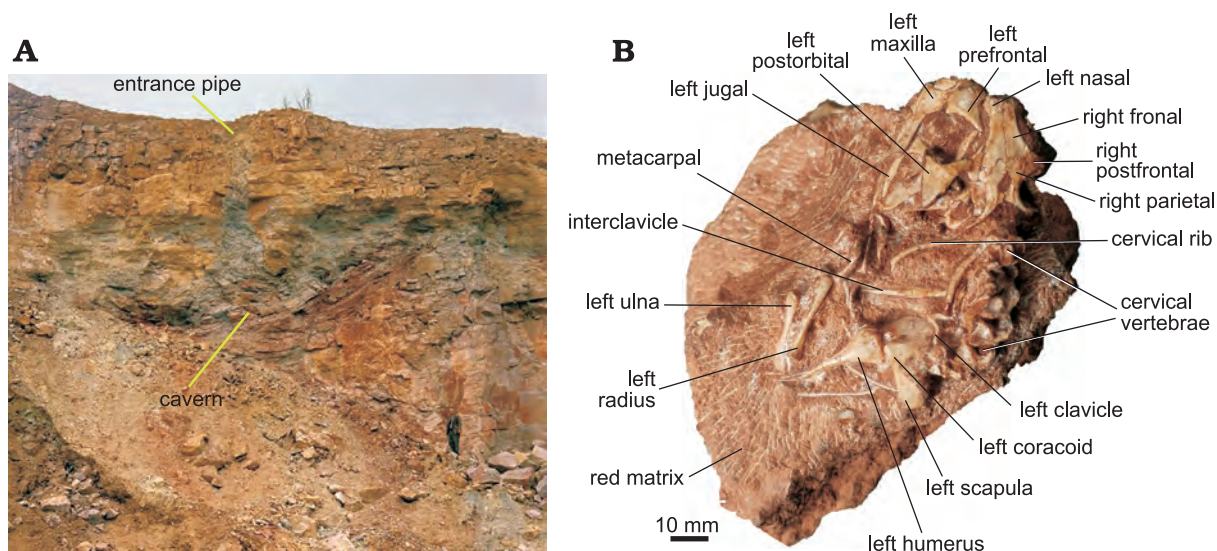
Fig. 5. Cromhall and its reptile fossils. **A**. Cromhall quarry fissure showing cavern development; note the upper green layers and the lower red beds. Both types of lithology have yielded terrestrial reptile bones. Note also the entrance pipe from the Carboniferous Limestone surface that is 3–4 m above the infilled cavern, The cavern extends on both the left and right sides; on the right-hand side the upper boundary of the cavern is about 2.5 m below the limestone surface. Photograph taken by C.A.F. Friend on 1/1/1965, from GeoScenic images, BGS archive. **B**. *Clevosaurus hudsoni* from Cromhall. This specimen (NHMUK PV R36832) in hard red marl has a skull that is dissociating into individual bones and the anterior skeleton consisting of cervical vertebrae, cervical ribs, pectoral girdle bones and parts of the left forearm. These articulated skeletons are rare but it is clear that this type of dissociation *in situ*, probably by bacterial action in subaqueous conditions, would produce great numbers of individual bones. The numerous bones may then be transported only short distances resulting in the jumbled conglomerations of disaggregated elements more typical of fissure deposits.

Whiteside and Marshall (2008) demonstrated that the Tytherington caverns or conduits were more plausibly formed in the fresh/saline water-mixing zone of freshwater lenses on small limestone palaeo-islands, rather than from flowing groundwaters dissolving limestone, as suggested by Simms and Ruffell (1990).

Fissure shapes and characteristics vary. Robinson (1957) described the Triassic reptile-dominated fissures as "underground water-course[s]", whereas Robinson (1971) and Kermack *et al.* (1973) identified the fissures of St. Brides palaeo-island as having a deep, narrow, "slot" morphology. However, these age-morphology distinctions are not clear-cut, as there are slot fissures at Cromhall (Walkden and Fraser 1993) and fissure 12 at Tytherington is a palaeo-doline (Whiteside and Marshall 2008), which looks slot-like in the exposure.

The sedimentary infills of the fissures comprise a great range of carbonate lithologies, including breccias, conglomerates, red, yellow and green marls, recrystallised limestones, and black and grey shales and siltstones, as well as calcareous sandstones. Dolomitised limestone breccias and/or limonitic deposits containing bones are found at Tytherington, Durdham Down and Pant-y-ffynnon; dolomitised limestone is recorded in the fissures at Cromhall (Fraser 1994), and pockets of ochre are also recorded from the near vicinity of the Emborough fissure (Robinson 1957; Savage 1977). The large-clast breccias that contain the bones of *Thecodontosaurus* at Tytherington and Durdham Down include dolomitised and ochreous rocks, and dolomite metasomatism of the host limestone may have played a part in the collapse of the breccia into a cavern. The low pyrite content found inside the *Thecodontosaurus* bones by Wings (2004), and the fact that the bones are frequently coloured white, suggests an aerated environment at deposition. The *Thecodontosaurus* breccias at Tytherington have therefore been interpreted as resulting from final gravitational collapse caused by oxygenated meteoric waters flowing around the loosened roof rocks into caverns developed at the edge of a freshwater lens (Whiteside and Marshall 2008). The breccias contain a wide range of tetrapod species and include bones of the largest and smallest terrestrial vertebrates known from the fissures (Van den Berg *et al.* 2012): *Diphydontosaurus* (0.1 m long) is found alongside *Thecodontosaurus* (approximately 2.0 m long).

Most of the fissure bones are disarticulated, suggesting considerable transport, although articulated complete and/or partial skeletons have been found at Cromhall (Fig. 5B), Emborough, Batscombe, Durdham Down, Twyn-yr-Odyn, and Pant-y-ffynnon. These articulated specimens occur in red or green marls, but there are exceptions, such as the articulated forearm of *Diphydontosaurus* in a conglomerate from Durdham Down (BRSMG Cb4715). There are associated bones of *Clevosaurus* from Woodleaze (Klein *et al.* 2015), a

very few co-ossified or sutured bones of *Oligokyphus* from Windsor Hill (Kühne 1956), a partial skull with articulated lower jaws of *Morganucodon* from Pontalun (Parrington 1978), and a *Morganucodon* articular complex from Ewenny (Kermack *et al.* 1973), as well as occasional associated elements from Tytherington, and of *Gephyrosaurus* (a coronoid and dentary; Evans 1980) from St. Brides quarries. However, partially articulated or complete skeletons are very rare or absent from the St. Brides quarries, Tytherington, Ruthin, Windsor Hill and Holwell.

The size ranges of bones also suggest transport, with for example bones from Tytherington similar in size to the reworked Carboniferous Limestone clasts, and presumably possessing similar hydrodynamic properties. On the other hand, other localities yield mixtures of small bones and teeth of larger animals and larger bones of small reptiles. In some small-clast conglomerates, the bones can be well preserved, with fine details intact, such as the rock that yielded *Diphydontosaurus* at Tytherington (Whiteside 1986). Similarly exquisite white-coloured fossils of *Planocephalosaurus* (Fraser 1982) from Cromhall are found in recrystallised limestones containing remanié fossils such as crinoid ossicles and chondrichthyan teeth derived from the Carboniferous Limestone; recrystallised limestones also preserve bones of *Clevosaurus* and *Diphydontosaurus* in fissure 8 at Tytherington.

Red and yellow marly clays yielded most of the isolated bones and teeth collected from Holwell by Moore (1867), and some of the St. Brides fossil material derives from soft red, yellow, green and grey clays as well as harder marls. Many of the red marls from the St. Brides fissures contain abundant haematitic ooids or pisoliths (Kermack *et al.* 1973; Gill *et al.* 2006). Dark grey and black siltstones yielded palynomorphs with terrestrial and marine vertebrates at Tytherington to Whiteside and Marshall (2008) who additionally found palynomorphs in finely laminated greyish limestones at the same locality. Dark grey shales at Cnap Twt and other quarries on St. Brides palaeo-island also contain palynomorphs (Harris 1957; Lewarne and Pallot 1957).

The tetrapod bones in red matrix are generally preserved in light colours such as white or yellow, whereas bones in green and yellow rocks can be coloured from white to brown or black. Bones in black rocks are often black, but fragments can be white and those in a grey matrix range from white to black.

THE FAUNAS

As noted, the standard assumption, proposed by Robinson (1957, 1971) and Shubin and Sues (1991), is that the faunas from the fissures can be separated into two groups: (1) a biota dominated by terrestrial reptile genera and, with the exception of Emborough where Fraser *et al.* (1985) recorded two *Kuehneotherium* teeth, no mammaliamorphs; and (2) a terrestrial tetrapod biota that includes a significant proportion of mammaliamorphs.

The pattern, however, is more complex (Table 2). In the group 1, "sauropsid" fissures, there are, in addition to the reptiles, non-marine fishes of either *Pholidophorus* or *Legnonotus* type in the fissures at Cromhall and Tytherington, and in great numbers at Twyn-yr-Odyn (Howgate 1976), from which no tetrapods have been reported. Teeth of Rhaetian marine fishes have also been found with the reptiles in the Cromhall "slot fissures" and the capping sequence over these (Fraser 1994; Whiteside and Marshall 2008), Tytherington (Whiteside 1983; Whiteside and Marshall 2008), and Durdham Down (Foffa *et al.* 2014). Despite extensive work at the site, Robinson (1957) did not report fish fossils at Cromhall, a key example of a "sauropsid" fissure locality, but she may have missed them because many of the coeval fish teeth are recovered only by sieving the acid-digested sediment through very fine mesh sizes (*e.g.*, Van den Berg *et al.* 2012; Foffa *et al.* 2014). In more recent studies, actinopterygian elements, comprising *Gyrolepis* scales and aff. *Gyrolepis* teeth (Fig. 2K), were found by Mike Curtis at Cromhall (site 4 of Fraser 1994) in rock that contained *Planocephalosaurus* (Whiteside and Marshall 2008; BRSMG CC 6087). This finding contradicts the report of Behan *et al.* (2012) that all fish teeth found in the Cromhall terrestrial deposits were derived from the Carboniferous; those authors only considered chondrichthyan teeth and all are above 0.5 mm and mostly much larger, possibly indicating a sieving sample bias. The narrowest dimension of aff. *Gyrolepis* teeth is *c.* 0.4 mm or shorter, and reworked Carboniferous chondrichthyan fossils are widely recognised (*e.g.*, Whiteside 1983; Whiteside and Marshall 2008; Van den Berg *et al.* 2012), having a different preservation from the terrestrial reptiles and coeval fish fossils.

The group 2, "mammaliamorph" fissures deposits at Holwell, Windsor Hill and in the St. Brides quarries show a range of faunal compositions, from single species to richer faunas with a wide variety

Table 2. Summary of the key localities and faunal compositions, for Triassic and Jurassic ("St. Brides") fissure faunas. Holwell also has the aquatic reptiles *Pachystropheus* and *Psephoderma* and a number of marine fish genera not found in any other locality. Data based on Robinson (1957), Kermack *et al.* (1973), Howgate (1976), Evans and Kermack (1994), Fraser (1994), Säilä (2005), Edwards and Evans (2006), Gill *et al.* (2006), Whiteside and Marshall (2008), Van den Berg *et al.* (2012), Foffa *et al.* (2014), Dalla Vecchia and Cau (2015), and Klein *et al.* (2015), as well as personal observations by the authors and Fraser (personal communication). Abbreviations: C, Cromhall; Ty, Tytherington; D, Durdham Down; W, Woodleaze; P, Pant-y-ffynnon; R, Ruthin; E, Emborough; B, Batscombe; T, Twyn-yr-Odyn; H, Holwell; M, St. Brides *Morganucodon* fauna; MS, St. Brides *Morganucodon*-sphenodont fauna; Wh, Windsor Hill; ×, taxon present, ?, taxon possibly present; blank, absent or no data. *Lissodus* can also be euryhaline.

	Taxon quarry	Sauropsid type fissures										Mammaliamorph type fissures		
		C	Ty	D	W	P	R	E	B	T	H	M	MS	Wh
Terrestrial reptiles	*Gephyrosaurus*											×	×	
	Clevosaurus convallis												×	
	Clevosaurus hudsoni/minor/sectumsemper	×	×	×	×	×	?	×			×			
	Diphydontosaurus	×	×	×	×	×	×				×			
	Planocephalosaurus	×	×	?			×							
	Pelecymala	×	×											
	Sigmala	×	×											
	other/unidentified lepidosaurs		×		?						×		×	
	kuehneosaur	×				×	?	×	×					
	Thecodontosaurus/Pantydraco		×	×		×	×				×			
	coelophysoid/"theropod"	×	×	×		×							×	
	sphenosuchiid/aff. *Terrestrisuchus*	×	×			×	×						×	
	"thecodont"/suchian/scleromochlid/*Agnosphitys*	×	×			×	×							
	"*Palaeosaurus*"/phytosaur aff. *Nicrosaurus*/*Angistorhinopsis*		×	×							×			
	aetosaur	×												
	drepanosaur	×	×											
	pterosaur	?	?									×	×	
	Tricuspisaurus/aff. *Tricuspisaurus*	×	×				×	×						
	procolophonid	×					×							
Cynodont	*Oligokyphus*												×	×
	other tritylodont										×			
	Pseudotriconodon										×			
Mammalia-formes	*Morganucodon* and *Eozostrodon*										×	×	×	
	Kuehneotherium						×					×	×	
	Bridetherium and *Paceyodon*												×	
	haramiyid										×		×	
Non-marine fish	*Pholidophorus/Legnonotus/Semionotus*	×	×							×	×			
Marine fish	*Gyrolepis*	×	×								×			
	Severnichthys	×	×								×			×
	*Lissodus**	×	?	×							×			×
Fish unknown	unidentified osteichthyan teeth		×	×	×									
Coeval invertebrates	gastropods	?	×								×	×		
	Euestheria	×	×			×								
	terrestrial arthropods	×									×			
Remanié	reworked Carboniferous fossils	×	×	×	×						×	×		
Tetrapod assemblage comparisons	nos. of identified tetrapod genera/types	13	13	5	2	7	7	4	1	0	9	3	11	1
	% of fauna in common with Tytherington	77	100	100	100	86	86	50	0	0	44	0	18	0
	% in common with *Morganucodon*-sphenodont fauna	15	15	20	0	29	14	25	0	0	22	100	100	100

of small tetrapods. The deposits at Duchy, Ewenny, Pontalun and Pant fissures 1–3 have a relatively im-poverished fauna (Fraser 1989), comprising the lepidosaur *Gephyrosaurus bridensis* (60% of the fossils, Evans and Kermack 1994), together with *Morganucodon watsoni* and to a lesser extent, and not present at Ewenny, *Kuehneotherium praecursoris* (see Kermack *et al.* 1968). Yet, there are several species of both *Kuehneotherium* and *Morganucodon* in the St. Brides fissures (PGG, personal observation), and any one fissure usually has a single species of either genus, possibly representing time differences between the fissures. Furthermore, Pant fissures discovered later, including Pant 4 and 5, have a more diverse biota, in-cluding *Gephyrosaurus*, *Kuehneotherium* and *Morganucodon*, but also possible pterosaurs as well as sphe-nodontians, sphenosuchian crocodylomorphs, theropods, tritylodonts and haramiyids (Evans and Kermack 1994; Gill *et al.* 2006). Bones and teeth of *Clevosaurus convallis* constitute 65–70% of the tetrapod fossils (Säilä 2005; Gill *et al.* 2006) and there is also a greater diversity of morganucodontans in these Pant de-posits, including *Bridetherium* and a large form known from one tooth, *Paceyodon* (Clemens 2011). These slot fissures and their tetrapods were termed the "*Hirmeriella* association" by Kermack *et al.* (1973), based on the relative abundance of the conifer *Hirmeriella*, but they are better described as two distinct biotas, the "*Morganucodon*" and *Morganucodon*-sphenodont" faunas of Gill *et al.* (2006), as both are found with *Hirmeriella*, being abundant in dark clay at Pant 5 and occasionally in red sediments of Pant 4.

Tritylodonts also occur at Windsor Hill, where *Oligokyphus* is represented by more than 2000 bones (Kühne 1956), and at Holwell, represented by a single partial right maxilla (Savage and Waldman 1966; Savage 1971) whose affinities are not yet established. Tritylodonts therefore had a more restricted occur-rence than mammaliaforms in the fissures. Holwell and Windsor Hill are neptunian dyke fissures and also include numerous fish teeth and marine invertebrates. Therefore these fissures starkly contrast with the St. Brides mammaliamorph-bearing fissures where no fishes have been reported and the invertebrate fauna is restricted to the gastropod "*Natica*" (= *Naticopsina*) *oppelii* (Kermack *et al.* 1973). However the beetle *Metacupes harrisi* has been recorded (Gardiner 1961) with lepidosaurs at Cnap Twt.

In contrast to the neptunian dyke fissures, contemporaneous invertebrates are rare at the other localities. Most commonly found is the predominantly freshwater branchiopod crustacean *Euestheria*, which is known from Cromhall, Tytherington, and Pant-y-ffynnon (Robinson 1957; Whiteside 1983; Whiteside and Marshall 2008) but has been given little attention. A millipede from Cromhall was depicted by Fraser (1988b) and annelids from that locality noted by Walkden and Fraser (1993). Robinson (1957) remarked on the absence of marine invertebrates in the sauropsid fissures. However, gastropod steinkerns, resembling *Hydrobia*-type specimens from Westbury Formation littoral deposits, were reported in the Tytherington deposits, particu-larly fissure 2, together with other marine and terrestrial components (Whiteside and Marshall 2008).

The faunal composition of each fissure at a particular locality often varies considerably. At Cromhall, Fraser (1994) showed that *Diphydontosaurus* is ubiquitous at the eight sites, but *Planocephalosaurus* and *Clevosaurus hudsoni* do not occur together in any deposit. Further, at *Planocephalosaurus* sites there is a greater overall diversity of tetrapods, and genus *Clevosaurus* is represented by a different species, *C. minor*. Whiteside and Marshall (2008) and Klein *et al.* (2015) also noted that deposits containing abundant *Planocephalosaurus* fossils at Tytherington are indicative of a diverse tetrapod biota. Unfortunately, similar faunal lists at particular sites in other sauropsid localities do not exist. There is evidence that a high propor-tion of *Gephyrosaurus* in the slot fissures is associated with a low overall diversity of tetrapods, from the description of the St. Brides faunas by Gill *et al.* (2006).

Some fissure localities are so dominated by one tetrapod that they are either monospecific or nearly so. The putatively gliding genera *Kuehneosaurus* and *Kuehneosuchus* predominate, respectively, at Emborough and Batscombe. At Windsor Hill, only *Oligokyphus* has been reported, despite the recovery of about 2000 bones (Evans and Kermack 1994), and at the more recently discovered locality of Woodleaze quarry, nearly all specimens are attributable to a single species, *Clevosaurus sectumsemper* (see Klein *et al.* 2015). It is likely that at least some of the lack of diversity is a result of the small land area available on tiny palaeo-is-lands (*e.g.*, Kühne 1956).

The notion that the tetrapods lived on islands is vital when considering differences between localities. Although the earliest faunas presumably arose from species that lived in the same area before the Rhaetian transgression, these would have become isolated on emergent islands, and would have evolved their own unique species with time, a pattern that in turn would have been complicated by repeated pulses of sea level rise and fall through the Rhaetian (*e.g.*, Hamilton 1962). Floras on these islands may have been richer than in the preceding Norian arid, sabkha environments thanks to the freshwater lens on these islands postulated

in the model of Whiteside and Robinson (1983) and Whiteside and Marshall (2008). Moreover, although it is likely that the fissures, which presumably represented natural pitfall traps, give a representative sample of the vertebrates living on the limestone surface (Fraser and Walkden 1983; Whiteside 1983), they may have received remains from only a small local area. Whiteside and Marshall (2008) and Klein *et al.* (2015) have suggested that there may be a relationship between the regional differences (*e.g.*, sandstone versus limestone surfaces) on an island and the fauna recovered in the fissures. These differences are hard to differentiate from the expected changes in the faunal composition even over just a few thousand years. Nevertheless it is likely that contemporaneous islands nearest to each other should have had a greater similarity in faunal composition than those further away, in both time and space.

Several biogeographic and temporal associations may be seen among the fissures. For example, Woodleaze and Durdham Down are most similar to Tytherington (Table 2). However Pant-y-ffynnon, Ruthin, and Cromhall all have over 75% and Emborough about 50%, of their tetrapods in common with Tytherington. Batscombe has a recorded *Kuehneosuchus* biota only, a reptile not yet found at Tytherington, although kuehneosaurs are present at Cromhall and Pant-y-ffynnon, as well as Emborough, suggesting that they are part of the same association. In the mammaliamorph-bearing localities, Windsor Hill and the "*Morganucodon*" biota have their limited genera in common with the much more diverse "*Morganucodon*-sphenodont" fauna. Holwell has genera such as *Thecodontosaurus* and *Diphydontosaurus* shared with the Tytherington group but also haramiyids and a morganucodontid, otherwise only jointly present in the "*Morganucodon*-sphenodont" biota of St. Brides. Twyn-yr-Odyn has the fish *Legnonotus*, a taxon not recorded elsewhere in the fissures, but may be closest to the Tytherington group or Cromhall, which includes significant deposits containing actinopterygians such as *Pholidophorus* with abundant terrestrial reptiles fossils. The repeated finding of the associated remains of actinopterygian fossils in terrestrial deposits indicates that the fishes are non-marine. Howgate (1976) regarded the Twyn-yr-Odyn *Legnonotus* as either a fresh- or brackish-water species based on his reconstruction of the enclosing fissure as a cavern collapse.

There are other possible associations between genera, such as the presence of *Diphydontosaurus* and *Clevosaurus* with *Thecodontosaurus* (or the closely related *Pantydraco*) at Durdham Down (Foffa *et al.* 2014), Tytherington fissure 2 (Van den Berg *et al.* 2012) and Pant-y-ffynnon (DIW, personal observation). It is also notable that Tytherington fissure 14 is faunally very similar to the Cromhall deposits (Whiteside 1983; Whiteside and Marshall 2008), as *Planocephalosaurus* is found in high proportions, and *Sigmala*, *Pelecymala* and *Tricuspisaurus* are present at both localities, yet both seem to lack *Thecodontosaurus* (N.C. Fraser, personal communication about Cromhall). *Diphydontosaurus, Clevosaurus* (Fraser 1994), and *Thecodontosaurus* (Moore 1881) are also all recorded from fissure deposits at Holwell, but it is not known if they are from the same fissure site.

DATING THE FISSURES

BACKGROUND

Assigning a date to the fissure faunas has proved problematic. Put simply, the fissure fill at any locality has to be younger than the host Carboniferous Limestone but older than any capping strata. A wide range of dates has been suggested for the fissures (Fig. 6). Robinson (1957), aiming to date the sauropsid fissures, described field relationships around the Emborough fissure, and projected beds of the nearest "Rhaetic", suggesting that they would have covered the deposit. Whiteside and Marshall (2008) gave counter-arguments and noted that the mapping model failed to demonstrate that the fissure deposit was demonstrably below the base of the Penarth Group and was more likely to date from after the onset of the transgression.

Dating the neptunian dyke fissures has also proved problematic, although embedded marine fossils enable a direct comparison with normal bedded sequences. Moore (1867) dated the Holwell "*Microlestes*" quarry, which yielded teeth of the haramiyid *Thomasia moorei*, as "Rhaetic" based on the associated marine fauna, but Kühne (1947) emphasised the lack of precision in this dating as the invertebrate faunal list published by Moore (1867) included fossils from several different fissures at Holwell, plus material from other localities such as the nearby Marston Road Quarry, which exposed unequivocal bedded Rhaetian (Westbury Formation) deposits (Nordén *et al.* 2015).

	Mid-Triassic	Late Triassic			Early Jurassic			Mid Jurassic
		Carnian Norian	E. Rhaetian	L. Rhaetian	Hettangian Sinemurian	Pliensbachian	Toarcian	
Cromhall		>>> >>>>>>>>> ◆◆◆◆◆◆ ◆◆◆◆◆◆						
Tytherington		⇦⇦◆◆◆◆ ◆◆◆◆◆◆						
Durdham Down	⇦⇦⇦⇦	◆◆◆◆◆◆ ◆◆◆◆◆◆						
Pant-y-ffynnon		>>>>>>>>>>>>						
Ruthin		>>>>>>>>>>>>						
Emborough		●●●●●						
Holwell "*Microlestes*" fissure								
Holwell, other fissures and Windsor Hill				⇨⇨⇨⇨⇨ ⇨⇨⇨⇨⇨	⇨⇨⇨⇨⇨⇨	⇨⇨⇨⇨ ⇨⇨⇨⇨	
St. Brides island		●●●●●●	●●●●●●	●●●●●● ●●●●				
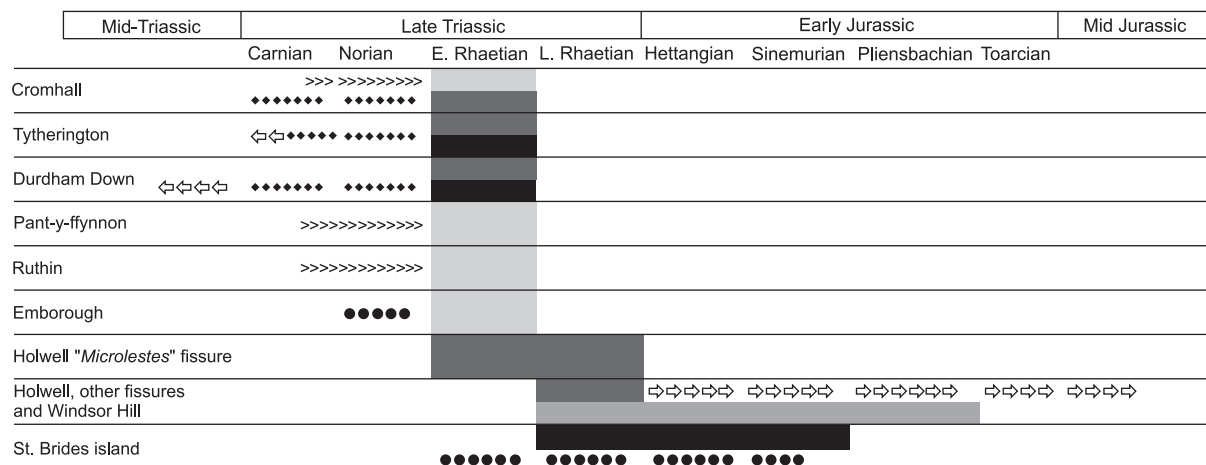
KEY for main evidence

■■■ From palynological dating: St. Brides (Kermack *et al.* 1973), Tytherington (Marshall and Whiteside 1980; Whiteside 1983),Tytherington and Durdham Down (Whiteside and Marshall 2008)

■■■ From associated marine fish: Holwell (Moore 1867), Tytherington (Whiteside 1983; Whiteside and Marshall 2008; Van den Berg *et al.* 2012), Cromhall (Fraser 1994), Durdham Down (Foffa *et al.* 2014)

■■■ From associated marine invertebrates: Holwell (Moore 1867), Windsor Hill (Kühne 1956)

■■■ From close similarity of terrestrial faunal assemblages: various (Whiteside 1983, 1986; Whiteside and Marshall 2008)

>>>>>>> From suggested lithological similarities to nearby horizontal beds: various (Robinson 1957), Cromhall (Halstead and Nicoll 1971; Fraser and Walkden 1983)

●●●●● From geological map and palaeogeographical reconstructions: Robinson (1957, 1971).

◆◆◆◆◆◆ From other suggested comparisons, *e.g.*, faunal, sedimentological, and geomorphological: Durdham Down (Moore 1881), various (Benton and Spencer 1995), Tytherington (Simms and Ruffell 1990), Cromhall (Walkden and Fraser 1993), various (Simms *et al.* 1994)

⇦⇦⇦⇨ Possible range from some authors, *e.g.*, Durdham Down (Moore 1881), Holwell (Kühne 1947; Savage and Waldman 1966), Windsor Hill (Savage 1977), Tytherington (Simms *et al.* 1994)

Fig. 6. Suggested dating of the fissures showing different approaches and conclusions by various authors. The principal historical means of dating the fissures is using faunal comparisons, palaeogeographical reconstructions and presumed lithological similarities with normally bedded strata in the UK. Comparisons with global faunas have also been used since the time of Charles Moore. Palynological evidence has been used to give an age assignment for St. Brides fissures initially by Harris (1957) and Lewarne and Pallott (1957), and in a precedent for sauropsid fissures by Marshall and Whiteside (1980).

Although not recording any invertebrate remains from the "*Microlestes*" fissure, it is clear from Moore's earlier papers (Moore 1859a, b, 1861, 1863) that the three tons of "coarse friable sand" which he had collected from a single fissure and had removed by horse and cart from the quarry to sort at his home in Bath yielded not only *Thomasia*, but the full complement of marine and terrestrial faunal components discussed below for the fissure. The composition of the broader vertebrate fauna of the Holwell "*Microlestes*" fissure thus fully supports a Rhaetian age. Likewise the fauna of Marston Road Quarry includes all the typical Westbury Formation fishes and reptiles (including *Pachystropheus* and a placodont), as well as a small lepidosaur, probably a sphenodontian, a terrestrial wash-in (Nordén *et al.* 2015). Kühne (1947) made a further collection of haramiyid teeth at Holwell and assigned these to the "Rhaetic" based on the associated marine fishes. Kühne (1956) examined the range of marine invertebrates and vertebrate fossils in the Windsor Hill neptunian dyke fissure and determined that the deposit, containing *Oligokyphus*, could be assigned a Pliensbachian age based on the youngest invertebrates such as the belemnite *Pseudohastites* and the brachiopod *Squamirhynchia* (= *Cirpo*) *fronto*. Savage (1977) counter-argued for a younger "Inferior Oolite" (Aalenian–Bathonian) age, as he interpreted the fissure as a swallet that filled subaerially with reworked "Lias" sediments along with contemporaneous mammaliamorph bones.

Although Robinson (1957) discounted Durdham Down as an "underground water-course" fissure, later authors (*e.g.*, Halstead and Nicoll 1971; Whiteside 1983) recognised that the deposit was a fill in a cavern. Moore (1867) claimed that the *Thecodontosaurus* fossils from Durdham Down were "Rhaetic" based on his recognition of similar dinosaur teeth from Holwell and the nearby presence of bone-bed fossils, but later (Moore 1881), suggested that the teeth were older and of "Keuper" age. Foffa *et al.* (2014) reported a few marine fish teeth, considered the palaeogeography, and confirmed Moore's original suggestion of a Rhaetian date. In fact, Holwell and the associated Marston Road site provide unique insights into mixing of terrestrial vertebrates and Rhaetian marine fossils.

HOLWELL

The fauna from the fissure in Moore's "*Microlestes*" Quarry at Holwell is unique in that the terrestrial tetrapod remains (mammaliamorphs, *Thecodontosaurus*, *Diphydontosaurus* and *Clevosaurus*) are far outnumbered by specimens of aquatic reptiles and fishes (see Fig. 2 for examples). Amongst the latter, teeth of *Rhomphaiodon* (*Hybodus*) *minor* have been reported from Ladinian to Rhaetian rocks (see discussion in Duffin and Delsate 1993), although the pre-Rhaetian records are unverified. It is a common taxon in the marine Rhaetian throughout northwest Europe and is well known from the classic basal Rhaetian bone bed and other Westbury Formation deposits of Aust, Westbury Garden Cliff, and Barnstone, for example (Sykes *et al.* 1970). Moore claimed to have up to 50,000 teeth of *Lissodus minimus*, formerly assigned to *Acrodus* (Duffin 1985, 2001; Fischer 2008) from Holwell; *Lissodus* is a long-ranging euryhaline genus, although *L. minimus*, like *R. minor*, is recorded from Ladinian to Rhaetian deposits. Once again, these records require verification, but in the British area, *L. minimus* is an extremely common shark mostly confined to the Westbury Formation; for example it is recorded in abundance from the basal Westbury Formation with rarer occurrences in the top of the Westbury strata and basal Cotham Member, Lilstock Formation in Manor Farm Quarry (Allard *et al.* 2015). The preservation and time range of *Lissodus* fossils demonstrate that the fossils are coeval with the Westbury strata and not derived. The largest hybodont shark teeth from Holwell belong to *Hybodus cloacinus*, which are often highly abraded and fragmented components of Rhaetian Bone Bed faunas; the species may range into the Sinemurian (Duffin 1993). *Palaeobates* is represented by a small number of teeth belonging to *P. reticulatus*, a taxon that is currently unique to the Holwell fauna (Duffin 1998a). Teeth originally ascribed to *Polyacrodus holwellensis* Duffin, 1998b have since been assigned to the monotypic genus *Duffinselache* (Andreev and Cuny 2012), which has been recorded from the Westbury Formation at several British localities (*e.g.*, Korneisel *et al.* 2015; Nordén *et al.* 2015) as well as equivalents in France and Belgium (Andreev and Cuny 2012). The taxonomic relations of *Pseudocetorhinus*, originally described from Holwell, but since recorded from the Rhaetian of Belgium, Luxembourg, and France (Delsate 1995, 2000; Cuny *et al.* 2000), are the subject of some discussion (Cappetta 2012), but the thorn-like teeth and possible associated gill rakers were originally described as belonging to a filter-feeding neoselachian shark (Duffin 1998a). The neoselachian sharks are further represented at Holwell by teeth, fin spines and probable scales of *Synechodus rhaeticus* which, although not common in the Rhaetian fauna, has been recorded from the Westbury Formation and other Rhaetian deposits in continental Europe (Duffin 1982, 1998b; Cuny *et al.* 2000; Korneisel *et al.* 2015; Nordén *et al.* 2015). The chondrichthyan complement of the fauna is completed by the crushing toothplates of the myriacanthid holocephalan *Agkistracanthus mitgelensis*, which has also been recorded from the Cotham Member of the Lilstock Formation at St. Audries Bay, as well as from the Rhaetian and Hettangian of Switzerland and Austria (Duffin and Furrer 1981).

Bony fishes are represented at Holwell by a series of genera that are all typical of the bedded marine deposits of the British Penarth Group — *Gyrolepis albertii*, *Severnichthys acuminata*, and *Sargodon tomicus*. Although the last has also been reported from the Ladinian and Carnian of Germany and the Norian of Italy (see discussion in Duffin and Delsate 1993), the fish specimens in Moore's collection from Holwell all testify to a Rhaetian age (Duffin 1999) for the deposit.

Amongst the reptile remains from Holwell, vertebrae of the putative choristodere or thalattosaur *Pachystropheus rhaeticus* are also well known from the British marine Rhaetian, especially from Blue Anchor, Aust, and Westbury Garden Cliff (Storrs and Gower 1993; Storrs 1994; Renesto 2005), as well as from the Rhaetian of Gaisbrunnen and Olgahain in southern Germany (Huene 1933). Placodont reptiles, represented by teeth and osteoderms of *Psephoderma alpinum* Meyer, 1858 (originally described as *P. anglicum* Meyer, 1867), although poorly represented in marine deposits outside the area of the Mendips (Storrs 1994), have been recorded from the nearby Rhaetian section at Marston Road (Nordén *et al.* 2015).

Moore described collecting material from a number of fissures at Holwell, and it is true that his collection, now housed in the BATGM, does not discriminate between the specimens obtained from different fissures. His faunal lists for the "*Microlestes*" fissure (Moore 1859a, b, 1861, 1863), which clearly formed numerically the greatest part of his collection and involved a huge investment of time and effort to obtain, indicate beyond reasonable doubt that *Thomasia*, *Thecodontosaurus*, *Pachystropheus*, *Psephoderma*, lepidosaurs and the wide range of Rhaetian fishes discussed above were all obtained from the same fissure infill.

It has been suggested that all the bones in the Rhaetian basal bonebed of the Westbury Formation might be derived from older horizons (Martill 1999). This cannot be demonstrated, however, by considering the strati-

graphic ranges elsewhere of bonebed taxa, which, as noted above, all range either below or above that horizon. Further, in a rare earth element (REE) study, Trueman and Benton (1997) showed that the provenance of bone and sediment could be compared; sites with heavily abraded, massive bone lumps, such as Aust Cliff, showed differentiation of bones and source sediments, and hence evidence that each had been derived from separate sources, whereas sites such as Westbury Garden Cliff, where the fish and reptile bones and teeth are small and show no signs of physical abrasion, also show perfect matching of REE signatures between fossils and sediment, hence indicating derivation of both from the same source. Further, the widespread occurrence of such bone beds across Europe at the base of the Rhaetian, all containing the same fauna, makes it hard to understand how older bone-bearing horizons could have been reworked uniformly over such a wide area and leave no remnant of the original horizon(s). More likely the bones and teeth came from fishes and reptiles that were parts of the contemporaneous fauna, and the energy of the transgressive movements of water and sediments churned and winnowed the phosphatic components on the seabed. Contemporaneity of erosion and bonebed deposition at the base of the Westbury Formation is confirmed by *Thalassinoides* burrows formed by callianassid shrimps extending into the top of the underlying Blue Anchor Formation, and infilled with basal Rhaetian bonebed that accompanied the influx of waters as the first act of the Rhaetian transgression (Korneisel *et al.* 2015).

DATING BY PALYNOLOGY

Establishing the ages of the fissure faunas has been controversial, but we propose two approaches that can be applied in a reasonably objective manner: palynology and mapping-scale topographic comparison. Both methods point to the somewhat radical suggestion that all the "sauropsid", green, yellow or red-bed fissures are Rhaetian, and most of the mammaliamorph-bearing fissures are younger, of Hettangian–Sinemurian age.

The first precise age assignment for a sauropsid fissure deposit was made by Marshall and Whiteside (1980), who recovered an assemblage of early Rhaetian palynomorphs and marine phytoplankton associated with *Thecodontosaurus* and *Clevosaurus* bones in fissure 2 at Tytherington. Further palynomorph assemblages were discovered at ten sites in six fissures at Tytherington, and one fissure near the Clifton Suspension Bridge by Whiteside and Marshall (2008). They were able to compare the palynological assemblages at Tytherington with the normally bedded Penarth Group sequence lying unconformably on Carboniferous Limestone at nearby Hampstead Farm Quarry, Chipping Sodbury. These assemblages confirmed the age as early Rhaetian, equivalent to the Westbury Formation. Recent investigations on archival collection material have produced another productive palynological, assemblage from Tytherington. Importantly this is from dark-coloured mudstone clasts embedded in a matrix that also contains bones of *Thecodontosaurus*. The palynological assemblage (Table 3) is dominated by *Rhaetogonyaulax rhaetica* (but only rare *Cymatiosphaera*

Table 3. Palynological analysis of the fissure 2 breccia, bearing the principal *Thecodontosaurus* bones found in Tytherington quarry. Palynomorphs are distinguished into terrestrial and marine forms.

	Taxon	Count	Percentage
	Classopollis classoides	35	16.0
	Ovalipollis pseudoalatus	35	16.0
	Ricciisporites tuberculatus	29	13.2
	simple spores	19	8.7
	indeterminate	12	5.5
Terrestrial 71.7%	*Vesicaspora fuscus*	11	5.0
	Rhaetipollis germanicus	5	2.3
	Classopollis spp.	4	1.8
	Vitreisporites pallidus	4	1.8
	?*Krauselisporites reissingeri*	1	0.5
	apiculate spore	1	0.5
	Alisporites thomasii	1	0.5
	Rhaetogonyaulax rhaetica	58	26.5
Marine 28.3%	*Dapcodinium priscum*	2	0.9
	Cymatiosphaera polypartita	1	0.5
	indeterminate cyst	1	0.5
Total	16 taxa	219	100.2

polypartita), *Classopollis classoides*, *Ricciisporites tuberculatus*, *Ovalipollis pseudoalatus*, and *Vesicaspora fuscus*. The content of *Rhaetipollis germanicus* is low. The taxa and their relative proportions are similar to those from the normally bedded Rhaetian Penarth Group section at Hampstead Farm Quarry near Chipping Sodbury recorded by Whiteside and Marshall (2008), The Hampstead Farm Rhaetian strata are located on the same palaeo-island as the Tytherington fissure deposits, confirming the new palynological assemblage age as equivalent to the lower part of the Westbury Formation (lower and middle Bed 5 using the bed number in Whiteside and Marshall [2008], based on the work of Curtis and Curtis in Donovan *et al.* [1989]). The high relative abundance of *Ovalipollis pseudoalatus*, *Ricciisporites tuberculatus* and *Rhaetogonyaulax rhaetica* shown in Table 3 also agrees with this age assignment (*cf.* Whiteside and Marshall 2008, fig. 15). This new discovery of *Thecodontosaurus* with fragments of lower Westbury Formation provides unequivocal evidence for the Rhaetian age of this reptile and its associated fauna. The assemblage includes a mixture of terrestrial and marine palynomorphs demonstrating the marginal location of the deposit near the Rhaetian sea.

Unfortunately, despite extensive sampling, palynomorphs have not yet been found in the other major Triassic fissure fills, but comparisons of the vertebrate faunas have been used to extend the argument. Based on the tetrapod similarities of Tytherington to Cromhall, Durdham Down, Pant-y-ffynnon and Ruthin, Whiteside and Marshall (2008) concluded that those fissures were infilled during the Rhaetian. The new, distinctive clevosaur, *Clevosaurus sectumsemper* at Woodleaze (Fig. 2G) has similar features to a species from fissure 2 (Fig. 2H) at Tytherington (Klein *et al.* 2015) and Pant-y-ffynnon (DIW, personal observation), suggesting that the deposits are coeval. Whiteside and Marshall (1985, 2008) additionally suggest that the presence of *Kuehneotherium* at Emborough indicates a Rhaetian age for that deposit and the co-occurrence of abundant kuehneosaur fossils also indicates a Rhaetian date for Batscombe. Whiteside and Marshall (2008) argued that no tetrapod-bearing fissure has been dated as older than earliest Rhaetian, or in particular pre-transgression, and that has not been contradicted.

The dates of the younger, *Hirmeriella* faunas are founded on established palynological evidence. Macrophytic fossils of the conifer *Hirmeriella muensteri* had been collected at Cnap Twt (Harris 1957), and more were discovered in many other St. Brides quarries by the University College London team led by K.A. Kermack. *Hirmeriella muensteri* is found with the tetrapods in St. Brides fissure fills, particularly at Ewenny, and Kermack *et al.* (1973) referred to the overall assemblage as the "*Hirmeriella* association". Evans and Kermack (1994) noted that the plant and palynomorph evidence used to date the St. Brides fauna included *Hirmeriella*, and *H. muensteri* is also found in southern German Lower Lias beds equating to the *Thaumatopteris* Zone of East Greenland, southern Germany, Poland, and Sweden. They identified the significant presence (6%) of *Krauselisporites* (*Heliosporites)* at Cnap Twt, which related to the late or "latest" Rhaetian *Heliosporites* Zone of Orbell (1973) and probably extended into the early Hettangian. They also emphasized the absence in St. Brides deposits of *Ovalipollis*, *Rhaetipollis* and *Ricciisporites,* palynomorphs that are typical of the Penarth Group (mainly Rhaetian), but absent from the base of the Jurassic and higher units. These studies indicated to Evans and Kermack (1994) a latest Rhaetian or Early Jurassic date for the Cnap Twt deposit, a typical *Hirmeriella* locality. Robinson (1971) considered the Early Jurassic palaeogeography of the area and suggested that St. Brides island was finally submerged in the early Sinemurian; Evans and Kermack (1994) concurred, stating that "the *Hirmeriella* association cannot be younger than that". Some later authors (Gill 2004, in Clemens 2007) considered that the depauparate *Morganucodon* fauna, possibly extant at a time when the island was smallest, might be younger than the more diverse *Morganucodon*-sphenodont fauna.

These conclusions are generally confirmed by comparison with the geochronologically dated Newark Supergroup in eastern North America. There, the palynomorph assemblages document a "fern spike" at the top of the Triassic (latest Rhaetian; J. Whiteside *et al.* 2010), indicating significant ecological change (Fowell *et al.* 1994). Although the palynoflora below the fern spike is diverse, the overwhelmingly dominant palynomorph that follows is *Classopollis*, and the collapse in diversity is attributed to the ETE environmental crisis. Hounslow *et al.* (2004) report a high proportion of *Classopollis* just above the Langport Beds in the Wilmcote Limestone Member (formerly the Pre-planorbis Beds and Planorbis Beds; Rhaetian–Hettangian) of the Blue Lias Formation. In their reassessment of the palynomorphs from Ewenny quarry, Whiteside and Marshall (2009) noted the absence of any marine taxa, as seen in the older, Rhaetian, assemblages, and the remarkable dominance by *Classopollis*, comprising over 95% of all palynomorphs. *Classopollis* is the pollen of *Hirmeriella* and related cheirolepidacean conifers, and indicates a very monotonous conifer-dominated vegetation. They also noted that trilete spores are very rare, being represented by only two specimens, *Carnisporites megaspiniger* and *Krauselisporites reissingeri*, which range into the Early Jurassic.

Further work on the assemblage has confirmed the absence of typical UK Rhaetian palynomorphs including *Rhaetipollis germanicus* and *Ovalipollis pseudoalatus*; the last occurrence of these at St. Audries Bay (for location see Fig. 4) is at the top of the Cotham Member, Lilstock Formation (Hildebrandt *et al.* 2013) and therefore before the Triassic–Jurassic boundary. Warrington *et al.* (2008, fig. 14) also show the last appearance datums (LADs) of *Rhaetipollis germanicus* and *Ricciisporites tuberculatus* at just below their proposed Triassic–Jurassic boundary for the St. Audrie's-Doniford Bay section. The horizon with an abundance of *Classopollis* in the basal Wilmcote Limestone Member at St. Audries Bay that correlates with the GSSP base of the Jurassic System at Kuhjoch (Austria; shown by Hildebrandt *et al.* [2013, fig. 27]) indicates that it is at the base of the Hettangian. Our sample from Ewenny is nearly all *Classopollis classoides* (= *C. torosus*), as opposed to *C. meyeriana*, and it is perhaps noteworthy that this species has a similar dominance in the mid–upper *Planorbis* Zone, as shown by Warrington *et al.* (2008, fig. 10) at St. Audries Bay. Specifically, the St. Brides palynomorph assemblage therefore demonstrates equivalence to the basal Blue Lias Formation and a dating of at least early Hettangian for the *Morganucodon* fauna from Ewenny quarry.

DATING BY TOPOGRAPHY

The second approach to establishing the relative ages of the different vertebrate-bearing units is to explore their field relationships and topographic levels. We have considered the height of the host Carboniferous Limestone surface overlying the fissures, or where that is imprecisely known, or where there are many tetrapod-bearing fissures, the maximum height of the pre-quarrying Carboniferous Limestone within 50 m of the quarry. The height of the base of the nearest outcrops of the Penarth Group strata from the appropriate BGS digimap© is then compared and the difference plotted in a simple bar chart (Fig. 7). This approach produces a pattern which shows that, where specific palynological or coeval fish dating of the sauropsid fissures is known, the limestone surface at the entrance to the fissures stands at 2–9 m above the base of the Penarth Group.

There are reservations to this approach. For example the Carboniferous Limestone at the mouth of the fissures may have undergone some erosion since its exhumation from younger Mesozoic strata, reducing its height relative to the Penarth Group base. Also, the base of the Penarth Group may not be chronologically equivalent everywhere. Furthermore, we know that there were cycles of sea level rise and fall in the Rhaetian, indicated for example by cycles in the Westbury Formation, and therefore all fissures in one quarry need not be contemporaneous. However, even with these provisos, we suggest that there is a pattern that provides evidence to indicate, in general, the relative ages of the fissure localities. The rationale is that final infilling would have occurred as the rising Rhaetian sea lapped up around the top of the fissure. Caverns on the palaeo-islands presumably formed phreatically in a freshwater lens maintained by a high sea level similar to those described by Mylroie (2013) on modern Bahamian islands. The top of the freshwater lens on islands such as the Bahamas is at most only 1–2 m above sea level (J. Mylroie, personal communication). In particular,
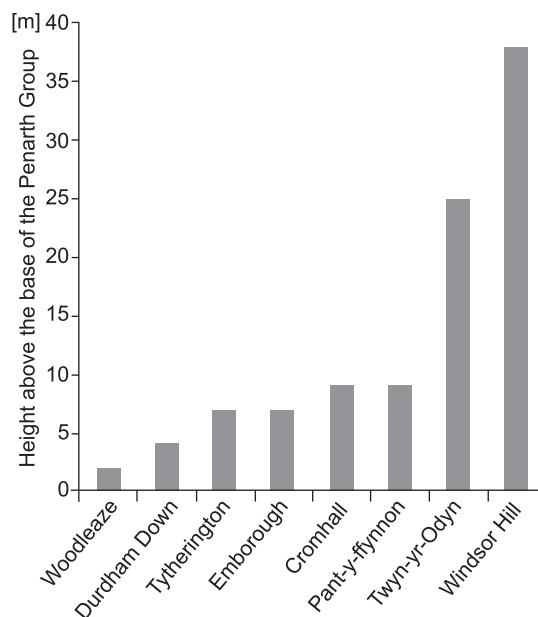
Fig. 7. Heights of Carboniferous Limestone in sauropsid fissure localities above the base of nearest Penarth Group. The height of the limestone surface in the near vicinity of a terrestrial vertebrate-bearing fissure is plotted with respect to the base of the nearest occurrence of bedded Penarth Group. The field relationships of the fissures and the Penarth Group are most reliable for Cromhall, Tytherington, Woodleaze, Durdham Down, Emborough and Windsor Hill. There is some uncertainty in the plots of Pant-y-ffynnon (where a mid-range figure is given) and Twyn-yr-Odyn due to some faulting in the vicinity; however, the fissure entrances are above the Penarth Group base. Holwell and Ruthin are not plotted, as the former is a neptunian dyke, and the geology around the latter is heavily faulted and sufficiently complex that some nearby Penarth Group strata are below the fissure entrance, whereas other sites are above. Batscombe fissure was not specifically located and was presumably quarried away, but the limestone surface in that vicinity is substantially higher (more than 12 m) than the nearest White Lias and therefore the Penarth Group base. Based on BGS digimap© geological maps, quarry maps where available, Ordnance survey digimap© and Google Earth© images of the area.

the presence of non-reworked fish teeth suggests a nearby sea and the presence of palynomorphs signifies a position below the vadose zone, as oxygenated water is destructive to pollen and spores. Furthermore, amorphous organic material in the palynological assemblages (Marshall and Whiteside 1980; Whiteside and Marshall 2008) indicates anoxic depositional environments that are likely to have been below, at, or near to sea level. Indeed, fissures just a few metres above sea level may still have been eroding, particularly at freshwater/saline water mixing zones (Whiteside and Marshall 2008). Vertical solution-formed voids such as "banana holes" and pit caves (Harris *et al.* 1995) are known to continue to widen and deepen a few metres above sea level (J. Mylroie, personal communication). Landlocked karstic water-filled voids in these locations with a connection to the sea are termed anchialine.

Comparison of the main sauropsid sites shows that putative Rhaetian fissures, such as Emborough, Pant-y-ffynnon and Twyn-yr-Odyn are also significantly above the base of the Penarth Group. From this analysis, it appears that Emborough has a similar field relationship as Tytherington to the Penarth Group and that Twyn-yr-Odyn may have been infilled later in the Rhaetian. However, it is worth noting that the base of the White and Blue Lias that lies within 500 m of Emborough is just 1 m below the top of the fissure, so all three localities may well be younger than those at Tytherington. We have not plotted Holwell, as the fissure is a neptunian dyke, nor the Ruthin fissure deposit, as the geology near the quarry is complex, with significant faulting, and calculations show some nearby basal Penarth Group sediments below the limestone surface whereas others are higher. The geology around Pant-y-ffynnon is also more complex than the other fissures plotted in Fig. 7 due to a greater degree of nearby faulting, so a middle figure has been plotted.

Windsor Hill, interpreted as a Pliensbachian neptunian dyke by Kühne (1956), but as an "Inferior Oolite" (Aalenian–Bathonian) "swallet" (*i.e.*, doline) by Savage (1977), shows, as predicted, the top of the fissure high above (nearly 40 m) the base of the Penarth Group.

The same technique can be extended to consider the field relations of the St. Brides palaeo-island fissures to local normally bedded strata. However, in these cases, the base of the Penarth Group lies at or below present-day sea level in the vicinity of the Carboniferous Limestone hill that encompasses the quarries. Using the regional geological model (Fig. 8A) of Wilson *et al.* (1990), and giving the threshold as the nearest mapped base of the Porthkerry Member, Blue Lias Formation, (the unit succeeding the Lavernock Shales Member), that lies just in the *Alsatites liasicus* Zone of the (mid) Hettangian, the relative position of the St. Brides fissures can be inferred (Fig. 8B). This analysis indicates that Ewenny contains the oldest deposits, of early–mid Hettangian age; Pant 2, Pontalun and Duchy form a second, later Hettangian group; and Pant 4 and 5 have the youngest deposits, perhaps of latest Hettangian or early Sinemurian age. This pattern fits with the three observed faunal groups: Ewenny has *Morganucodon* and *Gephyrosaurus* only (Kermack *et al.* 1973; PGG, personal observation); Pant 2, Pontalun and Duchy have *Kuehneotherium* in addition to those genera; while Pant 4 and 5 have a fauna where *Clevosaurus convallis* numerically dominates and *Gephyrosaurus* is very rare. Pant 4 and 5 also yield haramiyids, *Kuehneotherium*, and *Oligokyphus*, as well as the greatest diversity of morganucodontans, which are present in significant numbers (Gill *et al.* 2006; Clemens 2011). This pattern also accords with the palynological data from Ewenny, which indicate an age of at least early Hettangian, and the initial low tetrapod diversity concurs with an assignment just into the Early Jurassic following the ETE. As an indicator of the time for the proposed faunal succession, the Hettangian is between 1.5–2.5 Myr long, and the minimum duration of the Sinemurian *Arietites bucklandi* Zone is given as 342 ka by Weedon *et al.* (1999).

A criticism of this method could be that Pleistocene ice sheets and subsequent flooding (Crampton 1966) have variously depressed and eroded the Carboniferous Limestone around the Severn estuary, and so the match of topography to fissure age could be compromised. Such periglacial effects, for example, could have deepened the Triassic landscape of the Pant, St. Brides, and Afon Alun valleys, where the lower boundaries of the quarries lie. However, all the South Wales fissures are likely to have been affected to the same extent, and so the relative ages estimated for the fissures may still be accurate. It might also be argued that the greater diversity in Pant 4 and 5 was caused by the animals occupying different topographic levels, namely on the surface of the High Tor limestone rather than the Gully Oolite of the other localities. However, the area is so small (*c.* 20 km^2) that it is unlikely to have hosted substantially different habitats that would then be associated with different vertebrate diversities.

We can use these analyses to suggest a faunal succession of the fissures of the Bristol and South Wales region (Fig. 9). The faunas of Tytherington have a palynologically dated early Rhaetian age for
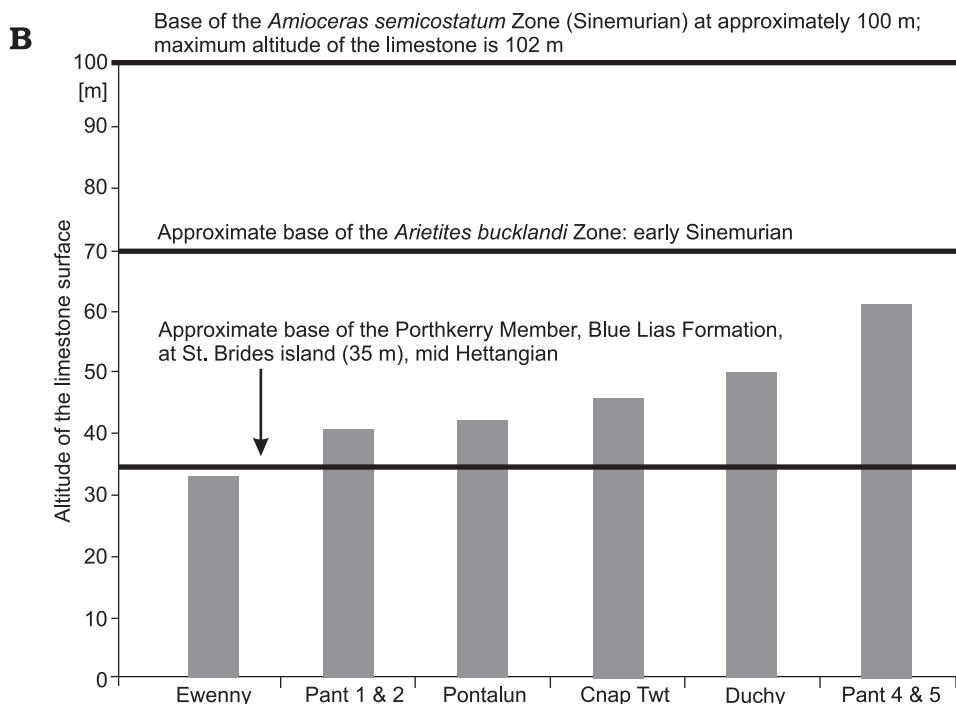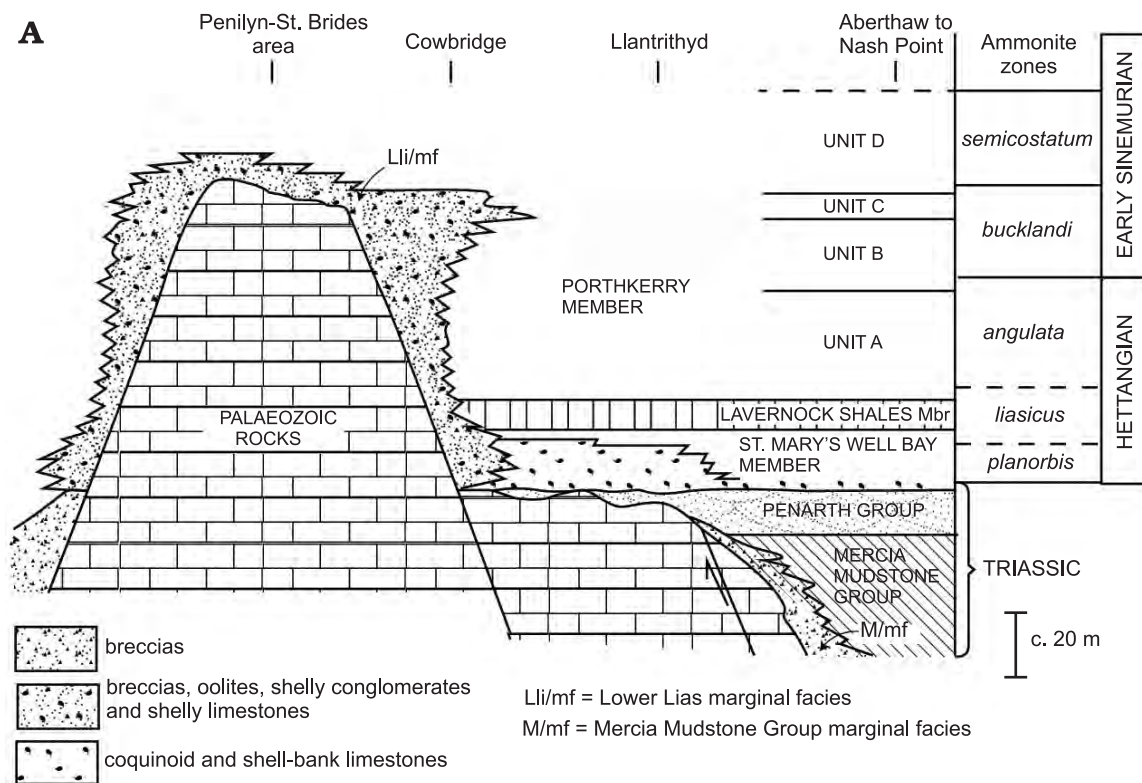
Fig. 8. Model of St. Brides area during the Early Jurassic transgression and altitude plot of the St. Brides fissures. **A**. Geological model in the Bridgend area as the Liassic transgression progressed. Simplified modern restatement of basement/cover relationships in South Wales (from BGS Memoir Sheets 261 and 262; Wilson *et al*. 1990). Note that it is not a simple transgressive flooding as relative sea levels throughout the period are likely to have gone down as well as up. **B**. Altitude of Carboniferous Limestone surface above the principal St. Brides fissure localities. The model shows the approximate topographical heights reached by named strata with respect to areas of Palaeozoic rocks in the Bridgend area as the transgression progressed. The base of the Porthkerry Member, Blue Lias Formation, and the Lower Sinemurian is the best estimate from this model, but mapping of the nearest Lavernock Shale Member suggests that the base of the Porthkerry Member may extend down to 20 m. Based on BGS Memoir for sheets 261 and 262 (Wilson *et al.* 1990), BGS geological maps, Ordnance Survey maps, quarry company historical maps, and Google Earth© images of the area.

A early Rhaetian ——————→ ←—— late Rhaetian ——————→ ←—— Hettangian ——————→ ←— early Sinemurian

Overall decreasing land area but fluctuating during multiple transgressive and regressive phases

Diverse palynoflora
Significant marine component of fish or dinoflagellates
Brackish or freshwater fish such as *Pholidophorus* or *Legnonotus* present
Animals up to 3 metres long
Terrestrial invertebrates include conchostracans, annelids and millipedes

Very low palynofloral diversity
No marine palynomorphs   (no fish?)
Animals less than 1.5 metres long
Metacupes (beetle) is the only recorded terrestrial invertebrate

Thecodontosaurus
coelophysoid
suchian/*Agnosphitys*
aetosaur
Diphydontosaurus
Planocephalosaurus
Pelycymala
Sigmala
drepanosaur
tricuspisaur
phytosaur
procolophonids

Kuehneosaurus

Gephyrosaurus

?
?
?

tritylodonts
haramiyids
Kuehneotherium
morganucodontans

Oligokyphus

Pseudotriconodon

Clevosaurus, sphenosuchians, theropods, and ?pterosaurs

B Early Rhaetian ——————→ T/J ←—— (mid) Hettangian ——————→ ←— Early Sinemurian

Kuehneotherium

Clevosaurus convallis

??? *Gephyrosaurus*

reduced population in the presence of *C. convallis*?

??? *Morganucodon*

morganucodontans

Oligokyphus
haramyids

theropods, sphenosuchians, and ?pterosaurs

Fig. 9. Changes in the tetrapod biota of the fissures of southwestern UK. **A**. Overall changes in the fissure terrestrial tetrapod assemblages: a summary of the suggested changes in the tetrapod biota from the early Rhaetian to the Pliensbachian based on analyses in this paper. Reptiles and mammaliamorphs are grouped separately, and the lower arrows show reptiles that probably spanned the time range, but evidence for them at some time periods is scant, *e.g.*, pterosaur metacarpals have been recorded at Cromhall but that identification is disputed. All assemblages are dominated by short tetrapods (< 0.5 m). However, the sauropsid assemblages include animals such as phytosaurs, sauropodomorphs, and coelophysoids, that range from 2–3 m in length whereas larger forms are very rare in the St. Brides deposits; the largest tooth recovered in those fissures derives from an archosauromorph 1–1.5 m long. **B**. Changes in the fissure terrestrial tetrapod assemblages of St. Brides palaeo-island. We propose three faunal assemblages for the St. Brides palaeo-island tetrapod community. The earliest assemblage comprises *Morganucodon watsoni* and *Gephyrosaurus bridensis* only, followed by a second younger biota that includes those genera as well as *Kuehneotherium*. The third and youngest fauna includes all three plus *Clevosaurus convallis*, morganucodontans including *Bridetherium* and *Paceyodon*, together with the tritylodont *Oligokyphus*. Pterosaurs were probably present in the second assemblage and also in the youngest biota alongside sphenosuchian crocodylomorphs and theropods.

Planocephalosaurus, Diphydontosaurus and *Thecodontosaurus*; the presence of at least two of these genera unites the fissures in Tytherington, Cromhall, Ruthin, Holwell, and Durdham Down. The new clevosaur found at Woodleaze by Klein *et al.* (2015) is also present at Pant-y-ffynnon as well as being similar to the species in the palynologically dated fissure 2 at Tytherington; moreover *Terrestrisuchus* is found at Pant-y-ffynnon (Crush 1984), as well as at Tytherington and Cromhall. Assuming that the two teeth are not contaminants from processing other fissures, the *Kuehneotherium* found at Emborough (Fraser *et al.* 1985) suggests at least a Rhaetian age (Whiteside and Marshall 1985) and is found with huge numbers of *Kuehneosaurus* fossils; kuehneosaurs are also present in Batscombe as well as the probable Rhaetian deposits at Cromhall and Pant-y-ffynnon. The suggestion that *Oligokyphus* (Fig. 1F) is present in the youngest of the known St. Brides faunas is also in accord with its presence at Windsor Hill, probably the youngest of the fissure deposits in the Bristol region. The morganucodontids and haramiyids of Holwell may indicate that some fissures there include deposits younger than early Rhaetian. It is worth emphasising that these fissure faunas are from island communities and, as such, immigration, genetic drift and local extinctions could have significantly changed the biota quickly. In addition, there may be species that are only found in certain habitats on an island and therefore it may never be possible to achieve a precise chronology of faunal changes.

COMPARISON WITH GLOBAL FAUNAS

Individual taxa found in the fissures are recorded from pre-basal Rhaetian normally bedded strata from elsewhere in the world. An example is cf. *Diphydontosaurus* from the Ladinian of Germany (Jones *et al.* 2013) and Norian of Italy (Renesto 1995), *Clevosaurus* from the Norian of Brazil (Bonaparte and Sues 2006), and a probable *Planocephalosaurus* from the Carnian of North America (H.-D. Sues, personal communication). Heckert (2004) also ascribed some jaw fragments from the Carnian of Texas to *Planocephalosaurus*. However, none of these genera or other abundant fissure tetrapods, except procolophonids, is reported from tetrapod assemblages in pre-Rhaetian sites in the UK. Moreover, some distinctive reptile genera and species, including *Clevosaurus hudsoni*, *C. sectumsemper*, *Sigmala*, *Pelecymala*, and *Thecodontosaurus*, appear to be unique to the sauropsid fissures, with no direct equivalents reported from elsewhere. The procolophonid genera of the fissure deposits have not yet been established, so they cannot currently be compared directly with UK genera such as specimens from the Anisian Otter Sandstone Formation of Devon. The single aetosaur scute found at Cromhall (Lucas *et al.* 1999) does not convey any clear age evidence (Whiteside and Marshall 2008). In contrast, cf. *Clevosaurus* and *Diphydontosaurus* are recorded from European sites closest to the fissure localities, such as in the Belgian Rhaetian by Duffin (1995). Individual taxa may have long, and currently unknown, stratigraphic ranges and the rarity and incompleteness of small tetrapod skeletons makes it hard to use individual genera in a strictly biostratigraphic manner.

Comparison of the fissure vertebrate assemblages to global biotas is somewhat more informative (Fig. 10), despite the problems with assigning ages to known normally bedded terrestrial strata. In particular, many formations traditionally regarded as Late Triassic were shown some time ago to be of Early Jurassic age (Olsen and Galton 1977). Fine-tuning of this dating continues and there is some uncertainty about the ages of major fossiliferous successions, such as the Newark Supergroup of the USA, the Chinese Lower Lufeng Formation, and units in parts of Europe. For example, the basal part of the McCoy Brook Formation (Newark Supergroup) was regarded as Hettangian by Sues *et al.* (1994) but is now considered "latest" Rhaetian (Fedak *et al.* 2015). The richest comparative European fauna from a normally bedded sequence is the "Grès infraliasiques" Formation at St. Nicolas-de-Port (SNP) near Nancy, France, regarded as post-transgression Rhaetian (Debuysschere *et al.* 2015, p. 2). The collection sites at the locality are from lenticular beds with considerable lateral variation and "for this reason, the precise level from which the mammalian teeth described by Sigogneau-Russell [*e.g.*, *Brachyzostrodon*, *Delsatia*, and *Morganucodon*] were collected remains uncertain" (Debuysschere *et al.* 2015, p. 2); the original site is lost (E. Chenal, personal communication). Cf. *Diphydontosaurus* has been found at a Rhaetian horizon (the basal lower conglomerate) at Serres, 11 km to the northeast of SNP and *cf. Planocephalosaurus* from Vaubexy 36 km to the south of SNP (M. Debuysschere and E. Chenal, personal communication). E. Chenal (personal communication) has also recovered specimens of cf. *Diphydontosaurus* from SNP. Overall, the tetrapod fauna from SNP and nearby localities is in accord with a dating of the Bristol fissures as Rhaetian. However, *Clevosaurus*, prevalent in the "sauropsid" fissures and the *Morganucodon*-sphenodont fauna from St. Brides palaeo-island, is not

	Ladinian– Carnian	Norian	Rhaetian SNP. Seres and Vaubexy	late Rhaetian McCoy	Hettangian	Sinemurian
	Worldwide	Worldwide	French, Belgian, Luxemburg and UK non-fissure sites	Brook Fm. N. America	Lufeng Fm. China	Kayenta Fm. N. America
SAUROPSID TYPE						
"*Palaeosaurus*" aff. phytosaurs	?					
aff. *Thecodontosaurus*	?					
Diphydontosaurus						
aff. *Planocephalosaurus*		?				
Sigmala and/or *Pelycymala*						
aff. *Clevosaurus hudsoni*						
Procolophonid						
Kuehneosaur						
aff. *Tricuspisaurus*		?				
Aetosaur						
Drepanosaur						
Coelophysoid/theropod						
aff. *Terrestrisuchus*	?		?			
MAMMALIAMORPH TYPE						
Pterosaur			?	?	?	
Haramiyid sp.				?	?	
Pseudotriconodon/cynodont					?	
Morganucodon sp.		?				
Eozostrodon						
Kuehneotherium praecursoris		?		?	?	?
Paceyodon davidi						
Gephyrosaurus						
aff. *Clevosaurus convallis*	?					?
aff. *Oligokyphus major*						

■ present   ▬ present or similar taxa   [?] uncertain data   [ ] absent

Fig. 10. Comparison of the fissure tetrapod faunas with global examples. Light gray is where the deposit has been well sampled, but no evidence of a taxon has been found. Black refers to a taxon or type being present, and dark gray is the presence of a closely related or possibly the same taxon. White is where no evidence of the taxon has been found, but further sampling may yield additional information. Some of the fossils found in normally bedded strata are similar but cannot with certainty be referred to a species, such as the cf. *Clevosaurus* and cf. *Diphydontosaurus* specimens of Duffin (1995). Data from Fraser (1994), Luo and Wu (1994). Shubin *et al.* (1994), Sigogneau-Russell and Hahn (1994), Storrs (1994), Cuny (1995), Curtis and Padian (1999), Bonaparte and Sues (2006), Lucas and Tanner (2006), Heckert (2004), Whiteside and Marshall (2008), Irmis *et al.* (2013), Jones *et al.* (2013), Debuysschere *et al.* (2015), and Fedak *et al.* (2015). M. Debuysschere, E. Chenal, and H.-D. Sues all provided written information (personal communication).

recorded from SNP or nearby localities despite over 1000 bones collected there. Also, the deposits of SNP have yielded many genera, including the mammaliamorphs *Megazostrodon*, *Brachyzostrodon*, *Rosierodon*, *Paikasigudodon*, *Woutersia*, *Delsatia*, and *Theroteinus* (Debuysschere *et al.* 2015), that have not been recorded in the Holwell or the St. Brides fissures. Furthermore, there are no records of any tritylodont from SNP, which is a significant additional difference from Pant 4 and 5 as well as from Holwell.

Many taxa characteristic of the sauropsid fauna, such as *Planocephalosaurus*, tricuspisaurs, procolophonids, and kuehneosaurs, are absent from global Early Jurassic deposits. However, comparisons with the Lower Lufeng Formation, China and the McCoy Brook and Kayenta formations in North America suggest some key similarities to the St. Brides and Windsor Hill fissures. The McCoy Brook Formation, of the latest Rhaetian and Early Jurassic, shares faunal similarities with St. Brides palaeo-island, notably *Oligokyphus* found in the latest Rhaetian Scots Bay Member (Fedak *et al.* 2015). *Oligokyphus* of probable Pliensbachian age has also been recorded in the Kayenta Formation (Sues 1985; Fedak *et al.* 2015), which is in accord with the same dating of *O. major* (including *O. minor*) by Kühne (1956) at Windsor Hill. As noted by Fraser (1994), *Clevosaurus convallis* from Pant 4 bears greater similarity to *C. bairdii* from the McCoy Brook Formation and the Chinese clevosaurs than to *Clevosaurus hudsoni* from the sauropsid fissure fills.

Comparing the fissure faunas further with the Chinese Dull Purplish and Dark Red Beds of the Lower Lufeng Formation shows some significant accord. Although Luo and Sun (1994) suggested that the Dark Red Beds are no older than Sinemurian and the Lower Dull Purplish Beds are no older than Hettangian,

Fedak *et al.* (2015) note that the Lower Lufeng Formation has not been precisely dated. What is agreed by both sets of authors is that *Oligokyphus lufengensis* from the Dark Red Beds lacks the accessory cuspules on the anterior margin of the postcanine molariform tooth crown found in *O. major*, *Oligokyphus* sp. from the Kayenta Formation and *Oligokyphus* sp. from the McCoy Formation. *Morganucodon*, ubiquitous in the St. Brides fissures, is found in the Dark Red Beds (possibly Sinemurian) of the Lower Lufeng Formation. It is interesting that the Lower Purplish Beds have a lower diversity than the Upper Red Beds, which matches our suggestions for the St. Brides biotas that the putatively younger Pant 4 and 5 assemblage is much more diverse than the other fissures.

The possible succession in the vertebrate assemblages of the fissures is in accord with the notion that they span the ETE. In this context, the sauropsid fissures contain a diverse, mainly reptile-dominated biota that was extant before the end-Triassic volcanic event, and this was followed by an Early Jurassic recovery with initially a depauparate "*Morganucodon*" fauna succeeded by greater tetrapod diversity exemplified by the *Morganucodon*-sphenodont fauna of Pant 4 and 5. The missing link in this suggestion is a probable late Rhaetian locality (equivalent to the Lilstock Formation), although some of the sauropsid-type fissures may actually be of this age, *e.g.*, Twyn-yr-Odyn, where the fish *Legnonotus* found in the Cotham Member at Aust (Egerton 1854), is abundant. It has also been suggested that the Holwell fissure, where Charles Moore collected a fossil later named *Pseudotriconodon,* may be late Rhaetian (*e.g.*, Cuny 2004).

REINTERPRETING THE PALAEOENVIRONMENT

The sauropsid tetrapods of the Rhaetian-age Bristol fissures were interpreted as members of a unique, higher-ground or upland fauna by Robinson (1957) and Halstead and Nicoll (1971), whereas Marshall and Whiteside (1980), Whiteside (1983) and Whiteside and Marshall (2008) argued that they lived on small, low-lying limestone islands. They noted that the fauna is best perceived as an insular biota, which could explain the small body size of the dinosaurs and some other taxa. Whiteside and Marshall (2008) also suggested that some caverns near the current limestone surface at Tytherington were the result of carbonate dissolution in a mixed freshwater/saline water regime at the edge of a freshwater lens maintained by a high nearby Rhaetian sea level. In a modern analogue, Mylroie (2013) has shown that caverns in Bahamian island limestone form at the top of the freshwater lens as well as near the halocline and at flank margins, with the lens maintained by the sea. It is likely that the cavern at Cromhall shown in Fig. 5A was also formed in a similar manner, indicating a high sea level at that locality, and similarly near the Durdham Down deposits (Foffa *et al.* 2014).

Further evidence of nearby saline waters for the sauropsid localities is suggested by the dolomitisation of the limestone in the Carboniferous host rock, and breccias that infill the fissures; Whiteside and Marshall (2008) reported authigenic dolomite crystals in mixed terrestrial and marine Rhaetian palynomorph-bearing rock. Dolomitic breccias are common at Tytherington and Durdham Down, and dolomitised rocks have been found at Cromhall (Walkden and Fraser 1993). The presence of coeval fish teeth in fissures at Cromhall, Durdham Down and Tytherington is in accord with a high sea level maintaining a freshwater lens a few metres below the surface of a limestone island. Therefore it is likely that fresh water was available for a relatively rich plant life that supported the reptiles and arthropods, which also formed their prey. The crevices and cracks (karren) on the surface and openings to the dolines would, perhaps, have been generally moist areas for the plants. In a more recent analogue, the Sawmill Sink blue hole on the Bahamian Abaco Island yields the wax myrtle as by far the most common pollen in Quaternary samples (Steadman *et al.* 2007), a plant that grows around the edge of sinkholes. This is similar to Tytherington, where the Rhaetian palynological sample from Fissure 16 is dominated by *Ovalipollis pseudoalatus* together with the fresh water alga *Botryococcus*, indicating a monotypic stand of vegetation surrounding a freshwater pool. Similarly, fissure 13 is another freshwater pool with *Botryococcus* and a minor marine component, but dominated by different vegetation, comprising mainly *Ricciisporites*. The *Ricciisporites* parent plant has now been identified (Mander *et al.* 2012) from ultrastructure as a gymnosperm with some similarity to the bennettitaleans, rather than a liverwort, *e.g.* Balme (1995).

This varied plant life provided a damp leaf litter that could sustain the millipedes, and a seasonal rainfall is indicated by the presence of the conchostracan ("clam shrimp") *Euestheria* at Tytherington, Cromhall and

Pant-y-ffynnon. Modern conchostracans live in the detritus of (mostly) temporary freshwater pools and have a life span of about 2–3 weeks (*e.g.*, Weeks *et al.* 1997). By analogy, the presence of *Euestheria* colonies comprising 50+ individuals of variable sizes and no preferred orientation in small rock hand specimens from the Cromhall collection of BRSUG indicates that deposition and fossilisation of their carapaces occurred *in situ* in the red-coloured sediment of their habitat. Had there been vadose flow, this would have selectively transported, separated and broken the delicate carapaces of these small crustaceans. Therefore, at the time that the animals died, the freshwater in the fissures would have ponded and dried, with a slow drainage denoting a raised water table as a consequence of a nearby high sea level.

The mammaliamorph-bearing fissures of St. Brides suggest a slightly different scenario. In common with the sauropsid fissures, the St. Brides fissure faunas represent a limestone island community, but the palaeogeography and modern topography indicate that the islands would have been higher, certainly 100 m or more, at the end of the Rhaetian. Although the vegetation of St. Brides was dominated by one plant, the conifer *Hirmeriella,* there is evidence for a variety of flora such as club mosses, bennettitaleans and possibly cycads and ferns (Evans and Kermack 1994; Gill *et al.* 2006). The palynological assemblages contain a vast proportion, over 95%, of *Classopollis* (the pollen of *Hirmeriella*) and this suggests a limited food resource for arthropods and their predators, the tetrapods, which may explain the depauparate *Morganucodon* fauna, comprising only insectivorous mammals and no herbivores (as noted by Gill *et al.* 2006). The more diverse *Morganucodon*-sphenodont fauna, consisting of the herbivorous haramiyids and *Oligokyphus* in addition to a wide range of insectivorous and (presumably) carnivorous mammaliaforms and reptiles, may have benefited from greater access to freshwater as the sea level rose, bringing the permanent water of the freshwater lens closer to the limestone surface, and/or it may be a result of recovery after the ETE. The general humidity is supported by reports of large quantities of haematitic pellets or ooids in some fissure deposits at Pontalun and particularly Pant, but not at Ewenny (Kermack *et al.* 1973; Evans and Kermack 1994; Gill *et al.* 2006). Based on the work of McFarlane (1976), these ferruginous ooids or pisoids were interpreted by Gill *et al.* (2006) as forming in a pedogenic laterite where fresh rock was subjected to alternating extreme wetting and drying cycles. In another example, Thorne *et al.* (2014) recorded microorganism-mediated iron pisoids from a modern fluvio-lacustrine wet/dry environment in Western Australia. This indicates a climate with heavy seasonal rains, as suggested by Evans and Kermack (1994), with waters running quickly into slot fissures and blocking them near or at the water table with surface debris including lateritic soils, vertebrate remains and plant material.

The St. Brides fissures may have been generally located further above the water table than the Rhaetian fissures, based on the modern topography of the area, which is higher than nearly all the sauropsid localities, and the greater frequency of narrow slot voids. There are exceptions; for example, the large caverns at Ewenny (Kermack *et al.* 1973), a cave in Cnap Twt (Harris 1957), and also a cave in Pant 4 fissure and one higher in the quarry at the western end (PGG, personal observation). Such large caverns suggest they were close to, or even below, sea level to maintain the phreatic conditions necessary for their formation. Furthermore, fossil charcoal present in abundance in the clay deposits of the slot fissures displays features of waterlogging (Gill *et al.* 2006), indicating a water table maintained for a sufficiently long time and therefore likely to have been near sea level. The presence of pollen and spores in these slot fissures also suggests deposition at the water table rather than under vadose conditions, which are highly oxygenated and destructive to palynomorphs. Although fishes are not recorded from these fissures, we know that modern-day solution pit caves commonly fill with terrestrial deposits and little marine sediments on "even small" Bahamian islands (J. Mylroie, personal communication). The occurrence of *Naticopsina oppelii* (see Kermack *et al.* 1973) in Pant 2 perhaps indicates the proximity of a marine environment at the time of deposition.

A notable feature of all the fissure deposits is the range of colour of the bones and teeth. The colour ranges from white, through yellows, browns, blues, greys, and black. The white bones may indicate deposition in an oxygenated environment and the black bones in anaerobic conditions, similar to the anoxic environment deduced for some Rhaetian Westbury Formation Beds reported by Macquaker (1999). Black terrestrial tetrapod bones have been found at Woodleaze (Fig. 2G), Tytherington, and Windsor Hill, whereas white bones predominate at Cromhall, Emborough, Batscombe, some deposits at Tytherington (Fig. 2H), such as the *Thecodontosaurus* breccia where bones have low pyrite (Wings 2004), and some lithologies such as the red matrix (Kermack *et al.* 1973) in St. Brides fissures. The St. Brides fissures also contain yellow, orange-stained, grey, and brown bones; bones at Ruthin are usually yellow or yellowish-white and Pant-y-ffynnon has a range of white and grey bones. Bones at Holwell range from yellow to dark brown, although some fish teeth are almost black. A variety of colours suggests different environments at deposition; white bones in an oxygenated

or vadose setting, through to black bones, perhaps settling at the halocline or just, below where sulphur-reducing bacteria moderated the formation of metal sulphides. Plant material in the form of charcoal is much more abundant in the grey clay matrix (Ewenny, Pontalun 3 and Pant 5) with brown bones.

The accumulations of bones in the fissures show some evidence for catastrophic killing, but it is most unlikely that they represent predator accumulations. In both the sauropsid fissures at Tytherington and in the St. Brides deposits, fossil charcoal or fusain has been discovered. This led Harris (1958) and Whiteside and Marshall (2008) to suggest that wildfire was a significant factor in the death of the tetrapods, through smoke inhalation or direct baking, and the subsequent decay of the animals' bodies would have provided an abundant supply of bones to be deposited in the fissures. The partial *Clevosaurus hudsoni* skeleton from Cromhall (NHMUK PV R36832; Fig. 5B) demonstrates that some articulated skeletons entered the sauropsid fissures where they started to dissociate; it is likely that this is a key source of disassociated bones in the fissure deposits, but other bones may have been individually washed into the fissures from the surface. The predator bone accumulation hypothesis (Kühne 1956; Kermack *et al.* 1973; Evans and Kermack 1994) as the key origin and constitution of the assemblages is rejected here on the basis of three lines of evidence. First, although some bones show tooth marks (*e.g.*, Evans and Kermack 1994), none of the bones shows any evidence of acid digestion in the gut of a predator (PGG, observation of material not prepared in acetic acid). Second, in most of the assemblages there is scant evidence of predators. In the *Morganucodon* fauna, any of the three genera are unlikely to have been a major predator on the others, as *Morganucodon* and *Kuehneotherium* are tiny and interpreted as insectivorous (Gill *et al.* 2014) whilst *Gephyrosaurus* was also probably insectivorous (Evans 1980). Furthermore, searching for other predatory animals amongst the thousands of specimens from the *Morganucodon* fauna yields only one possible pterosaur fossil (Fraser 1989) and some teeth from small archosaurs (Fraser 1989; Evans and Kermack 1994). Postulating that the *Morganucodon* faunal composition was a result of predator accumulations would require an extreme (and probably unfeasible) selection of prey, hunting the probably nocturnal or crepuscular *Morganucodon* and *Kuehneotherium* but also the possibly diurnal *Gephyrosaurus*. Yet this hypothesised predator was not catching sphenodontians or tritylodonts as none were found in the *Morganucodon* fauna although these animals are abundant in the *Morganucodon*-sphenodont fauna.

Thirdly, although there has been reported evidence of predatory bite marks on bones on the *Oligokyphus* accumulation of Windsor Hill, and despite (Kühne 1956) suggesting otherwise, the possibility of opportunistic cannibalism in times of starvation cannot be eliminated as the cause of bite marks; in that assemblage the putative predator again left no trace of its own teeth or bones.

Potential predators such as small archosaurs are found in greater abundance in the *Morganucodon*-sphenodont fauna accumulations of Pant 4 and 5, residing in the same assemblages as the rhynchocephalians and larger morganucodontans. Considerably bigger carnivorous archosaurs of *c.* 2.5 m long are indicated by isolated teeth or other remains in assemblages of the sauropsid fissures (*e.g.*, Van den Berg 2012; Foffa 2014) but not in the St. Brides deposits where the longest animal was perhaps a maximum of 1.5 m. Overall, however, as emphasised by Whiteside and Marshall (2008), the "washed-in" hypothesis better explains the great range of small and larger exquisitely preserved bones, as well as the occurrence of articulated or nearly articulated skeletons such as shown in Fig. 5B.

The fissure assemblages are similar to void-fills on modern day and Quaternary islands where species diversity is low, but individual species have numerous individuals (Whiteside 1983; Whiteside and Marshall 2008). The terrestrial animals on the small islands are frequently small, and can be found preserved as individual elements in fissure fills on limestone islands such as Aldabra (Arnold 1976) and New Providence in the Bahamas (Etheridge 1966). Furthermore, the differing species, biodiversity and variable proportions of reptile taxa that can be found in closely positioned fissures in localities such as Cromhall and Tytherington is paralleled in the Quaternary deposits such as those from Barbuda reported by Etheridge (1964).

CONCLUSIONS

The fissure deposits of the Bristol region and in South Wales provide a unique window on the Late Triassic and Early Jurassic faunal changes across the ETE. In general terms, our analysis supports the view of Robinson (1957), that the earlier faunas were dominated by reptiles and the later ones by mamma-

liamorphs. However, *contra* Robinson (1957), we have found no evidence of tetrapods in fissures that pre-date the Rhaetian transgression. The oldest faunas, from Durdham Down, Tytherington, Cromhall, Pant-y-ffynnon, and possibly Ruthin, are characterised by clevosaurs with large flanged teeth, *Diphydontosaurus* and, in some localities, *Planocephalosaurus* and *Thecodontosaurus* or *Thecodontosaurus*-like species. Phytosaurs are present in the earliest of these biotas. Sphenosuchian crocodylomorphs, procolophonids and coelophysoids are also found in most of these deposits. Kuehneosaurs are particularly known from Emborough and Batscombe, as well as more rarely from Cromhall and Pant-y-ffynnon. Despite the recovery of thousands of tetrapod bones from all sauropsid fissures, cynodonts and particularly mammaliaforms have not been recorded in sauropsid localities except for the two *Kuehneotherium* teeth at Emborough found by Fraser *et al.* (1985). Either the cynodonts were absent or exceptionally rare owing to the small land areas of fluctuating sizes as the Rhaetian sea transgressed and regressed, or to the relative isolation of the individual palaeo-islands.

The fauna at Holwell is an amalgam of most probably Rhaetian faunas, but as the fissure vertebrates derive from neptunian dykes, and the specific sites where Moore collected his specimens are uncertain, it is not possible to be certain about the precise dating. The presence in the fauna of *Thomasia*, *Eozostrodon*, *Pseudotriconodon* (Cuny 2004), and *Diphydontosaurus* is in accord with the Rhaetian biota of SNP in France. The finding of a probable haramiyid, *Hypsiprymnopsis rhaeticus* Boyd-Dawkins, 1864 (possibly = *Thomasia*) in the Rhaetian grey marls (Williton Member) at Watchet and the report of *Tricuspes*, a possible cynodont from the Westbury Formation of Vallis Vale, near Frome Somerset (Huene 1933; Storrs 1994), is also in accord with a Rhaetian date for the Holwell fauna. The additional presence of *Clevosaurus* and *Thecodontosaurus* agrees with the Rhaetian dating of Tytherington and Durdham Down. However, the presence of tritylodont *incertae sedis*, the affinities of which are not established (Savage 1971), makes further comparisons moot.

We have presented evidence that the St. Brides faunas range in age from Hettangian to possibly early Sinemurian, and that there is an increasing faunal diversity as the entrance to the fissures and the fossiliferous horizons became topographically higher. What remains unclear is whether any of the "sauropsid" or "mammaliamorph-type" fissure localities could be of late Rhaetian age, equivalent to the Lilstock Formation. There is no reliable evidence that any fissure is of that age, although the faunal content of Holwell does include some marine fishes more typical of the late Rhaetian; Cuny (2004) tentatively suggested a later Rhaetian age for Holwell. Holwell also has an intermediate fauna between sauropsid and mammaliamorph type fissures (Table 2). There are examples of animals that are known to be representative of the late Rhaetian such as *Euestheria brodieana* in Tytherington fissure 12 and the fish *Legnonotus* in Twyn-yr-Odyn, also recorded from the Cotham marble (Cotham Member, Lilstock Formation) at Aust Cliff (Egerton 1854). It seems likely that a fissure of confirmed late Rhaetian age may be found in the future.

Overall, the characteristics of all fissure faunas are animals of small to small-medium size, numerous individuals and a range in diversity from low to comparatively diverse depending on locality. Possibly owing to isolation by saline waters, amphibians are unconfirmed and probably absent from all fissures; yet non-marine (possibly brackish water) fishes are present in the older deposits, but fishes in general, appear to be absent in St. Brides infills. Although some of the animals may have derived from neighbouring sandstone areas, in general the tetrapods lived on the karstic landscape of small islands. A diverse reptile biota is found in the older fissures, with sphenodontians abundant, comprising at least seven species in five genera. Procolophonids, aetosaurs, phytosaurs, tricuspisaurs, kuehneosaurs and *Thecodontosaurus* are not recorded from the younger fissure fills of St. Brides. Mammaliamorphs became much more prominent members of the fauna, particularly after the ETE, but, although reptile diversity is much lower, two species of rhynchocephalians from the St. Brides deposits are the most dominant numerically.

It is a curiosity that *Gephyrosaurus*, generally regarded as a basal rhynchocephalian (*e.g.*, Jones *et al.* 2013), is present and common in many of the St. Brides fissures, but does not occur in the older fissures or (apparently) anywhere else in global faunas of the Late Triassic–Early Jurassic. Sphenodontian rhynchocephalians, usually considered to be more derived, dominate the earlier sauropsid fissures. It is likely that the abundance and diversity of acrodont sphenodontians in the sauropsid faunas was favoured by the absence of their probable competitors and possible predators, the cynodonts. Possibly also, the presence of a significant proportion of mammaliamorphs with shearing teeth in the St. Brides fissures favoured a niche suitable for a lizard-like species with a puncturing dentition, or there was a daytime/night-time niche separation, as suggested above.

NOTE: LOST SPECIMENS

It is worth reporting that many specimens from the Bristol fissures have been lost, or at least mislaid. From the vertebrate collections at Holwell made by Charles Moore over a number of years commencing in 1858, three of the mammaliamorph teeth are not accounted for (M. Williams, personal communication). From the sauropsid fissures, the millipede from Cromhall figured by Fraser (1988b) is lost (Fraser, personal communication) and some key fossils of a procolophonid, possibly *Hypsognathus,* from that locality are also missing. The many fish fossils from Twyn-yr-Odyn described by Howgate (1976) cannot currently be found.

From the Duchy deposit, a symmetrodont tooth of *Kuehneon* and dental fragments of a possible amphibian and a dipnoan, all found by Kühne, have been lost (Evans and Kermack 1994). Although not from a fissure deposit, the probable haramiyid *Hypsiprymnopsis rhaeticus* found at Watchet by Boyd-Dawkins (1864) has also been lost. These specimens could all have added greatly to our knowledge of the fissure faunas and their loss is to be greatly regretted.

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ADDENDUM

Since the acceptance of this paper and the arrival of the proofs we have been able to study in greater detail the fossils of small terrestrial reptiles from Moore's "*Microlestes*" quarry at Holwell held at the BATGM. We have recognised the presence of *Gephyrosaurus*, a procolophonid and *Variodens* as well as a number of previously undescribed rhynchocephalians. This has strengthened the view suggested in this paper that Holwell is a link between the sauropsid-type and mammaliamorph-type fissures.

Also a new species of sphenodontian, *Sphenotitan leyisi*, has been described from the Late Triassic of northwestern Argentina by Martinez *et al.* (2013). We have been able to compare the description with some new specimens of *Pelecymala* from Tytherington fissure 14 and, although *Sphenotitan* is much larger, there appear to be strong affinities between the genera. Martinez *et al.* (2013) regard the Quebrada del Barro Formation which has yielded *Sphenotitan* as Norian although Apaldetti *et al.* (2011) considered that it was younger, possibly Early Jurassic. Therefore essentially little modification is required to our Fig. 10 except to indicate that present or similar taxa could be added to the *Sigmala* and/or *Pelycymala* row under the category "Norian, Worldwide".

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DOES THE JURASSIC *AGILODOCODON* (MAMMALIAFORMES, DOCODONTA) HAVE ANY EXUDATIVOROUS DENTAL FEATURES?

JOHN R. WIBLE and ANNE M. BURROWS

Obligate exudativory, including active wounding of bark to acquire gum and/or sap, is rare among extant mammals and does not show a consistent dental signature. A recently described Middle Jurassic docodont *Agilodocodon* was reconstructed as an exudativore based on proposed similarities of its lower anterior dentition to some extant New World monkeys, specifically marmosets, spider monkeys, and howler monkeys. Oddly enough, of these, only marmosets are exudate-feeders. In our reinvestigation, we did not find any significant resemblance in the lower (and upper) anterior dentition between the Middle Jurassic fossil and these extant New World monkeys. The marmosets, the only obligate platyrrhine exudativores, have lower and upper incisors that are distinguished from *Agilodocodon* and other New World monkeys by having enamel restricted to the labial surface. Differential wear between the enamel and softer dentine maintains a chisel-like tooth that marmosets use in gouging bark. Additional comparisons of the anterior dentition of *Agilodocodon* and other extant mammals were conducted. The lower and upper anterior teeth of *Agilodocodon* were found to be most similar to some elephant shrews and South American marsupials, which have a primarily insectivorous diet. *Agilodocodon* does not show any dental adaptations found in extant mammals for exudativory.

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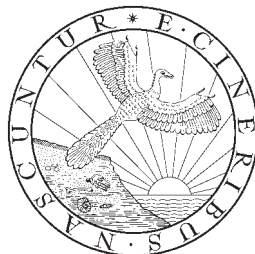
INTRODUCTION

New discoveries in the Mesozoic record of mammals and their near relatives (Mammaliaformes) reveal ecomorphological specializations that unexpectedly include many niches occupied by extant mammals (Luo 2007). The extinct mammaliaform clade Docodonta is a fitting example. It comprises about 14 genera from the Middle Jurassic to Early Cretaceous of Laurasia (Luo and Martin 2007; Luo *et al.* 2015; Meng *et al.* 2015) and one putative taxon from the Middle Jurassic of India (Prasad and Manhas 2007; Meng *et al.* 2015). Although the taxonomic diversity of Docodonta is low, its ecomorphological diversity is high and includes the beaver-like *Castorocauda* (Ji *et al.* 2006), the desman mole-like *Haldanodon* (Martin 2005, 2006), the golden mole-like *Docofossor* (Luo *et al.* 2015), and the arboreal or scansorial *Agilodocodon* (Meng *et al.* 2015). The last is the subject of this contribution.

In announcing *Agilodocodon scansorius* from the Middle Jurassic of China, Meng *et al.* (2015, p. 764) suggested that it had "dental characters indicative of an omnivorous diet that included plant sap". Specifically, it was said to have lower incisors similar to those of some extant New World monkeys, which use these teeth "to gnaw into the bark of trees to feed on exudates, such as gum and sap" (Meng *et al.* 2015, p. 765). They argued that the similarity of incisor morphology supported a similar dietary component for *Agilodocodon*, which makes this the oldest evidence for exudativory in mammaliaforms.

Among extant mammals, gum and sap feeders are either facultative (seasonal) or obligate (full-time), with the latter usually inflicting a wound through gouging to initiate exudate flow. It is not fully known how widespread the facultative type is, as appropriate field data are not available for many species; the occurrence of the obligate type is rare but includes members of Primates and Diprotodontia (Nash 1986; Nash and Burrows 2010). The vast majority of extant exudativores, both facultative and obligate, are found within the Order Primates, with at least 69 species having some level of exudativory (Smith 2010) out of a total of 376 species (Wilson and Reeder 2005). Among the New World monkeys, marmosets are the only obligate exudate-feeders whereas the closely related tamarins are facultative, feeding from exudate flows or semi-dried drops that are already present (Smith 2010). However, only the marmosets show any dental specializations for exudativory. Rosenberger (1978) described a loss of lingual enamel on the lower incisors of the marmosets *Callithrix jacchus, Cebuella pygmaea,* and *Mico argentatus* (*Callithrix argentata* therein), creating in effect a chisel-like, honed edge to these teeth used in gouging tree bark to open a wound. Additionally, marmosets are characterized as showing the "short-tusked" condition with the lower canine on the same occlusal plane as the lower incisors (Swindler 2002).

Here, we assess the claim by Meng *et al.* (2015) that the lower incisors of *Agilodocodon* resemble those of marmosets, spider monkeys (*Ateles*), and howler monkeys (*Alouatta*), which is an odd claim in that only the marmosets are exudate-feeders. Additionally, we assess the notion put forth by Meng *et al.* (2015) that this resemblance is consistent with those teeth being used by *Agilodocodon* to obtain exudates. We address whether there are other extant mammals not considered by Meng *et al.* (2015) with an anterior lower dentition similar to *Agilodocodon*. Finally, we review whether there are other craniodental features that might distinguish exudate-feeders.

Institutional abbreviations. — AMNH, Department of Mammalogy, American Museum of Natural History, New York, New York, USA; CM, Section of Mammals, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.

MATERIAL

Agilodocodon was studied only from the literature (Meng *et al.* 2015 and associated supplementary files). We studied the following New World monkey specimens in the Section of Mammals, Carnegie Museum of Natural History, Pittsburgh, PA. For dental terminology, we follow Hershkovitz (1977).
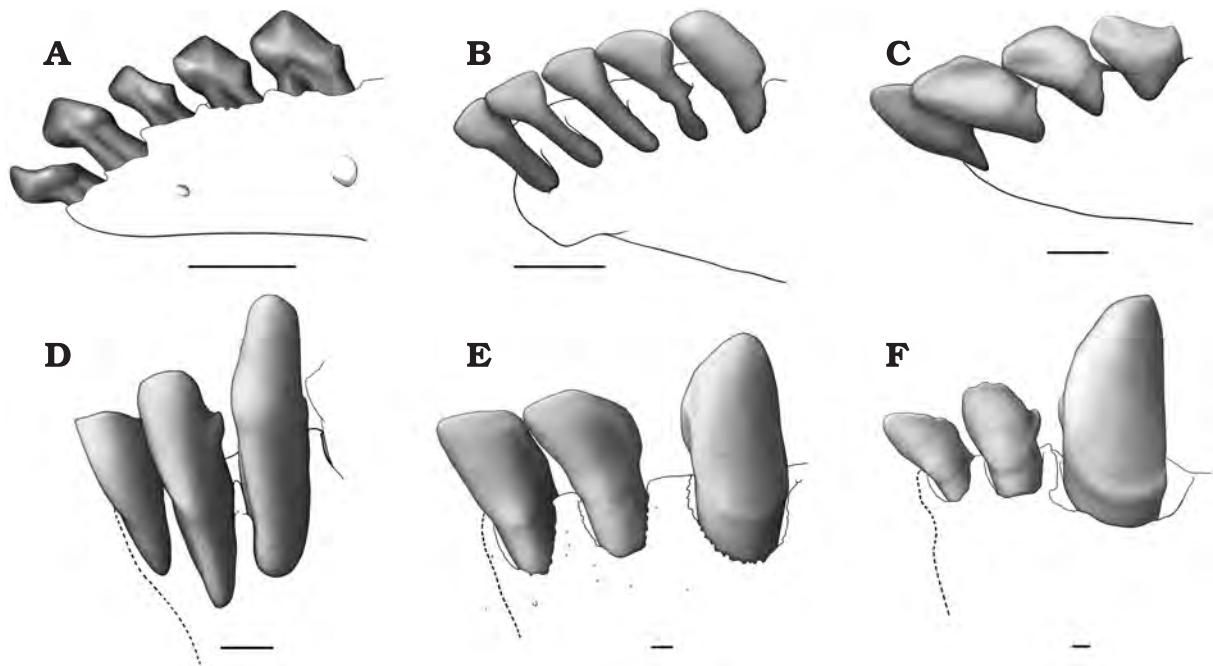
Fig. 1. Left lower anterior dentitions in labial view. **A**. *Agilodocodon* (reproduced with permission from Meng *et al.* 2015, fig. 2H), four incisors and canine. **B**. *Dromiciops australis* AMNH 92147 (male), four incisors and canine. **C**. *Elephantulus edwardii* CM 40801 (male), three incisors and canine. **D**. *Mico argentatus* CM 1964 (male), two incisors and canine. **E**. *Ateles paniscus* CM 68450 (female), two incisors and canine. **F**. *Alouatta seniculus* CM 2719 (female), two incisors and canine. Scale bars 1 mm.

Callithrix jacchus (common marmoset): female CM 12174; male CM 1720.
Mico argentatus (silvery marmoset): females CM 1964, 5011, 5013, 5016, 12187; males CM 1963, 1965, 1966, 4985, 5012.
Ateles belzebuth (white-fronted spider monkey): female CM 1559.
Ateles fusciceps (black-headed spider monkey): male CM 17455.
Ateles geoffroyi (Geoffroy's spider monkey): female CM 1576; male 1252.
Ateles paniscus (red-faced spider monkey): females CM 2772–2775, 68450, 76826; male CM 68451.
Alouatta caraya (black howler): female CM 61431; male CM 61430.
Alouatta guariba (brown howler): male CM 1719.
Alouatta seniculus (Venezuelan red howler): females CM 2712, 2719; males CM 2722, 68447, 68448.

DESCRIPTIONS

Although Meng *et al.* (2015) reported that it is the lower anterior dentition (incisors and canines) of *Agilodocodon* that shows exudativorous adaptations, our descriptions are not limited to these teeth but include the upper anterior dentition as well.

Anterior dentition of *Agilodocodon*. — *Agilodocodon* has a dental formula in the upper and lower jaws of four incisors, one canine, six premolars, and four molars. Meng *et al.* (2015, supplementary materials, pp. 16–17) (Figs 1A, 2A, 3A) described the incisors as spatulate and spade-shaped with crowns that are bucco-lingually compressed and mesiodistally broad. They also described the crowns as being curved with a convex buccal surface and a concave lingual surface ornamented with a low median ridge and a lingual cingulid at the crown base. Most of the eight left and right lower incisors have incipiently divided roots or divided roots. The canine is also spade-shaped and has an incipiently divided root. Overall, the canine is similar to the incisors and is small.

Based on their illustrations (Meng *et al.* 2015, fig. 2A, G, H), we also note that the roots of the upper and lower anterior teeth are not uniform in girth but taper to their narrowest at the crown-root junction (Figs 1A, 2A, 3A). The four lower incisors and the lower canine show decreasing procumbency from anterior to pos-
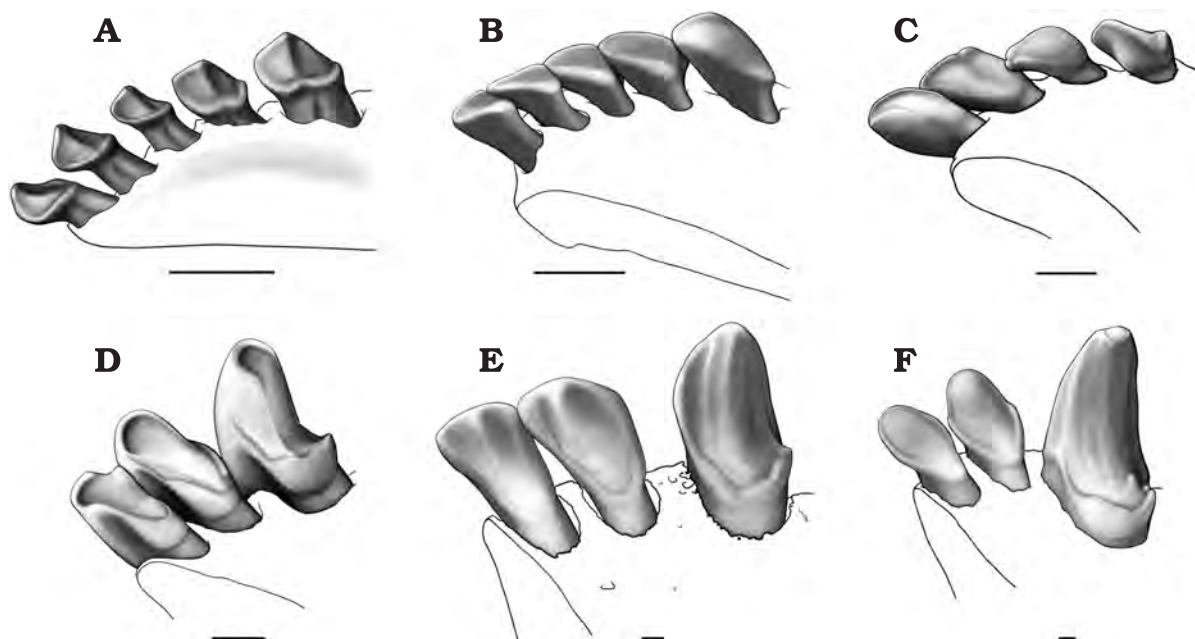
Fig. 2. Left lower anterior dentitions in lingual view. **A**. *Agilodocodon* (reproduced with permission from Meng *et al.* 2015, fig. 2G), four incisors and canine. **B**. *Dromiciops gliroides* AMNH 92147 (male), four incisors and canine. **C**. *Elephantulus edwardii* CM 40801 (male), three incisors and canine. **D**. *Mico argentatus* CM 1964 (male), two incisors and canine. **E**. *Ateles paniscus* CM 68450 (female), two incisors and canine. **F**. *Alouatta seniculus* CM 2719 (female), two incisors and canine. Scale bars 1 mm.

terior (Figs 1A, 2A). In contrast, the upper canine is vertical and the upper incisors have their tips directed posteriorly (Fig. 3A). The upper and lower anterior teeth are separated by small interdental spaces and none of the crowns come into contact (Figs 1A, 2A, 3A). The crowns of the lower anterior teeth are much broader than they are tall (Figs 1A, 2A). The first three lower incisors are triangular in shape and come to a blunt point at their apex. The upper incisors and canine have crowns as tall as wide and come to a blunt point except for the first, which is rounded (Fig. 3A).

Given that the mandible of *Agilodocodon* accommodates 15 teeth, it is long and low (Fig. 4A). It is of relatively uniform height under the postcanine teeth but shallowest under the anterior teeth, extremely so under the first incisor. What appears to be the surface of the symphysis is indicated by a shelf in Meng *et al.* (2015, fig. S3); it ends under the second premolar. In light of the long, low jaw, the symphysis must be narrow and horizontal. The preserved mandible is straight, which reconstructs as a V-shaped lower jaw (Fig. 4A).

Anterior dentition of marmosets. — We examined males and females of species from two of the three genera of marmosets (Garbino 2015): the common marmoset *Callithrix jacchus* and the silvery marmoset *Mico argentatus*. We found the anterior dentition (incisors and canine) to be relatively uniform across these two forms. The dental formula in the upper and lower jaws has two incisors, a canine, three premolars, and two molars.

The mandible is U-shaped and the two lower incisors are set anteroposteriorly in the bottom of the U (Fig. 4D). The second lower incisor is offset slightly posterior to the first and its root is set slightly obliquely compared to the sagittal placement of the first. The incisors are similar in their morphology, but the second is taller and anteroposteriorly broader than the first (Figs 1D, 2D). The lower incisors are tall, mediolaterally compressed with the anteroposterior dimension roughly twice the mediolateral, and only slightly procumbent with the first more so than the second. In labial view (Fig. 1D), the surface of the crown is strongly convex, much taller than wide, and only slightly wider than the root. Its apex is relatively flat. In lingual view (Fig. 2D), the apex of the tooth at the labial margin has a thick band of enamel with a very broad wear facet behind it in dentine that slopes posteroventrally and is relatively flat. This facet is flanked by mesial and distal ridges and ends posteriorly at a lingual cingulid. The medial and lateral faces of each incisor has a slight prominence (mesio- and distostylid), the latter being stronger; this is nearer the apex in the first incisor and halfway down the crown of the second. The incisors are tightly packed with little or no space between their crowns.
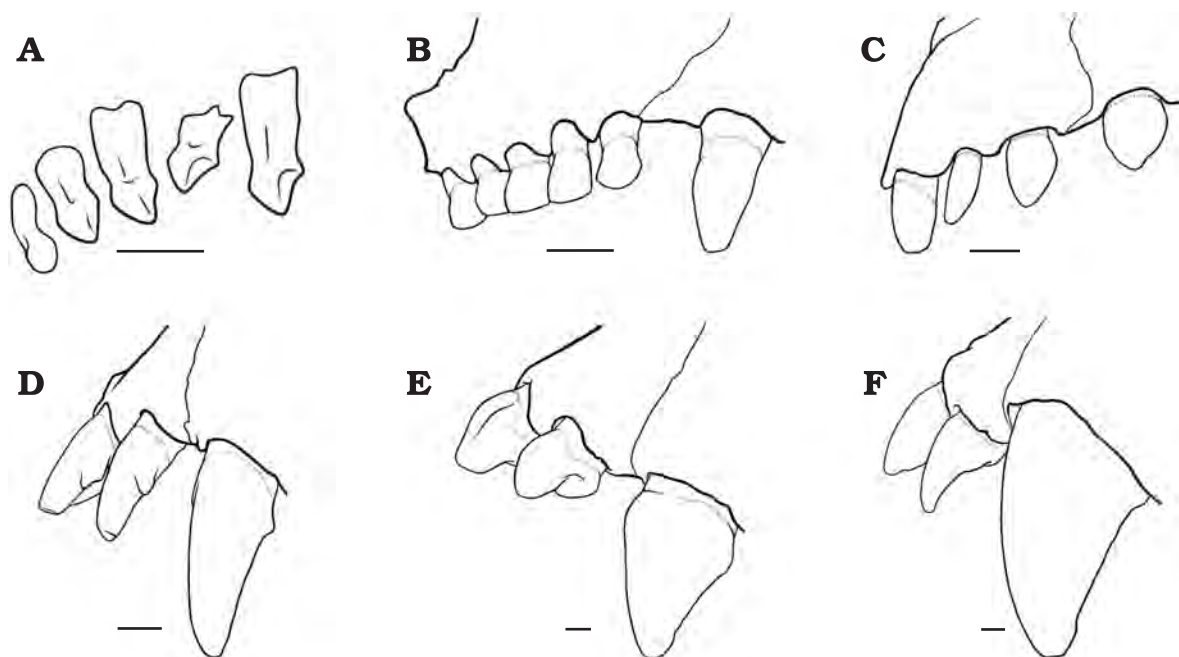
Fig. 3. Left upper anterior dentitions in lateral view. **A**. *Agilodocodon* (reproduced with permission from Meng *et al.* 2015, fig. 2A), four incisors and canine. **B**. *Dromiciops gliroides* AMNH 92147 (male), five incisors and canine. **C**. *Elephantulus edwardii* CM 40801 (male), three incisors and canine. **D**. *Mico argentatus* CM 1964 (male), two incisors and canine. **E**. *Ateles paniscus* CM 68450 (female), two incisors and canine. **F**. *Alouatta seniculus* CM 2719 (female), two incisors and canine. Scale bars 1 mm.

The absence of enamel on the lingual incisor face was reported by Rosenberger (1978) in these same two taxa studied here plus *Cebuella pygmaea*, the pygmy marmoset. "Differential wear of the softer dentine lingually serves to maintain a chisel-like edge to these teeth", which is used in gouging tree bark (Rosenberger 1978, p. 208). Subsequently, Gantt (1980, p. 209) showed that *Cebuella* has "a covering of enamel a few micra thick which is rapidly worn away and is absent in adult animals". Juveniles that could confirm this were not in our marmoset sample.

The lower canine is caniniform, taller and broader than the incisors with a sharper apex (Figs 1D, 2D). It is set posterolateral to the second incisor and separated from that tooth by only a narrow gap (Fig. 4D). As with the incisors, the canine is mediolaterally compressed. The surfaces of the crown are convex except for that facing the second incisor, which is flat. A distinct cingulid is present wrapping from the medial surface across the posterior surface onto the posterior one-third of the lateral surface (Fig. 2D). As with the incisors, the apex of the canine at the labial margin has a thick band of enamel with the surface posterior to it exposing dentine.

The mandible has a thick, fused symphysis that is obliquely oriented and extends to the level of the second premolar (Fig. 4D).

The two upper incisors are procumbent, subequal, and set anteroposteriorly, with the first more procumbent than the second (Fig. 3D). The first incisor is roughly mitten-shaped with the distostyle representing the "thumb"; however, the crown apex is flat and contacts the first incisor of the opposite side producing an expanded chisel-like surface. The second incisor is separated from the first by a narrow gap, has a mesio- and distostyle, and ends in a blunt point. Both the labial and lingual surfaces of the two incisors are convex. Additionally, the two incisors show the same restricted enamel reported by Rosenberger (1978) for the lowers.

The canine is a large caniniform tooth, projecting ventral to the incisors and separated from the second by a gap. The canine has a mesio- and distostyle, but these are not as well developed as on the second incisor.

Anterior dentition of spider monkeys. — We examined representatives of four of the seven species of *Ateles* (Groves 2005): *A. belzebuth*, *A. fusciceps*, *A. geoffroyi*, and *A. paniscus*. The anterior dentition was relatively uniform except for the moderate sexual dimorphism in canine size (Plavcan 2001). The dental formula in the upper and lower jaws has two incisors, a canine, three premolars, and three molars.

The shape of the mandible and position of the lower anterior dentition in the spider monkeys is reminiscent of that in the marmosets (Fig. 4E). The two lower incisors are similar to each other in their morphology, but the second is slightly larger in both mediolateral and anteroposterior dimensions (Figs 1E, 2E). The roots
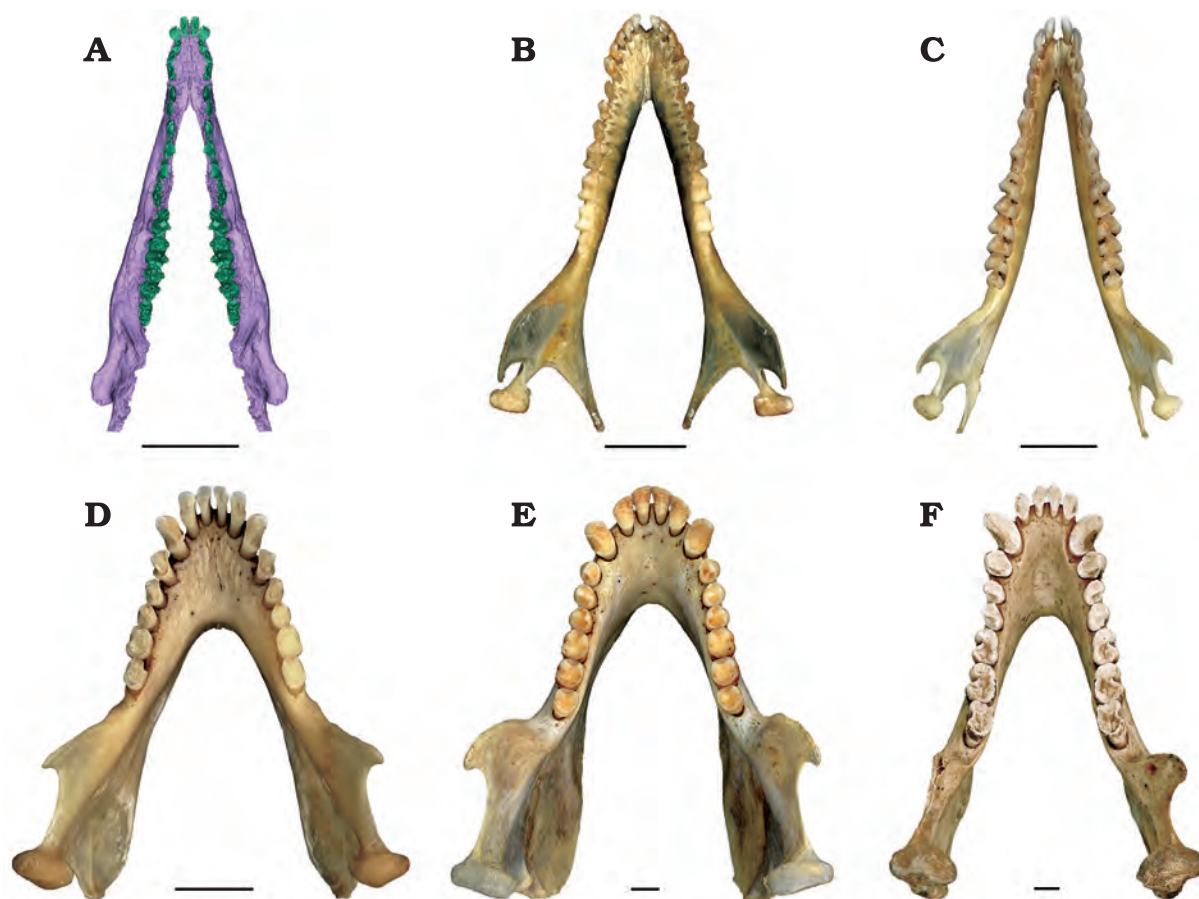
Fig. 4. Mandibles in occlusal view. **A**. *Agilodocodon* (modified from Meng *et al.* 2015, fig. S3B). **B**. *Dromiciops gliroides* CM 40621 (female). **C**. *Elephantulus edwardii* CM 40801 (male). **D**. *Mico argentatus* CM 1964 (male). **E**. *Ateles paniscus* CM 68450 (female). **F**. *Alouatta seniculus* CM 2719 (female). Scale bars 5 mm.

are mediolaterally compressed and of uniform girth. The base of the crown is of comparable girth to the root. The crown is triangular, taller than wide, with the widest part of the triangle at the crown apex. The apices of the two incisors are relatively flat, of similar height, and in contact. The greatest mediolateral and anteroposterior dimensions are subequal for each incisor. The labial surface of the crown is convex and vertical, whereas the lingual surface slopes posteroventrally and is relatively flat. The enamel is uniform.

The lower canine is caniniform, taller than the incisors with a sharper apex. The canine is mediolaterally compressed and separated from the second incisor by a small gap. The labial surface of the crown is convex; the lingual surface is relatively flat with a distinct cingulid.

The mandible has a thick, fused symphysis that is more vertical than that of the marmosets but also extends to the level between the first and second premolar (Fig. 4E).

In the uppers (Fig. 3E), the incisors are set anteroposteriorly with the first larger and more procumbent than the second. The first incisor has a flat apex and contacts the tooth of the opposite side at the midline. The second incisor is separated from the first by a narrow gap and its apex is more rounded. Both incisors are convex labially and have an extensive lingual heel; on the second this is a raised cingulum, but not on the first. Swindler (2002) reported the opposite distribution of the lingual cingulum in his sample. The canine is a stout caniniform tooth that projects well beyond the occlusal plane. It is separated from the second incisor by a wide gap. The enamel is uniform in the upper anterior teeth.

Anterior dentition of howler monkeys. — We examined representatives of three of the ten species of *Alouatta* (see Groves 2005): *A. caraya*, *A. guariba*, and *A. seniculus*. The anterior dentition was relatively uniform except for the strong sexual dimorphism in canine size (Plavcan 2001), lacking in the exudativorous marmosets. The dental formula in the upper and lower jaws has two incisors, a canine, three premolars, and three molars.

The shape of the mandible and position of the lower anterior dentition in the howler monkeys is reminis-

cent of that in the marmosets and spider monkeys (Fig. 4F). The shape of the two lower incisors is similar to each other, but the second is larger and taller than the first (Figs 1F, 2F). The roots are mediolaterally compressed and of uniform girth, with the base of the crown of comparable girth as the root. The crowns are taller than wide and roughly mitten-shaped in both labial and lingual views with the "thumb" eminence positioned laterally. In lingual view, the "thumb" eminence is a distostylid; a weaker mesiostylid is present on the second incisor. The incisors are much longer anteroposteriorly than they are mediolaterally wide. The labial surfaces are convex. The first incisor is slightly procumbent and has a narrow contact across the midline. The second incisor is more vertical and separated from its medial and lateral neighbors by narrow spaces. In lingual view (Fig. 2F), both incisors have a relatively flat surface that slopes posteroventrally from the apex, with the slope lower on the first incisor than the second. The second has a distinct ridge on the lateral margin, posterior to the distostylid. The enamel is uniform.

The lower canine is caniniform, much larger and taller than the incisors with a very sharp apex. The canine is subcircular in outline and has distinct medial and lateral ridges that delimit labial and lingual surfaces. The labial surface is strongly convex, whereas the lingual is mildly convex with a distinct cingulid.

The mandible has a thick, fused symphysis resembling that in the spider monkeys, but it extends to the level between the second and third premolar (Fig. 4F).

In the uppers (Fig. 3F), the anterior teeth are reminiscent of those in the spider monkeys with the following differences: both incisors come to a blunt point and have a lingual cingulum, and the canine is a more substantial caniniform tooth.

COMPARISONS

As noted above, Meng *et al.* (2015) made two claims for *Agilodocodon*: (1) that its lower anterior dentition resembles that of marmosets, spider monkeys, and howler monkeys; and (2) the resemblances are of a sort occurring in exudativores. We address each of these claims separately below and also whether there are other extant mammals with a lower anterior dentition more similar to *Agilodocodon* and whether there are craniodental features of exudativores beyond those of the lower anterior dentition.

Does the lower anterior dentition of *Agilodocodon* resemble that of marmosets, spider monkeys, and howler monkeys? — The New World monkeys studied here have lower incisors built on a similar bauplan (Figs 1D–F, 2D–F) that includes mediolateral compression, crowns taller than wide, and relatively flat posteroventrally sloping lingual faces; differences concern overall shape, relative sizes, interdental spacing, and procumbency, and in the case of the marmosets the presence of enamel restricted to the labial surface and roots that are comparable in girth to the crowns. However, there is little similarity between the New World monkey bauplan and *Agilodocodon*. In *Agilodocodon* (Figs 1A, 2A), the incisors are labio-lingually compressed, the crowns are much wider than tall, and the lingual faces are concave with a median ridge. Additionally, the shape of the incisors in *Agilodococon* changes considerably through the series: cup-shaped at the front and quadrangular at the rear. The first and third show a strongly concave distal margin, whereas the second and fourth are straight. Finally, *Agilodocodon* has incisors with uniformly strong lingual cingulids; in the New World monkeys this is either weak or entirely absent.

The New World monkey lower canines do not show a uniform morphology, but all are caniniform (Figs 1D–F, 2D–F). In contrast, the canine in *Agilodocodon* repeats the morphology of the most proximate incisor and the difference is one of the slightly greater size of the canine (Figs 1A, 2A).

The arrangement of the anterior dentition in the mandible is also quite different between the New World monkeys and *Agilodocodon*. In the former (Fig. 4D–F), the mandible is U-shaped, with the incisors and canine closely packed at the bottom of the U; the shape and position of the incisors in the marmosets and spider monkeys, in particular, creates an effective cutting edge. Additionally, the mandibular symphysis is fused and thick. In *Agilodocodon* (Fig. 4A), the mandible is V-shaped with the incisors and canines separated by interdental spaces, which reduces the cutting edge available for gouging seen in the marmosets. The symphysis of *Agilodocodon* is thin and mobile.

The upper anterior dentition in the New World monkeys is also built on a similar bauplan (Fig. 3D–F), with the incisors procumbent (the mesial more so than the distal) and the canine caniniform and larger than
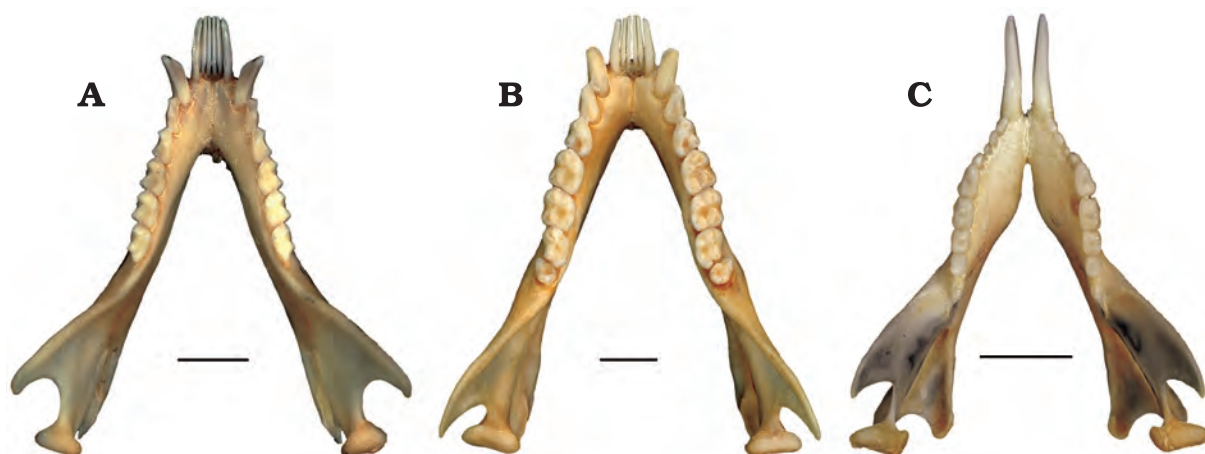
Fig. 5. Mandibles in occlusal view. **A**. *Euoticus elegantulus* CM 41122 (male). **B**. *Nycticebus coucang* CM 59519. **C**. *Petaurus breviceps* CM 116682 (male). Note in B, the small supernumerary tooth at the rear of the tooth row. Scale bars 5 mm.

the incisors. The marmosets differ in that their incisors have restricted enamel, the mesial incisors meet on the midline to form an effective cutting edge, and the size disparity between the incisors and canine is reduced. In contrast, in *Agilodocodon* (Fig. 3A), the incisors and canine are similar in morphology and size, are pointed (except the first incisor), are oriented posteriorly rather than procumbent, and separated by interdental spaces; this arrangement does not produce a cutting edge for gouging.

In light of the profound differences, we conclude that the anterior dentition of *Agilodocodon*, both lower and upper, has no resemblance to the anterior dentition of marmosets, spider monkeys, and howler monkeys.

Are there features of the lower anterior dentition of *Agilodocodon* expected in obligate exudativores? — Among New World monkeys, marmosets are the only obligate exudativores (Smith 2010). It has long been suggested that their ability to wound bark to procure exudates is a function of the restricted enamel on their lower incisors, which results in a chisel-like tooth (Rosenberger 1978; Swindler 2002). Restricted enamel is one dental characteristic that distinguishes marmosets from closely related tamarins (Rosenberger 1978), which are facultative exudativores, as well as other New World monkeys including spider monkeys and howler monkeys, which are not known to feed on exudates but are instead instensively frugivorous and folivorous, respectively (DiFiore *et al.* 2010). If restricted enamel on tightly packed incisors is indeed a mark of exudativory in marmosets, then *Agilodocodon* is not an exudativore of the marmoset type.

Other features of the lower anterior dentition of marmosets have been implicated in their ability to gouge trees. In a comparison between *Callithrix jacchus* and various species of the facultative exudativore *Saguinus*, the former has incisor features accommodating increased stresses linked to dissipating gouging forces, including root surface areas larger relative to symphyseal volume, labiolingually thicker crowns, and enamel with greater decussation (Hogg *et al.* 2011).

Of course, there are other obligate exudativores that have different morphological features of their lower anterior dentition. Beyond marmosets, the best known obligate exudate-feeders among Primates are certain strepsirhines, including the needle-clawed bushbaby *Euoticus elegantulus*, the greater bushbaby *Otolemur crassicaudatus*, and the slow loris *Nycticebus coucang*, all of which include exudates as at least 75% of their diet year round (Smith 2010; Starr and Nekaris 2013). The anterior lower dentition in these forms includes a procumbent toothcomb (Fig. 5A, B) composed of four incisors and two canines (Swindler 2002). *Euoticus elegantulus* and *O. crassicaudatus* do not gouge to acquire exudates. Instead, they scrape, twist, or flick away at semi-dried exudate drops or scoop flowing exudates with their anterior dentition (Charles-Dominique 1977; Nash 1986). In contrast, *N. coucang* is an active gouger (Wiens *et al.* 2006; Starr and Nekaris 2013). Although both *E. elegantulus* and *O. crassicaudatus* may use their toothcombs as scraping devices, they are characterized by robust posterior dentition (upper canines and upper and lower premolars) that may be more intensively used in exudate-feeding than the gracile and delicate teeth of the toothcomb, cracking away at dried exudate drops to re-stimulate flow (Burrows and Nash 2010). The toothcomb of the slow loris *N. coucang* (Fig. 5B) is short, robust, and well designed to resist increased forces that may be generated during gouging activities (Burrows *et al.* 2015).

Beyond Primates, the best known obligate exudativores are several petaurid marsupials, the sugar glider *Petaurus breviceps* (Smith 1982; Howard 1989), the yellow-bellied glider *Petaurus australis* (Goldingay 1987), and Leadbeater's possum *Gymnobelideus leadbeateri* (Smith 1984). As diprotodonts, these forms have a pair of curved, elongated, procumbent lower incisors (Fig. 5C), which are used to incise bark to acquire exudates (Smith 1982, 1984; Goldingay 1987; Howard 1989).

While there seems to be little in the way of a definitive dental signature for exudativory in the lower anterior dentition of extant mammals, *Agilodocodon* possesses none of the morphological characters seen in the dentition of extant exudate-feeders such as tightly packed incisors with reduced lingual enamel, curved, elongated lower incisors, or a short, robust toothcomb.

Does the anterior lower dentition of *Agilodocodon* resemble that of any other extant mammals? — Not many extant mammals have a lower anterior dentition resembling that of *Agilodocodon*, with lower incisors that are labio-lingually compressed and an incisiform canine (Thenius 1989; Hillson 2005). One South American marsupial in particular, the monito del monte *Dromiciops gliroides* (for illustrations of the entire dentition see Reig *et al.* 1987, fig. 6), shows some remarkable similarities to *Agilodocodon*. Its four lower incisors (Figs 1B, 2B, 4B) are generally similarly shaped to those of *Agilodocodon*, show decreasing procumbency posteriorly, are labio-lingually compressed with the crown much broader than the root, and lingual cingulid developed, and the canine is similar to the last incisor but is larger. The upper anterior teeth of *Dromciops* (Fig. 3B) also have some similarity in shape and orientation to those of *Agilodocodon* (Fig. 3A). The principal differences in both the upper and lower anterior teeth are that *Dromiciops* lacks interdental spaces (except for the upper canine) and the teeth form more of a cutting edge. According to Nowak (1991), *Dromiciops* has a natural diet consisting mainly of insects and other invertebrates. Many didelphid marsupials also have lower incisors (see Reig *et al.* 1987; Voss and Jansa 2009) that are reminiscent of *Agilodocodon*, such as the brown four-eyed opossum *Metachirus nudicaudatus*, which include a similar degree of decreasing procumbency, a pointed crown, and a low median ridge on the lingual surface (Fig. 6). The principal difference is the presence in *Metachirus* of a larger caniniform canine. *Metachirus* has a "diet that includes fruits, insects, mollusks, amphibians, reptiles, birds, eggs, and small mammals" (Nowak 1991, p. 19).

A placental group with resemblances to *Agilodocodon* in the anterior dentition is Macroscelidea (Thenius 1989; Hillson 2005), such as the Cape elephant shrew *Elephantulus edwardii*. Its three lower incisors (Figs 1C, 2C, 4C) are similar in shape to those of *Agilodocodon*, show decreasing procumbency posteriorly, are labio-lingually compressed with crowns that are much broader than the root, and its canine repeats the pattern of the last incisor. The principal difference is the lack of interdental spaces in *Elephantulus*. The upper anterior teeth of *E. edwardii* (Fig. 3C) are even more remarkable in their similarity to *Agilodocodon*; the upper incisors and canine are similarly shaped, oriented, and positioned with regard to one another with interdental spaces. The natural diet of *Elephantulus* is insects, especially ants and termites (Nowak 1991).

Are there other craniodental features expected in obligate exudativores occurring in *Agilodocodon*? — Extant marmosets are known to gouge in part by producing a relatively wide jaw gape (Eng *et al.* 2009; Hogg *et al.* 2011). Mandibular features seen in these extant gougers include a short coronoid process and a low mandibular condyle (Vinyard *et al.* 2003; Forsythe and Ford 2011). *Agilodocodon* bears no evidence of either of these traits compared to the closely related docodont *Haldanodon*, which is reconstructed as an insect-feeder by Martin and Nowotny (2000). In fact, the condyle is positioned well above the occlusal surface in *Agilodocodon* (Meng *et al.* 2015, fig. 2E) but is even with it in *Haldanodon* (Martin and Nowotny 2000, figs 14.4, 14.5).

In Primates, molar differences have been noted between obligate exudativores and other

Fig. 6. *Metachirus nudicaudatus* AMNH 266452 (reproduced with permission from Voss and Jansa 2009, fig. 9), lingual view of lower incisors.

forms. In New World monkeys, taxa that consume large amounts of fibrous foods or chitinous insects have molars with well-developed shearing crests, whereas those feeding on tree gum or less fibrous foods have flatter molars with more rounded cusps (Kay *et al.* 2002). A shearing quotient developed to quantify these differences separates exudativorous marmosets from folivores (*e.g.*, *Alouatta*) and insectivores (*e.g.*, *Saimiri*) but not from frugivores (*e.g.*, *Ateles*) (Kay *et al.* 2002). In strepsirhines, exudate-specialist galagos have relatively smaller lower molars than non-specialists, possibly indicating less use of molars in processing sap and gum (Burrows and Nash 2010; Burrows *et al.* 2015). Docodonts as a group are defined in part on the unique morphology of their molars, possessing high shearing crests that would be useful in crushing functions (Averianov 2004; Kielan-Jawaworska *et al.* 2004) with diverse dietary adaptations, from insectivory to omnivory and even carnivory (Luo and Martin 2007). Meng *et al.* (2015, p. 765) described the upper molars in *Agilodocodon* as having crest patterns "analogous to those of galagid and some lorisid primates that have a mixed diet of insects, other small animals, fruits, tree gums, and sap". The images they provided of the *Agilodocodon* upper molars with relatively high crests (Meng *et al.* 2015, fig. 2A, C) are not particularly reminiscent of the more rounded cusps found in the exudate-specialists *Otolemur crassicaudatus*, *Euoticus elegantulus*, and *Nycticebus coucang* (Swindler 2002). Consequently, there is no evidence in the molars to support an obligate exudativorous lifestyle in *Agilodocodon* as seen in marmosets or any obligate exudate-feeding strepsirhine.

CONCLUSIONS

We reviewed the claims by Meng *et al.* (2015) that the anterior lower dentition of the Middle Jurassic docodont *Agilodocodon* resembles that of some extant New World monkeys and that the resemblance is indicative of an exudativorous component in its diet. We found no particular resemblance in the lower anterior dentition of *Agilodocodon* on the one hand and marmosets, spider monkeys, and howler monkeys on the other. Moreover, the marmosets, the only obligate exudativores in the New World monkey sample, are distinguished by having lower (and upper) incisors with enamel restricted labially, lower incisors with root girth comparable to crown girth, and a "short-tusked" canine. Differential wear between the enamel and softer dentine on the tightly packed incisors maintains a chisel-like cutting edge and the broad incisor root dissipates stress produced in tree gouging. *Agilodocodon* does not share these features. Comparisons with other exudate- and nonexudate-feeding mammals reveal that the lower (and upper) anterior dentition of *Agilodocodon* has more similarities with some South American marsupials and placental elephant shrews, both of which have primarily insectivorous diets. Ultimately, we are unsure what *Agilodocodon* ate, but it was not an obligate exudativore of a type found among extant mammals.

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(*Compiled by Żaneta Bartosińska*)

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