Zofia Kielan-Jaworowska (1925–2015)

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Zofia Kielan-Jaworowska, a leading authority on early mammals, died on 13 March, just weeks before her 90th birthday. Kielan-Jaworowska was a founding staff member of the Institute of Paleobiology, Polish Academy of Sciences (PAS), and served important roles in the Institute and its antecedents for some 60 years. Internationally, she is best known for leading the now-legendary Polish-Mongolian Expeditions to the Gobi Desert from 1963–1971. These expeditions collected an enormously significant assemblage of vertebrate fossils dating to the latter part of the Cretaceous. In following years, publication of this assemblage by Kielan-Jaworowska and colleagues revealed hitherto unimagined diversity of major vertebrate groups of the Mesozoic, and made fundamental contributions to our understanding of vertebrate evolution in the waning years of the Age of Dinosaurs.

Like many of her generation, particularly in Eastern Europe, the Second World War had a profound influence on Kielan-Jaworowska. She was born 25 April 1925 in Sokołów Podlaski, central Poland and spent most of her life in and around Warsaw. Following the September 1939 and subsequent occupation by German armies, secondary and higher education were strongly curtailed, with violation punishable by death[1]. According to her own account (Kielan-Jaworowska 2005), most of Kielan-Jaworowska's wartime education took place surreptitiously, with classes being held in private apartments. By the time she finished high school and began secret classes at the University of Warsaw in 1943, Kielan-Jaworowska had set her sights on biology as a field of special interest. In parallel with her secondary and higher education, she also contributed to her country's war effort, joining the Grey Ranks (an underground paramilitary group organized from scouting troops) at age 14. She received training as a medic, caring for and transporting wounded, and participated in this capacity through the Warsaw Uprising (late 1944). Systematic destruction by retreating German forces left Warsaw mainly in ruins by January 1945. Finding shelter and work at the Zoological Museum, Kielan-Jaworowska rapidly developed an interest in paleontology (specifically, fossil vertebrates), and by fall 1945, when operations at the University of Warsaw resumed, she met and soon became a student of Roman Kozłowski (1889–1977), founder of Polish paleontology and, ultimately, the Institute of Paleobiology PAS.

Younger scientists are often surprised to learn that Kielan-Jaworowska's initial studies had nothing to do with early mammals. Kozłowski, an authority on Paleozoic graptolites, steered her into research on Devonian trilobites, which formed the basis for her M. Phil. (1949) and Ph.D. (1953) studies. During a chance mountaineering trip in 1950 she met Zbigniew Jaworowski (1927–2011), whom she married eight years later. Jaworowski, then a medical student, later became a renowned physician in radiation medicine, and an expert in monitoring atomic radiation and climate change. A Renaissance scholar with broad knowledge in practically any topic, Jaworowski was an inseparable part of Kielan-Jaworowska's life, and was well known to her colleagues and acquaintances. Their fields of interest intersected when, by chance, Kielan-Jaworowska happened to bring some Mongolian dinosaur bones to her home study while Jaworowski had a Geiger radiation counter there, leading to the discovery that part of the collection was highly radioactive (Jaworowski and Peńsko 1967). Their only child, Mariusz, was born in 1959. In the interim, Kielan-Jaworowska began (1952) an ambitious project on Ordovician trilobites, which would take her to field work at widely scattered sites, and research on collections in major institutions of Europe. This study, completed in 1959 immediately before Mariusz's birth, was published as a monograph a year later.

Kielan-Jaworowska's interest in vertebrates was to be delayed further when, in 1959, Kozłowski suggested that she take up study of another invertebrate group: polychaete worms. Using acid preparation of erratic (glacially-deposited) Ordovician–Silurian boulders, Kozłowski had discovered complete jaw apparatuses of these organisms, until then known mainly from disarticulated elements. Soon Kielan-Jaworowska had a large collection of well-preserved polychaete specimens, which she completed studying during a break from Mongolian field work in 1964.

In the meantime, important, career-changing opportunities had opened up. Kozłowski retired in 1960, and Kielan-Jaworowska, by then a senior scientist and highly-regarded administrator, succeeded him as Director of the Institute of Paleobiology, a post she would hold until 1982. Shortly thereafter, an Academy of Sciences was established in the Mongolian People's Republic. Kozłowski, still active with PAS, suggested the possibility of joint Polish-Mongolian

[1] Poland was also the only Nazi-occupied country in which the death penalty was imposed for offering help to Jews. In 1991, the Yad Vashem Authority of Israel awarded the Righteous Among Nations title to the Kielan family, including Zofia, for providing safe haven to one of Zofia's Jewish schoolmates during Nazi occupation of Warsaw.

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paleontological expeditions, and helped broker a scientific cooperation agreement to that end. Kielan-Jaworowska was appointed to organize and lead those expeditions. According to her own account, the opportunity for expedition support came from trade, wherein countries under Soviet influence accepted each other's currencies, and Poland found itself with Mongolian currency that could not be spent elsewhere.

Mongolia had been put on the map, paleontologically speaking, in the 1920s by the American Museum Central Asiatic Expeditions (Andrews 1932), which discovered (among others) the first Cretaceous mammal skulls known (Gregory and Simpson 1926). Soviet expeditions collected Mongolian fossils beginning in the 1940s, but early expeditions focused mainly on dinosaurs (see Benton et al. 2000). From 1963 to 1971, Polish-Mongolian teams collected a spectacular array of vertebrate fossils from Upper Cretaceous (Campanian–Maastrichtian) beds in the Gobi Desert. By all measures—impressive number of fossils, species diversity, and anatomical informativeness—this collection ranks among the most important assemblages of Mesozoic vertebrates ever found. The timing of these discoveries was also very opportune. After a hiatus of some 40 years since the American Museum Expeditions to Mongolia in the 1920s, the newer discoveries by the Polish Mongolian expedition brought new scientific information to light, just as paradigm shifts caused a worldwide renaissance in the studies of dinosaurs and early mammals.

Most celebrated among the other vertebrates collected are the dinosaurs: skeletons of large (*Tarbosaurus*) and small (*Velociraptor*) theropods, among them the famous "fighting dinosaurs" (*Velociraptor* locked in death struggle with *Protoceratops*); a complete sauropod skull and skeleton; and a host of ornithischian skeletons, including ankylosaurs and pachycephalosaurs. These formed the basis for some 50 scientific publications by various authors, supervised and edited by Kielan-Jaworowska. Zofia Kielan-Jaworowska herself discovered the type specimen of the awe-inspiring, 2.4 m-long forelimbs of the gigantic ornithomimosaur *Deinocheirus* in 1965 (Osmólska and Roniewicz 1970). The distinctive features of this dinosaur attracted intense interest in the paleontological community for another 40 years, until the case came to closure with the discoveries of two more complete specimens by Korean, Mongolian, and Belgian scientists (Lee et al. 2014).

The dinosaur fossils from the Polish-Mongolian expedition also provided source material for exhibits in Warsaw, Ulaanbaatar (the capital of Mongolia), and elsewhere.

Impressive as they were, the expeditions constituted only part of the larger program to make the Mongolian fossils available for study and display, both in Poland and Mongolia; and to disseminate knowledge to the public and professional communities. Here Kielan-Jaworowska demonstrated true organizational and administrative genius, succeeding brilliantly. Numerous publications, in the form of both preliminary studies and monographic treatises, were published as a series edited by her in *Palaeontologia Polonica* from 1968–1984, of which Kielan-Jaworowska herself contributed 13 of the 64 works. Concurrently, she orchestrated exhibits in Warsaw and elsewhere, wrote many popular works, generated considerable media attention, and began publishing studies in international venues, eventually contributing an impressive list of eight papers in *Nature*. These and some other works chronicle many important new discoveries or interpretations based on the Mongolian fossil mammals.

Of special interest to Kielan-Jaworowska were the fossil mammals from Mongolia, to which she would dedicate the next fifty years of research: about 180 specimens were found. Most were represented by skulls, and some by skeletons, in contrast to the previously-known record of mainly teeth and bits of jaws. One deserving of mention concerns *Deltatheridium* and allies, previously considered to be aberrant placentals (e.g., Van Valen 1966), but which Kielan-Jaworowska and coauthors place in Metatheria, as close relatives of Marsupialia (Butler and Kielan-Jaworowska 1973; Kielan-Jaworowska and Nessov 1990). Kielan-Jaworowska also made extensive contributions to understanding the evolutionary history of Eutheria, which include living placentals and fossil allies. Besides the many new eutherian species she established (e.g., Kielan-Jaworowska 1975b), she also published comparative studies on their skeletons, with the new insight that the eutherians from the Late Cretaceous of Mongolia were adapted to terrestrial locomotion (Kielan-Jaworowska 1977, 1978). This then-new interpretation is now part of the broader picture of ecomorphological diversity among early mammals (Luo 2007; Kielan-Jaworowska 2013). Kielan-Jaworowska's studies on brain endocasts of Cretaceous mammals also filled some previously blank areas of our knowledge (Kielan-Jaworowska 1983, 1984, 1986), and the original data from her work are still relevant to our understanding of mammalian brain evolution today (e.g., Rowe et al. 2011).

Zofia devoted much attention to an extinct, rodent-like group, Multituberculata, which are generally the most abundant and diverse mammals of Late Cretaceous assemblages from Laurasia. She discovered that they have a so-called "marsupial bone" (the epipubis), which may support the pouch in marsupials but which is also present in non-pouched mammals, such as monotremes and eutherians (Kielan-Jaworowska 1969, 1975). She proposed that, like living therians but unlike egg-laying monotremes, multituberculates probably gave live birth (Kielan-Jaworowska 1979). Kielan-Jaworowska also made important contributions to knowledge of multituberculate skull structure and their feeding adaptations (e.g., Kielan-Jaworowska 1970), a topic to which she repeatedly returned through the years. Perhaps the most comprehensive of her life's works are her studies on the evolutionary morphology and functional anatomy of multituberculate postcranial skeletons. She and Peter Gambaryan (1994) were the first to propose diverse locomotor modes within this taxonomically diverse group. This was a prescient idea that has now been well corroborated by newer discoveries (e.g., Yuan et al. 2013). Her persistent argument on the phylogenetic placement of multituberculates was the source of inspiration, to many, to evaluate and re-evaluate the overall phylogenetic relationships of all mammals and their kin (Kielan-Jaworowska 1997). With over 40 research papers on multituberculate species from many parts of the world, and on their evolution and paleobiology, Zofia's vast contribution is un-matched by anyone studying this extremely complex, yet also extremely important group for early mammal history. Her life's work on multituberculates had made them an indispensable group for mapping mammalian relationships. Kielan-Jaworowska's research work soon placed her in contact with most of the scientists in her field and took her to many countries. The geopolitical and ideological chasms before the fall of the Berlin Wall in 1989 made it difficult for scientists in the former Soviet Bloc to have free academic exchange. This circumstance, so overwhelming for scientists in formerly socialistic countries, is now unfamiliar to the younger generations who take

the internet for granted. Benefiting from her eminent stature and her indomitable, resourceful character, Zofia overcame the political hurdles, developing an extensive network of contacts and collaboration with her international colleagues, since the very beginning of her career. As early as the 1960s, Kielan-Jaworowska visited the British Museum and University College London. Her collaborative studies there contributed to a new model on the early evolution of mammals that emerged in the early 1970s (Kermack and Kielan-Jaworowska 1971). In 1973–1974 she was appointed by Harvard University as an Alexander Agassiz Visiting Professor at the Museum of Comparative Zoology, Cambridge, Massachusetts, where she studied evolution of the therian molar pattern (Crompton and Kielan-Jaworowska 1978). Of all of Kielan-Jaworowska's international colleagues and friends, she developed the deepest friendship with Malcolm C. McKenna (American Museum of Natural History), whom she visited many times (Kielan-Jaworowska 2005). In 1981, Kielan-Jaworowska spearheaded the Second Mesozoic Terrestrial Ecosystems Symposium bringing a large number of international paleontologists to Poland (Kielan-Jaworowska and Osmólska 1983).

In 1982 Kielan-Jaworowska stepped down from her position as Director of the Institute of Paleobiology, in order to undertake an extended period (1982–1984) of study as Visiting Professor at the Muséum national d'Histoire naturelle, Paris. Here she employed histological techniques to section multituberculate skulls, permitting reconstruction of the cranial vasculature and brain (Kielan-Jaworowska 1986; Kielan-Jaworowska et al. 1986), and forming the basis for subsequent studies, noted below. Although an improvement over serial grinding techniques (e.g., Stensiö 1927), the process of histological sectioning was laborious: Kielan-Jaworowska and her French colleague, Cecile Poplin, spent three months of 10-hour days to complete the task (Kielan-Jaworowska 2005).

She returned to Warsaw in 1984; however, as described in her autobiography (Kielan-Jaworowska 2005), the political climate was in turmoil in Poland at that time, and it was an inauspicious period for Polish science. She applied for a position in 1985 and was appointed in 1986 as Professor of Paleontology at the University of Oslo, where she moved in 1987. One of her important contributions was the renovation of exhibits at Oslo's Palaeontological Museum, which she accomplished by drawing on her previous experience in curating exhibits on a shoestring budget, and on casts obtained through her extensive network of professional acquaintances. Kielan-Jaworowska collaborated widely during her Oslo years, notably with the charismatic Lev Nessov (Kielan-Jaworowska and Nessov 1990, 1992; Nessov et al. 1998); and with the Russian anatomist Peter Gambaryan, with whom she reconstructed the musculature and paleobiology of multituberculates (Kielan-Jaworowska and Gambaryan 1994; Gambaryan and Kielan-Jaworowska 1995, 1997). Kielan-Jaworowska's serially-sectioned multituberculate skulls became the source material for the masters and Ph.D. studies of Jørn Hurum, her only Norwegian graduate student. She invited Zhe-Xi Luo, whom she had previously met in 1983 in Montana, to be a member of Hurum's Ph.D. committee. The seed for future collaboration was sown with Hurum's Ph.D. work (Hurum 1997), and Hurum and Kielan-Jaworowska would carry on their close collaboration on multituberculate anatomy and evolutionary relationships (e.g., Hurum et al. 1995; Kielan-Jaworowska and Hurum 1997, 2001, 2006; Kielan-Jaworowska et al. 2002, 2005). Together with Luo, they forwarded the novel and exciting hypothesis that venom spurs, as seen in living monotremes, may have evolved earlier than the extant mammals, as evidenced by its widespread presence among early mammaliaforms (Hurum et al. 2006).

Returning to Poland in 1995, Kielan-Jaworowska was appointed Professor Emerita at the Institute of Paleobiology PAS, ending her career where it began. Yet she remained as active as ever, publishing 35 scientific papers, two books, and 14 popular articles in the last two decades of her life. She also assumed editorship of this journal from 1996–2007 and significantly accelerated its rapid growth. Earlier in her career, Kielan-Jaworowska had collaborated with Jason A. Lillegraven and William A. Clemens in co-editing and writing the first general treatise on Mesozoic mammals (Lillegraven et al. 1979). This book instantly became the primary reference of its kind. In following years, the rapidly expanding fossil record, together with conceptual and methodological advances (such as cladistics and the advent of algorithm-based phylogenetic analysis), made it clear that a new synthesis was needed. Kielan-Jaworowska undertook this work as the major project in her "retirement" and the capstone to her prolific career. Her *Mammals from the Age of Dinosaurs* (Kielan-Jaworowska et al. 2004), with contributions by her two junior colleagues, Richard Cifelli and Zhe-Xi Luo, was published 25 years after the first compendium. She subsequently wrote a popular account of Mesozoic mammals, the history of their discoveries, as well as the people who discovered them, with rich first-hand experiences, many fond personal memories, and her reflection from her life's work on some teachable moments for the future scientists (Kielan-Jaworowska 2013).

Zofia Kielan-Jaworowska was a passionate and indomitable intellectual. She was tireless and persistent when advocating for her new research ideas (e.g., Kielan-Jaworowska 1997); and meticulous and exacting in her studies of fossils. She named some 20 genera of Mesozoic mammals, most of them based on information-rich specimens. Kielan-Jaworowska's greatest paleontologic legacies are empirical: they consist of the fossils collected under her leadership and the contributions to knowledge, in the form of basic data, derived from those fossils. Her research touched on diverse aspects of mammalian phylogeny and paleobiology, with many insights. Almost without exception, the foundation underlying those insightful interpretive works is an enormous body of descriptive and comparative morphology, basic systematics, and high-quality illustrations. This voluminous body of scientific work has provided essential context and has served as the foundation for understanding newly-discovered early mammals of recent decades (e.g., Zhou et al. 2013; Yuan et al. 2013; Bi et al. 2014). Kielan-Jaworowska's descriptive contributions will undoubtedly endure in future paleontological literature, like those of her scholarly predecessors do today (e.g., Owen 1871; Simpson 1928, 1929), as testament to the originality, scope, and significance of her achievements.

Zofia Kielan-Jaworowska served as mentor to each of us and to uncounted other scientists. She was a peerless role model. She was uniformly helpful and supportive, especially to scientists with limited resources. Her openness and honesty led her to be critical at times, but invariably her criticisms were well founded and helped improve our work. Zofia was enormously generous, warm, and hospitable; she and Zbigniew hosted an untold number of colleagues and students, many of whom they had not even previously met. Words cannot express the depth of our gratitude to and admiration of Zofia Kielan-Jaworowska, and we miss her dearly.

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For complete list of Zofia Kielan-Jaworowska publications see Supplementary Online Material available at http://app.pan.pl/SOM/app60-Cifelli_etal_SOM.pdf

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