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Between hard rock and open space: Constraints and freedom of Finnish paleontology

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Palaeontology is the science which treats of the life that has existed on the globe during former geological periods. It deals with all questions concerning the properties, classification, relationships, descent, conditions of existence, and the distribution in space and time of the ancient inhabitants of the earth, as well as with those theories of organic and cosmogonic evolution which result from such inquiries.

Grundzüge der Paläontologie (von Zittel 1895), English translation by Charles Eastman (1900)

I won't say the pieces were beginning to fall into place, but at least they were getting to look like parts of the same puzzle. Which is all I ever get or ask.

Raymond Chandler: *The Little Sister*, motto of Mikael Fortelius' Ph.D. thesis (1985)

Introduction

Science in any particular place and time depends on factors acting at many different levels. Global *Zeitgeist* and technology are filtered through local conditions to shape research environments and to be received and in turn reshaped by individual actors. The role of single individuals and what may even appear as pure chance is likely to be especially conspicuous in small environments.

This has certainly been true of the distinguished but tenuous tradition of Finnish paleontology. Natural conditions are not favourable. The Ice Age cleared away and reshuffled most that had remained of post-Cambrian sediments, leaving, with few exceptions, ancient bedrock covered by postglacial soft tissue. In spite of occasional pieces of mammoth (*see* e.g. Ukkonen *et al*. 1999), fossil-hunting is not a promising source of inspiration for hopeful young naturalists. Finnish geology has not contributed anything to the classical debates about the Age of Earth, or the History of Life on time scales of tens to hundreds of millions of years.

On the other hand, although small in itself, Finland has enjoyed the benefits of two strong politico-cultural contexts: first the Kingdom of Sweden, then the Russian Empire. Scientifically, Sweden remained a great power throughout the 18th century, and the Linnaean heritage influenced Natural History in Finland well into the 1900s. The Royal Academy in Åbo (Turku), founded in 1640, was one of the main Swedish universities, deeply involved in Linnaeus' project of collecting and systematizing the biological treasures of the whole world. Two of his foremost apostles were Finns: Pehr Kalm, travelling in North America and subsequently becoming Professor of Natural History in Turku, and Petter Forsskåhl, travelling (and perishing) in Arabia. In the 19th century, as subjects of the Emperor of Russia and Grand Duke of Finland, Finns had "domestic" access to all the corners of the world's largest empire, spanning from the Arctic to the Black Sea and from Poland to northern California. This included the main Russian centres of learning, with the capital St. Petersburg only some 300 km away from Helsinki.

While most Finnish paleontologists have been zoologists in the first place and only secondarily geologists, it should be noted that a strong line of Quaternary geology goes back at least to Wilhelm Ramsay (Professor of Geology 1899–1928), and some of it may well qualify as paleontology, or maybe paleobiology. Especially noteworthy is the palynological tradition from Matti Sauramo, who became the first professor of a discipline that was actually renamed "Geology and Paleontology" in 1940 (Donner 2003, 2005). Sauramo's production even includes a study of older fossils from the nearby Estonian coast around the island of Vorms. Palynological chronology, since the 1950s supported by isotope techniques, has remained important. Beyond the far border of the Finnish geological time gap, Precambrian microfossils have more recently attracted considerable attention (e.g. Tynni 1980, Tynni & Donner 1980, Tynni & Uutela 1984). In the present article, however, I shall focus on the main line of Finnish paleontology, which is firmly rooted in the study of *animals* (Cenozoic mammals) — even when the institutional affiliation of the investigators may have been Geology, now part of Geosciences and Geography at the University of Helsinki.

Alexander von Nordmann

Southern Russia was the main arena of the first paleontologist of Finnish origin, Alexander von Nordmann (1803–1866), who had enrolled at the University in Turku in 1821 to study Natural History. His professor was the prominent entomologist Carl Reinhold Sahlberg, who in the same year founded the first scientific society in Finland together with some of his students, von Nordmann among them. Recruiting the Linnaean heritage in the service of the ascending National Project, the society was named *Societas pro Fauna et Flora Fennica*. Only six years later, Turku burned down almost completely and most of the biological collections were lost. This, together with the death of his father, gave von Nordmann the decisive impulse to go abroad, first to Berlin. Light microscopy was then undergoing the fast technological developments that laid the foundations for modern cytology, and had already produced remarkable results in the ontogenetic studies of Karl von Baer and Heinrich Rathke. Microscopic investigation of invertebrates became von Nordmann's speciality. *Mikrographische Beiträge zur Naturgeschichte der Wirbellosen Thiere* (von Nordmann 1832) was his scientific breakthrough, with identifications and life history descriptions of, e.g., parasitic crustaceans. On these merits, he was offered the post as Professor of Botany and Zoology at the Richelieu Lyceum in Odessa, soon becoming Director of the Botanical Garden as well. His activities during those happy years were diverse and wide-ranging, including no less than 14 scientific expeditions in the southern parts of the Russian Empire. Most important in the present context are his excavations of several rich "diluvian" sites of mussel shells with later clay intrusions holding masses of disordered mammalian bone fragments. The first one was discovered in 1846 in Odessa itself in connection with urban construction work. In 1849, von Nordmann returned to Finland to take up the chair of Natural History at the University, which had by then moved to Helsinki. He presented his rich fossil material in four instalments at meetings of the *Societas pro Fauna et Flora Fennica* in 1854 (I–III) and 1860 (IV). The reports were printed in 1859–1860 (Hjelt 1867, Moring 1984).

Thus the science of paleontology makes its entrance in Finland with a solid study entitled *Palaeontologie Süd-Russlands*. It is a descriptive, taxonomically organized catalogue of the bone fragments, accompanied by 28 beautiful lithographic plates ("Being a draughtsman myself, I have drawn the sketches for the illustrations …”). The first part is entirely devoted to cave bears, and its few conclusions give a flavour of the strict empiricist ethos: “The benevolent Reader … will doubtlessly ask, what results can be deduced from all the above data, descriptions and comparative measures of various bones?” Well, first that the Odessa bear is identical to the cave bears described from other parts of Europe, second, that the bears now living are so different that they cannot be regarded as transformed (or maybe deviant, “*entartete*”) forms of the cave bear, but represent a separate species. It is amusing to compare von Nordmann’s modest conclusions with the grand scenarios that his successors have derived from basically similar material.

Von Nordmann rejected the idea of species transformations larger than such that would have been acceptable to Bonnet or even Linnaeus. His framework was purely Cuvierian — morphological analysis illuminating taxonomy and functional anatomy. There can be no talk of macroevolution. Of course, given the nature of the localities (e.g., “*Eine Diluviallehmgrube in Odessa*”), his fossils lend themselves readily to Cuvierian catastrophe theory. Interestingly, von Nordmann was personally acquainted with many of the leading contemporary figures of embryology and comparative anatomy (von Baer, Rathke, and the *Naturphilosoph* Lorenz Oken), disciplines that would soon, in the hands of Haeckel, be effectively recruited in support of evolution. He also contributed to the revised edition of Lamarck’s *Histoire des animaux sans vertèbres*, thus acknowledging the author’s expertise in zoology without being bothered by his radical evolutionism. Incidentally, Darwin’s *Origin* appeared just as *Palaeontologie Süd-Russlands* was being printed, but although von Nordmann lived for six more years, his views on Darwinism remain unclear (Moring 1984). Anyway, he shunned speculation, and his paleontology is only part of a versatile biological oeuvre.

Von Nordmann had no direct followers, which may be partly explained by a certain social marginalization of this half-Russian/German cosmopolite in a time of mounting national sentiment. After him, there is a gap of some 70 years in the line of Finnish paleontology. But when continued, it is by no means unaffected by von Nordmann’s legacy: his *Palaeontologie*, his lasting reputation, and most tangibly, his fossil collection, of which a significant part including the cave bear material was finally purchased by the University in Helsinki.

Björn Kurtén

In 1945, Björn Kurtén (1924–1988) from the Ostrobothnian town of Vaasa entered the same university to study geology and zoology. His was a lively imagination nourished on many kinds of literature, including books about dinosaurs and other beasts. While still a schoolboy, he had published an adventure novel in his native Swedish, and two more appeared during his first years at university. Paleontology was just then experiencing the paradigm shift marked by George Gaylord Simpson’s pivotal *Tempo and Mode in Evolution* (1944), whereby it became an integral part of the “modern synthesis” of genetics and population biology with Darwinian evolution (Dobzhansky 1937). Simpson’s book set the scene for Kurtén’s entire scientific work. At the University he was introduced to population dynamics, quantitative ecology and functional anatomy by his zoology teachers, most notably Olavi Kalela and Pontus Palmgren. Through Palmgren, he got the opportunity to study with the paleontologist Birger Bohlin in Uppsala (Sweden). Thus he came to analyze Bohlin’s (previously published) material on crown height in bovid teeth in a population framework, finding that the distribution corresponded to an age distribution (*see* Wallgren 1989).

Valio Armas Korvenkontio

Kurtén was to become the founding father of the current school of paleontology in Finland. Before him, however, there is a remarkable but solitary figure that deserves to be mentioned. In 1934, Valio Armas Korvenkontio (1889–1944) defended his Ph.D. thesis *Mikroskopische Untersuchungen an Nagerincisiven unter Hinweis auf die Schmelzstruktur der Backenzähne*. It is a meticulous study of dental growth and wear in rodents, both extinct and extant, largely based on enamel fine structure. The dedicatee is Henry

Fairfield Osborn (1837–1935), dinosaur hunter, controversial eugenicist, and influential head of the American Museum of Natural History in New York, who had provided most of the fossil material. Korvenkontio's aim was primarily "phyletic", using dental characters for resolving difficult systematic relations, and secondarily functional and mechanistic. His analysis of fine structure allowed him to discern how similar function may emerge from different growth patterns, genetically fixed in different phyletic lines, in their interaction with physical forces. The thesis ends with a discussion of how well the results can be explained by each of four major evolutionary theories (1–4) as perceived by the author. Korvenkontio concludes that pure "Selectionism" (theory 1) fares poorly, as does theory 2, pure "Lamarckism". Theory 3, "Orthogenesis" receives quite a favourable assessment. It is an eclectic mix adopted from the German zoologist Theodor Eimer (Eimer 1888), embodying the sound idea that evolution is constrained to specific pathways by (genetic) restrictions in the possible directions of variation. However, adaptations are largely ascribed to the inheritance of acquired characters. Korvenkontio's most unreserved approval is accorded to the "further developed orthogenetic views by one of the greatest minds in the field of modern evolutionist research, a man with the widest experience regarding the concrete facts of the history of the organic world, Henry Fairfield Osborn." This theory 4, named "Aristogenesis", is an elaboration of theory 3 with the virtues of downplaying the Lamarckian elements and including allometric growth among fundamental explanatory factors.

Korvenkontio led his later life mainly outside Academia as a school teacher, and his dissertation therefore remained an isolated landmark. Obviously, his empirical studies have the most lasting value, but he does conceptually foreshadow modern ideas of how form and function depend on the interaction of genetic-molecular networks with the environment during ontogeny and throughout life. It was not *only* a joke when Mikael Fortelius and Jukka Jernvall (*see* further below) in the 1990s styled themselves as "The Valio Armas Korvenkontio Unit of Dental Anatomy in Relation to Evolutionary Theory" (acronym VAKUDARET).

Population thinking and paleoecology

To return to Björn Kurtén, he appears in retrospect as just the kind of mind paleontology needed at that juncture. He combined strict quantitative analysis of large fossil materials with a synthetic imagination that helped him to see the big picture. Population thinking was evident already in his Master's thesis on the Chinese *Hipparion* fauna, and fully developed in his Ph.D. thesis *On the Variation and Population Dynamics of Fossil and Recent Mammal Populations* (Kurtén 1953). Its motto, *sero venientibus ossa*, "to the latecomers (only) bones remain", suggests what may have been for him the most fundamental appeal of paleontology: the reconstruction of past conditions and events from sparse fossil clues is not unlike a good detective story. Of course, his kind of paleontology required that the bones be abundant enough to allow analyses of populations and communities [cf. his ingeniously simple idea of the "half-life" of taxa (Kurtén 1972)]. Kurtén also used to say that "being a paleontologist without fossils at home is best, as a collection swallows its keeper, and only the traveller sees the whole picture". Nevertheless he stayed, in a way, close to home, devoting his strictly scientific activities wholly to Cenozoic mammals rather than, for example, dinosaurs. Among other things, he made good use of von Nordmann's collections, particularly the cave bear material. The cave bear (bear = *björn* in Swedish) remained a lasting favourite, on which he was to publish at least 15 original studies as well as a popular book, *The Cave Bear Story* (Kurtén 1976, *see* also Kurtén 1975).

It is not necessary here to review Kurtén's production and career as "a paleontologist's paleontologist … [and] 'world-class' evolutionary biologist", as George Gaylord Simpson called him in a foreword to a collection of his early articles. Basic facts are easily accessible, for example, in a memorial volume of *Annales Zoologici Fennici* (e.g. Leikola 1991, Anderson 1991). However, I should like to comment on some aspects of his particular spiritual heritage — his "paleoecology", and how it was done.

The central fact is that he was both a scientist *and* a literary man. Rigorous formulation and testing of hypotheses may, generally speaking, be a necessary condition for science in contrast to other forms of knowledge, but it is not a sufficient condition for good science. A more interesting and much less transparent process is the generation of relevant theories and hypotheses, requiring in biology an integrative grasp of the living world, a creative imagination, and a capacity to commute between synthetic and analytic modes of thought. To an unusual extent, Kurtén puts different levels of his own scientific creativity on public display through his writings in different genres. There is a continuum from original research articles through synthetic monographs/textbooks and popular science books to scientifically informed fiction, with different claims to scientific rigour and "truth".

The level of science next to original research articles is represented by two grand monographs, *Pleistocene Mammals of Europe* (Kurtén 1968a) and *Pleistocene Mammals of North America* (Kurtén & Anderson 1980), syntheses that truly create new understanding. Outside strict science writing, Kurtén excelled in two other literary genres cultivated mainly in his native Swedish: first, popularization of paleontology and evolutionary biology (e.g. Kurtén 1968b, 1969, 1971a, 1971b, 1975, 1976). Only three months before his death he gave a lecture on "Reconstructing the life of the past" at the Finnish Society of Sciences and Letters (Kurtén 1989). Second, there is his "paleofiction": novels set in human prehistory but firmly based on the best knowledge about the world of that time. To these literary expressions may be added a visual aspect of his imagination, realized in collaborations and friendships with artists like the British wildlife artist Hubert Pepper (1928–1985), illustrator of some of Kurtén's books and painter of his portrait, and Eirik Granqvist (born in 1944), eminent young taxidermist/sculptor ("Conservator") of the Zoological Museum of the University of Helsinki. In the 1970s and early 1980s, Granqvist replaced the "stuffed animal" exhibits with vivid dioramas of animals in their environments. Inspired by Kurtén, he also recreated mammoths and transformed an old lioness into a black sabre tooth tiger. *Den svarta tigern* [*The Black Tiger*] (Kurtén 1978) is the title of Kurtén's most successful paleonovel — known in English as *Dance of the Tiger* (1980). Kurtén and Granqvist also shared a living delight in supposed Cro-Magnon and Neanderthal lifestyles, which later gave rise to Granqvist's *Préhistorama*, a museum in southern France devoted to human prehistory.

The scientific value of Kurtén's paleofiction was perceptively assessed by Stephen Jay Gould in his foreword to *Dance of the Tiger*: "I believe that Kurtén's novel is a more appropriate place than the professional literature itself for discussing many of the truly scientific issues … Evolutionary biology has been severely hampered by a speculative style of argument that records anatomy and ecology and then tries to construct historical adaptive explanations … These speculations have been charitably called "scenarios" … [and] presented in the professional literature where they are taken too seriously and literally. Then they become "facts" and enter the popular literature … Yet these stories have a role in science. They probe the range of alternatives; they channel thought into the construction of testable hypotheses … But they are stories. So why not treat them as such, get all the benefits and pleasures, and avoid the wrangles that arise from their usual, inappropriate placement?"

In Finnish paleontology, Kurtén remains a towering presence both in the scientific themes and by virtue of the personal example he set as a "world-class" paleontologist. Nearly all Finnish paleontologists active today (and a good number of foreign ones, too) trace their scientific ancestry to him. Yet he had few doctoral students. He was basically an old-school individualist rather than a team player, and although internationally well-connected, definitely no organizer of collaborative consortia. He was usually a soft-spoken and kind man, social to a degree, but somewhat shy. Incidentally, his two Finnish students, Ann Forstén and Mikael Fortelius, were also the only ones who chose to work with non-carnivores, which was of some importance for the further developments in Finland.

Ann Forstén

Ann Forstén (1939–2002) is internationally renowned for her fine and extensive work on fossil horses. Ever since her Ph.D. thesis *Revision of the Palearctic Hipparion* (published in 1968 and still a classic in its field), her research was focussed entirely on this group. She applied the modern quantitative methods of Simpson and Kurtén but without evident concessions to literary imagination. She belonged to a species of museum-taxonomist "lonely riders": among her 91 original research articles, all but 15 are single-authored, and only three have more than one co-author. Forstén and Fortelius have collaborated on a single paper dealing with cheek tooth patterns in Tertiary horses (Rensberger *et al*. 1984). At the level of international museum exchange Forstén had a wide and effective network, though. She spent a total of seven years abroad, harvesting her data in big museums as well as little-known local fossil collections around the world, in the United States as well as the (former) Soviet Republics. As Curator of the Vertebrate Division of the Zoological Museum in Helsinki since 1988, she was strongly committed to maintaining the collections and making them useful to visiting scientists. Although she had no direct pupils or scientific successors, she was an active and generous supporter especially of young female scientists.

Mikael Fortelius

Through Mikael Fortelius (born in 1954) and his group, the single stem of Finnish paleontology has grown into a tree branching in several directions and intertwining with quite different research traditions. Received themes have been developed and new ground has been broken in ways that could not have been foreseen by the predecessors. Of course, the sprouting has been partly conditioned by changes in the research environment: on one hand, the developments in molecular biology and information technology that have revolutionized all biological sciences, on the other hand public funding policies that favour multidisciplinary research programs and big consortia. Fortelius, among many other talents, has had the receptive mind and social skills to welcome these opportunities/challenges and turn them to advantage, which he could hardly have learnt from his beloved mentor.

Early years

Like Kurtén, Fortelius came to the University of Helsinki from a mainly Swedish-speaking family then living in Vaasa. Like Kurtén, he had had an early dinosaur phase, although the book he got for his fourth birthday "at his own request" (according to his father's inscription) was about evolution and fossil mammals. His father was a medical doctor, his mother is a dentist. To what extent these early interests and family background have influenced his later choices can only be guessed. In 1973, Fortelius applied to study biology at the Faculty of Science, which required less physics and mathematics than the Faculty of Medicine (a common "lazy" reason for choosing biology). At that time students could still compose their curricula quite freely, without undue pressure to graduate in the shortest possible time, so his main subjects, chemistry and microbiology, could well be combined with Björn Kurtén's lectures on Cenozoic mammals and the origins of humans. Fortelius had previously read some of Kurtén's books without being terribly impressed, and Kurtén was by no means a brilliant lecturer, yet his quiet authority exerted a strange fascination. Fortelius switched to zoology and geology and chose to do his B.Sc., M.Sc. and Ph.D. for Kurtén.

The subject of his Master's thesis, rhinoceros teeth, could have been expanded in different directions for a Ph.D. A monograph on rhinoceroses was one obvious possibility. While studying fossils in Lyon, however, Fortelius found that this was already being undertaken by the Curator of the collection, and so he decided to focus instead on tooth function, a fortunate choice. In one direction there was the question how teeth become the beautiful tools that they are, leading to the study of genetic programming, developmental growth rules, structure, use, and wear. In another direction there was the question what teeth can tell us about the life of the animal and the qualities of its biological and physical environment.

The Ph.D. thesis is a monograph entitled *Ungulate cheek teeth: developmental, functional and evolutionary interrelations* (Fortelius 1985). It brings into play an abundance of themes and ideas, connecting the fossil past and the living present, the evolutionary and the developmental, the genetic and the functional, all set in a broad comparative context – all in all an intimidating chunk to embrace, and the final achievement justifies the modest satisfaction expressed by the motto quoted at the top of the present article. Whilst firmly rooted in received traditions, the thesis contains the seeds of most of the future work. Whilst forward-looking in content, it (now) appears delightfully old-fashioned in its monograph form, which allows synthesizing and intermixing ideas and data, results and discussion in a way that would not be possible in a series of small articles in standard journals.

It conveys a strong impression of paleontology as a science about *life*, not fossils *per se*. One telling example is Fortelius' simple empirical approach to an apparent dilemma regarding the scaling of metabolic rate and tooth size, respectively, with body mass (Pilbeam & Gould 1974, Gould 1975). Ungulate teeth scale roughly isometrically, whereby the occlusion areas of teeth of equal shape will be allometrically related to body mass M with the exponent 2/3 (i.e., proportional to $M^{2/3}$). Metabolic rates, however, increase more steeply, in proportion to $M^{3/4}$ on average. As virtually all energy available for metabolism is processed by the teeth, how can this work? Fortelius pointed out, firstly, that it is not occlusion area, but the volume of food between the teeth that defines the amount comminuted per chewing stroke. Given that teeth scale isometrically with body size (i.e., are proportional to M^1), so will the food volume between the teeth. Secondly, the *rate* of energy intake will depend not only on single-stroke volume but also on chewing rate. But alas, accurate enough data on the scaling of chewing rate with body size were not to be found in the literature! So Mikael together with his brother Walter went straight to the Helsinki Zoo, stopwatch in hand, and recorded chewing rates of 20 ungulate species. They found that the chewing rates decreased with body size with a mean allometric exponent not significantly different from –1/4. The isometry of single-stroke volume and the negative allometry of chewing rate give an allometric exponent of (1 – 1/4) = 3/4 for food processing rate *vs*. body mass — just right to satisfy the metabolic needs. This has a further important implication. As the lifespan of mammals is known to scale as $M^{1/4}$ on average, the *lifetime* number of chews and dental wear will, *ceteris paribus*, be independent of body size M. This means that functional demands on teeth are primarily dictated only by the properties of the foods they are made to process, not the size of the animal.

Scaling has remained one of Fortelius' lasting interests and has given rise to some fun work like an article about "the largest land mammal ever *imagined*" (Fortelius & Kappelman 1993). By this exercise in allometric scaling, the monstrous 20–30 tonnes reconstruction of *Indricotherium* (*Baluchitherium*) from the 1930s was reduced to about 11 tonnes — rather like the biggest species known from other taxa, e.g., fossil proboscideans. Beyond the single organism, rather different questions of scaling in space and time are central to ecology and evolutionary biology. For example, Fortelius' more recent work involves welding together disparate evidence reflecting ecosystem and climate changes on different spatio-temporal scales into a coherent picture (*see* below).

What's in a tooth? Evolution, ecology and climate

Teeth are the kernel from which most of the wide-spanning research motifs have grown, giving the lie to some early criticism of Fortelius' science being narrow ("rhino teeth? — come on!"). Teeth are not only the most durable and best fossilized parts of mammals; they also have a high degree of morphological articulation and thus "offer good opportunities to link morphology to ecology through diet" (Jernvall *et al*. 1996, Polly *et al*. 2011). Their wear tells about the individual's food and life history, their morphology about the deeper history of the clade, their growth about the genetic-molecular control of morphogenesis. The space of evolutionary constraints and adaptations of teeth is firmly structured by properties that are amenable to study. When large materials from many species are available, conclusions can be extended to populations, communities and ecosystems, including vegetation, and ultimately climate. Indeed, one overriding theme in Fortelius' research is the refinement and validation of reasonably accessible dental measures for use as proxies of ecological conditions.

Crown height is a classical, easily measured parameter correlated with diet. High-crowned molar teeth (hypsodonty) may unquestionably be seen as an "adaptation" for a high degree of wear, as associated with grazing abrasive grasses. The durability problem is complex, however, since wear-resistance may depend on combinations of many functional variables, including cusp patterning, enamel thickness and chewing direction. In a judiciously argued review, Janis and Fortelius (1988) considered hypsodonty in the general context of several lines of evolutionary adaptations. Yet they note that "by far the most common solution to the problem of increasing the durability of the dentition is increased tooth height, frequently accompanied by a modification of occlusal morphology", that "increased crown height of the cheek teeth is extremely common among herbivorous animals", and that "hypsodonty and hypselodonty have evolved in parallel many times in many mammalian orders." Hypsodonty emerges as an "easy" invention that has recurred over and over again in evolutionary time.

The realization that ecomorphology cuts across phylogenetic boundaries was crucial for solving a riddle that Fortelius had originally presented in lecture notes for undergraduate students. Whilst the strong taxonomic radiation of ungulates in the Eocene correlated with a strong increase in tooth diversity, the taxonomic radiation of the Miocene coincided with *fewer*, and more disparate, radiations of tooth morphology for different vegetation zones. The solution was formulated several years later in the first fruit of the Jernvall–Fortelius collaboration: the blooming Eocene offered a rich diversity of high-quality niches accommodating a corresponding diversity of dietary specializations and feeding styles, whereas the partly dry and gradually cooling Miocene offered fibrous vegetation of low primary production and loss of intermediate niches. Tooth morphology was forced into fewer streams with loss of intermediate crown types, although taxonomic diversity could still increase driven e.g. by increased provinciality and subdivision of resources. The authors conclude that "the analysis of morphological trends describes the ecological aspect of ungulate radiations better than taxonomically based analyses alone" (Jernvall *et al*. 1996).

The decoupling of diet and climate signals from taxonomy was taken one step further in two articles with nearly self-explanatory titles: *Common mammals drive the evolutionary increase of hypsodonty in the Neogene* and *Maintenance of trophic structure in fossil mammal communities: site occupancy and taxon resilience* (Jernvall & Fortelius 2002, 2004). Even without any adaptive evolution of tooth morphology, the proportion of hypsodont teeth in the fossil material will increase as the climate gets drier just because hypsodont species conquer space at the expense of less well-adapted species. Hypsodonty is not costly to maintain, so there are no strong selective pressures against it during intervals of higher humidity, but low-crowned species can then spread and become more dominant. Thus Fortelius *et al*. (2006) reaffirm that "mean hypsodonty provides a reasonably faithful record of relative rainfall within and between intervals".

In the 1990s and 2000s, there is a consistent pursuit of better-resolved as well as more comprehensive methods to reconstruct the environment including precipitation, climate and primary production during the Neogene (the period from Miocene to Pleistocene, i.e. ca. 23–2.5 Mya). In this endeavour, it becomes a major challenge to weld together disparate data reflecting different time scales (ecological/paleontological/geological). In tooth morphology, growth patterning tells about phylogenetic history and selection pressures in deep time. Wear, on the other hand, reflects the diet of the individual, and can in turn be further resolved. Traditional measures at the microscopic level (microwear) tell about recent events, which may differ significantly from the ecologically more relevant lifetime average. It is also rather laborious to measure (cf. Korvenkontio). In the "mesowear" method, Fortelius and Solounias (2000) devised a felicitous solution allowing lifetime wear to be assessed from measures that can be observed by the unaided eye or at low magnification. The authors found that, contrary to previous belief, the morphology of occlusal surfaces is not too dependent on wear stage to be of use for functional characterization of species (very young and very old excluded). Cluster analysis based on mesowear variables, combined with hypsodonty, proved remarkably successful in classifying extant ungulate species either as grazers, mixed feeders, or browsers (i.e., on an abrasion to attrition axis).

Obviously, ecosystem reconstruction may be guided by measures derived from the entire fossil material, not only from teeth. This is implemented in "ecometrics", a method making fuller use of traits that may characterize the dynamic interaction of organisms and their environments (Fortelius *et al*. 2002, Polly *et al*. 2011). In plants useful traits may be leaf physiognomy, venal density and stomatal density, in animals, e.g. ectothermic body size and limb proportions – as well as tooth crown complexity. The key idea is to identify specific trait–environment pairings that hold across different scales (species, communities, etc.), and to study their dynamics over space and time. This may then be correlated with other climate measures like isotope distributions, and wax composition in plants. Some recent advances in this ongoing research program are the explicit combination of ecometrics and biogeography with a climate model (Eronen *et al*. 2009) and the prediction of primary production from ecometrics data (Liu *et al*. 2012). For tooth aficionados it is still gratifying to note that the distribution of tooth types alone predicts 70% of Earth's (global) net primary production today.

The insights into the highly non-linear dynamics of climate variation on different time scales, causes as well as consequences, are bound to arouse in the investigator a sense of responsibility in the context of current climate debates. Fortelius now participates not only in the efforts of the international scientific community to formulate scenarios for the near future of the biosphere (Barnosky *et al*. 2012), but also in societal actions like a PM on climate change presented to the Governor of California in 2013 (Barnosky *et al*. 2014).

Data- and other bases

Naturally, these remarkable achievements have had several prerequisites of a more technical nature. A crucial tool for assembling and mastering the enormous data bodies has been the open-access "New and Old World (NOW) Database of Fossil Mammals", which is coordinated by Fortelius. Its starting point was a workshop organized in 1992 at Schloss Reisensburg in Germany with the purpose to review the evidence for provinciality and diachrony of change between central Europe and the eastern Mediterranean realm during the Middle and Late Miocene. Fortelius was strongly involved in setting up the database, and the first major results were published in 1996 (Fortelius *et al*. 1996). The acronym originally stood for "Neogene of the Old World", but the name was recently changed, as the database now encompasses the entire Eurasian post-Oligocene, ca. 25–0.01 Mya.

Another indispensable element has been solid theoretical and computational skills for modelling and statistics, which in Fortelius' case have been provided by collaboration with the computer scientist Heikki Mannila (now President of the Academy of Finland) and the physicist Kai Puolamäki (*see* e.g. Puolamäki *et al*. 2006).

Thirdly, the use of fossil teeth for environmental reconstruction would have been unthinkable without the solid mechanistic understanding of tooth function that Fortelius acquired at an early stage. Already before defending his doctoral thesis, he went to the lab of the enamel specialist Alan Boyde at University College London to work at EM resolution on the 3-D structure and wear of rhinoceros teeth (Boyde & Fortelius 1986). The authors managed to explain the profiles and wear resistance more or less completely on the basis of the decussation patterns of the enamel prisms as formed by the patterns of ameloblast streams during development. They went to impressive lengths to validate their conclusions by direct observation, studying development in preparations from fetal rhinoceroses, and wear by applying a whole battery of experimental abrasion and polishing procedures.

At this point of a possibly glorious career as an experimental biologist, Fortelius' activities took a different direction. Chance intervened and the prepared mind responded: at Boyde's lab, he happened to meet Lawrence B. Martin, a British Ph.D. student working on the enamel structure of hominid primates under Boyde's supervision. On behalf of his second supervisor Peter

Andrews from the Natural History Museum, Martin invited Fortelius to participate in excavations at the Miocene site Paşalar in western Anatolia (Turkey), and field work became an important part of his activities for many years. Several seasons in Turkey were followed by projects in Iran and China, also involving increasing administrative responsibilities. Besides the networking benefit, it may be assumed that working with international teams on fossil faunas at several sites across Eurasia catalyzed thinking in terms of communities, ecosystems and climate. For example, in a special issue of the *Journal of Human Evolution* about Paşalar, Peter Andrews writes: "the fossil assemblage approximates to a life assemblage accumulated over a short period of time and from a limited geographical area", albeit with some identifiable bias (Andrews & Ersoya 1990).

The public paleontologist

In the eyes of the Finnish public, the excavations also gave Fortelius the street credibility of a *real* paleontologist. He has found no hominins or dinosaurs himself but he knows the thrill, having been present at such discoveries. As a more recent spin-off, he has visited Turkana in northern Kenya — once again through the agency of Lawrence Martin, now leader of the Turkana Basin Institute. Currently, there are plans for an ambitious project to use the exceptionally well-resolved Turkana data in conjunction with coarser data for the entire African continent in order to understand better how changes at ecological and evolutionary time scales are related. Moreover, in Turkana, it is difficult not to reflect on the specific environment that allowed our kind of ape to evolve. Owen-Smith (2013) recently proposed that a precondition not present elsewhere were the African grasslands, dryish but nourishing thanks to volcanic nutrient supply, breeding a fauna of "grazers" of just the right (intermediate) prey size. In a critical examination of this scenario, Fortelius (2013) adds the suggestion that "… some of our more remote fossil relatives went for the grass (or sedge) directly, [while] our direct ancestors opted to harvest the same resource at a higher trophic level."

It is easy to discern a *Wahlverwandtschaft* between Fortelius and Kurtén in the holistic drive to reconstruct the entire living world of past periods. Differences are equally obvious, and can at least partly be related to the changes in the general scientific and technological environment. Kurtén's synthetic mode of expression was literary. The powerful tools for handling and analyzing enormous databases offered by the IT revolution has set new standards for scientific modelling and relegated literary syntheses further into the popular periphery. At one point in the early 1990s our mutual friend Jan-Henrik Kock, then science secretary at the European Science Foundation, explicitly encouraged Fortelius to embark on databases rather than write a planned book on the Miocene.

There may also be personal reasons for the change in focus. Obviously Fortelius' mentor was a hard act to follow on the literary arena. Although he himself has a lively imagination as well as a beautiful command of language both written and spoken, he did not, of course, write fiction as a schoolboy. When we met as students in the 1970s, his imagination was fired more by rock music and the Star Wars movies. Whatever the reasons, his "scenario" writing has been limited, although interesting, mainly exemplified by articles on human evolution (*see* above, Fortelius 2013, and also Fortelius 2009).

What has not changed at all from Kurtén to Fortelius is how paleontology as an academic discipline falls between all possible chairs. Kurtén got his first permanent position as professor extraordinary of paleontology at the University of Helsinki in 1972, when he had already prepared to move abroad for good. Fortelius has gone through a long sequence of temporary positions at the Department of Geology, the Finnish Museum of Natural History and the Academy of Finland, before finally getting tenure as full Professor of Evolutionary Paleontology at the Department of Geology in 2004.

Jukka Jernvall and tooth evo-devo

Fortelius' first (co-)supervised doctoral student was Jukka Jernvall (born in 1963): friend, associate and presently Academy Professor at the

Institute of Biotechnology of the University of Helsinki. Jernvall's research has sprung from the cross-fertilization of two long and distinguished research traditions, paleontology and developmental biology. The latter line came from co-supervisor Irma Thesleff, at the time Professor of Orthodontics doing cutting-edge (*sic*) research on tooth development. Her scientific pedigree goes back to the founders of Finnish developmental biology, Gunnar Ekman (1883–1937) and Sulo Toivonen (1909–1995), via her uncle Lauri Saxén (1927–2005). When Saxén was asked by his dentist niece, Thesleff (née Saxén), for advice on subjects for proper hard-core research, he encouraged her to do developmental biology on the organs she knew best, mouth and teeth. Thesleff's Ph.D. thesis (Saxén 1975) was about the etiology of cleft lip and palate, but from the 1980s she focussed on molecular mechanisms of tooth development and morphogenesis, which involve patterns of sequential and reciprocal signalling between cells and tissues representative of very general principles in organogenesis. Thesleff and Fortelius had met briefly already in 1986 at a workshop on tooth morphology, but collaboration materialized only through Jernvall.

Jernvall had been excited by a book about "Lucy", the 3.2 million-year-old hominid skeleton discovered in Ethiopia in 1974 and then hailed as "the Mother of Mankind" (Johanson & Edey 1981). As a young student looking for a subject, he contacted Eirik Granqvist at the Zoological Museum (*see* above), who directed him to Fortelius' lectures. This sowed the seeds of things to come. In 1987, Jernvall already participated in the excavations in Paşalar and met Lawrence Martin, who once again catalyzed Finnish science by inviting him to work at his university, SUNY at Stony Brook. One thing led to another — not least, Martin's colleague, primatologist Patricia C. Wright, became Jernvall's long-standing collaborator and first wife. He spent a total of eight years mainly at Stony Brook.

Before this, however, he had joined Irma Thesleff's group, having responded to a job announcement he happened to see on the notice board of the Department of Zoology. The task was to study the expression of the matrix glycoprotein tenascin in mouse tooth development. In Jernvall's hands, the study soon took a comparative turn, as he required species with teeth of different sizes and cusp patterns to unravel basic mechanisms of tooth morphogenesis. A major breakthrough was the (re)discovery of the enamel knot, now understood as a developmental control centre. The work evolved into the Ph.D. thesis "*Mammalian molar cusp patterns: Developmental mechanisms of diversity*" (Jernvall 1995), published as a monograph in *Acta Zoologica Fennica*, like those of Kurtén and Fortelius. Like theirs, it also has a motto worth citing, not least because the choice (in its contrast to Kurtén's paleofiction) illustrates the progressive carnivalization of science as a social enterprise in the late 20th century. It is taken from the Roy Lewis novel *The Evolution Man (Or How I Ate My Father)*, purportedly written by the son of the first man to discover the use of fire. Through this discovery, fuel has become a commodity of immense value, and the storyteller explains that "it was the elephants and mammoths who kept us warm with their thoughtful habit of tearing up trees to test the strength of their tusks and trunks. *Elephas antiquus* was even more given to this than is the modern type, for he was still hard at it evolving, *and there is nothing that an evolving animal worries about more than how his teeth are getting along*", the italicized part being Jernvall's motto.

Much of the joint work with Fortelius has been described above. Jernvall recalls how the most creative ideas arose during lunch table discussions, sometimes with John Hunter (Fulbright Exchange Fellow and co-author on some key papers) as the third party. While collaboration has continued, the centre of gravity in Jernvall's research has shifted outside the scope of the present article. He has recently been appointed Head of a Centre of Excellence in Experimental and Computational Developmental Biology (EC Dev) at the University of Helsinki, with former postdoctoral fellow Isaac Salazar-Ciudad from Barcelona as an important partner.

The Fortelian radiation

Jernvall's line of tooth evo-devo and morphometrics certainly represents the most novel recent ramification, but the heritage is diverse and dynamic also closer to paleontology/paleobiology in a more traditional sense. I should like to bring this account of the discipline up to the present by saying something about the activities of Fortelius' other former Ph.D. students, albeit this may be little more than "journalism with footnotes" (as historian Henrik Meinander has described some forms of contemporary history).

The thesis completed next to Jernvall's is a piece of classical paleobiology by Suvi Viranta, *European Miocene Amphicyonidae — taxonomy, systematics and ecology* (Viranta 1996). Viranta-Kovanen now works as a Docent at the University of Helsinki, lecturing to geoscientists about fossil mammals and teaching anatomy to medical students. In true Kurténian spirit, she has published several popular books and articles, mainly about carnivores.

Pirkko Ukkonen has carried on the tradition of Ice Age paleobiology. Her Ph.D. thesis is titled *Shaped by the Ice Age: reconstructing the history of mammals in Finland during the late Pleistocene and early Holocene* (Ukkonen 2001). She has continued on these lines with special emphasis on the occurrence of mammoths in the Baltic region. Her affiliations have included Lund University and the Natural History Museum in Helsinki, and she teaches as Docent of Paleobiology at the Department of Geosciences and Geography.

Liu Liping is a Chinese student recruited through Fortelius' excavations in China, where her dissertation on *Chinese fossil Suoidea: Systematics, Evolution, and Paleoecology* (Liu 2003) originated. She now works at the renowned Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences in Beijing, but spends part of her time in Stockholm with her husband. This facilitates continued collaboration with Fortelius, as well as another of Kurtén's disciples, Lars Werdelin in Stockholm.

The Chinese connection also forms the basis of Anu Kaakinen's *A long terrestrial sequence in Lantian – a window into the late Neogene palaeoenvironments of Northern China* (Kaakinen 2005). She now pursues a successful research career as Academy of Finland Research Fellow, with a wide collaborative network mainly focussed on China.

Jussi Eronen's thesis title, *Eurasian Neogene large herbivorous mammals and climate* (Eronen 2006), well describes his general research orientation. He has been deeply involved in the NOW network and is the person chiefly responsible for maintaining the database. As a postdoc with a grant from the University of Helsinki, he has been highly productive in research as well as active in teaching and supervision.

Another NOW product is Diana Pushkina's dissertation *Eurasian large mammal dynamics in response to changing environments during the Late Neogene* (Pushkina 2007). The author is now mainly doing riding, dancing and skating at near-professional levels, but she also goes on with research and academic teaching at a lower intensity.

The Iranian Ph.D. student Majid Mirzaie Ataabadi defended his thesis *The Miocene of Western Asia: fossil mammals at the crossroads of faunal provinces and climate regimes* in 2010 (Mirzaie Ataabadi 2010) and then went to do a postdoc in Beijing. This was interrupted when he had to return home for four years of civil service (*in lieu* of national military service). He now serves as a lecturer at a provincial university in Iran, where he has also had the opportunity to pursue paleontological projects. Collaboration with Fortelius may continue depending on political developments.

Most recently, in June 2013, a young Chinese student described as a "modelling wizard", Hui Tang, successfully defended his thesis *The spatio-temporal evolution of the Asian monsoon climate in the Late Miocene and its causes: A regional climate model study* (Tang 2013). He now works as a postdoc in Anu Kaakinen's project.

Besides these core activities, Fortelius has been associated with an interesting research program concerned with defining bone measures that can be correlated with the performance of different sensory modalities of mammals. This began when Sirpa Nummela as a student of Fortelius in the early 1990s asked him for a subject where she could combine her enthusiasm for bones and senses. He took her to his former zoology teacher, physiologist Tom Reuter, and this led to a series of studies on the function and scaling of middle ear bones and how they constrain hearing in land mammals. This venture, where biophysicist Simo Hemilä played a central role (Fortelius acting only as an essential catalyst at that stage), was enlarged to a ground-breaking analysis of whale hearing and how it evolved when these mammals returned to the sea [*see* Nummela's Ph.D. thesis (1999)]. The program was extended to the senses of olfaction and vision through Ph.D. student Henry Pihlström's work on the predictive value of, respectively, the cribriform plate and the orbit of land mammals (Pihlström 2012). In a recent article, the authors have sketched a cross-modality synthesis, introducing the novel concept of the "sensory space" of an animal (Nummela *et al*. 2013). As always with functional modelling based on bone measures, the work is motivated also by the possibility to reconstruct the performance of extinct species from fossil material.

Conclusion

Mikael Fortelius' personal reprint copy of an essay on Alexander von Nordmann published thirty years ago by historian Beatrice Moring, his wife at that time, bears her inscription "About the first to the fourth". Having since then added 100% to his age and immeasurably to his scientific *oeuvre*, Fortelius can rightfully claim this position in the lineage of von Nordmann, Korvenkontio and Kurtén. In his work, paleontology by far transcends mere fossil systematics – as it did in the hands of Darwin, Simpson and Kurtén. The science "which treats of the life that has existed on the globe during former geological periods" (von Zittel 1895) reaffirms its role as part of the great multidisciplinary enterprise towards understanding Life on Earth in general and the Human Condition in particular.

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