Tracing transitions : an overview of the evolution and migrations of the genus Mammuthus BROOKES, 1828 (Mammalia, Proboscidea)

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The above compilation of papers discusses aspects of a comparatively large part of the evolutionary history of mammoths (genus *Mammuthus* BROOKES, 1828), which started in Africa between 7.0 and 6.0 Ma, perhaps even earlier, and ended only a few thousand years ago in the far northeast of Siberia. The earlier part of this time span is summarily treated in the Introduction, that presents mammoths as the outcome of a still not entirely unravelled process of diversification of the earliest elephants during the late Miocene and the early Pliocene. The later part is discussed in the papers, which almost exclusively deal with Eurasian (Palaearctic) mammoths and cover nearly three million years of their evolution. Since the mammoth lineage has become extinct, the living African and Indian species are all that remains of the subfamily Elephantinae, as well as of the order Proboscidea as a whole. Although threatened by extinction, they still represent two thirds of the main lineages with respect to Elephantinae, but with respect to Proboscidea only a deplorable remnant of a glorious past.

The first paper in the series treats the earliest mammoth in Europe, the Pliocene *M. rumanus* (ŞTEFĂNESCU, 1924) from the Dacic Basin, Romania (between 3.5 and 3.0 Ma). The series ends with a survey of late Early to early Middle Pleistocene stocks of *M. meridionalis* (NESTI, 1825) and their replacement by the steppe mammoth, *M. trogontherii* (POHLIG, 1885), a process that was completed when *M. meridionalis* became extinct, before or around 0.7 Ma.

Within any context, but especially within the Eurasian one, *M. rumanus* may count as a dentally very primitive species. Although in part dated to a later age, molar samples of comparable primitivity from other European regions were - tentatively or with confidence - referred to this taxon, viz., those from the Red Crag Formation (eastern England), Montopoli and Laiatico (Lower Valdarno, Central Italy), and Bossilkovtsi (Bulgaria). In particular the complete M^3 from Cernăteşti (Romania) with its eight true lamellae displays a primitivity that can only bring to mind African taxa such as *M. subplanifrons* (OSBORN, 1928), mentioned in the Introduction. Primitive molar specimens referred to *M. rumanus* were also reported from northeastern China - c. 8000 km further to the East - and preliminarily dated to the time span 3.4-2.8 Ma. A find from the Baikal region was considered to be of similar age, but referred to *Archidiskodon* sp. For the time being this enumeration exhausts the list of occurrences of very early Eurasian mammoths, so that far-reaching conclusions on this group are not yet possible. Since this earliest evidence appears to date back to about the same late Pliocene times, the colonization of Eurasia may have been a more or less continuous process, but its rate remains unknown and its routes to the Pacific have yet to become apparent from future sites and data. It is also obvious that the amount of morphological information obtained from the small samples now available is still at a basal level: the greater part of the dentition is not represented yet, and range widths may be surmised, but not yet observed. Similarly, nothing in particular is known about the earliest northward migration of mammoths from northeastern Africa, before their dispersal across Eurasia: all theoretical outlines have yet to be corroborated by data.

Equally unknown are the details of the evolution of *M. rumanus* into its successor, the at least dentally more advanced *M. meridionalis*, which taxon here includes *M. gromovi* (ALEKSEEVA & GARUTT, 1965). The southern mammoth is known mainly from Early Pleistocene sites, some of which are as far apart geographically as those that yielded *M. rumanus*, but its representatives were found in greater numbers. However, there is no material yet that documents the very speciation of *M. meridionalis*, a situation that is fully analogous with that regarding the speciation of *M. trogontherii*, because the earliest molars referable to this taxon indicate that speciation had already been completed at an earlier stage. In both cases the model of punctuated equilibrium may be applicable, because it implies a reduced chance to find evidence of such relatively short and regional intermezzos as speciation processes. Many questions therefore still remain: whether the evolution of *M. meridionalis* was comparatively fast or gradual after all, whether it first took place in eastern Asia, in Europe, or in between, and whether *meridionalis* morphology accordingly spread in westerly or in easterly direction, or in both directions. One could also ask oneself if it could have arisen more or less simultaneously in eastern and western Eurasia, and if there were two or more groups of meridionaloid mammoths, now united under the name *M. meridionalis*. By analogy there may be more than one way to interpret the North-African taxon *M. africanavus* (ARAMBOURG, 1952): does it represent a separate evolutionary branch from a presumably East-African population of *M. subplanifrons*, and was it 'cornered' in the area west of Chad and Libya only to become extinct? Was it perhaps the ancestor of the North-African mammoths referred to *M. meridionalis*, or do these in fact represent a link in the Eurasian chain?

The East-West scenario is now advocated by Wei *et al.* (2010), who see the entire Eurasian evolution of *Mammuthus* as driven by recurrent major climatic changes in the far reaches of the continent. Morphologically evolved mammoths seem to have occurred here sooner than anywhere else, and hence to have spread westward, replacing the more primitive ancestral forms on the way. Within this context the evolution of *M. rumanus* into *M. meridionalis* was the first instance of a pattern that was later repeated in the transition from *M. meridionalis* to *M. trogontherii*, and lastly from *M. trogontherii* to *M. primigenius* (BLUMENBACH, 1799). Although this model is attractive because of its parsimony and the so far earlier dates for *M. meridionalis* from northeastern China and the Khapry Faunal Complex, it does not explain why there were only three 'speciation events' in *Mammuthus* since *M. rumanus*, while several more glacial stages occurred within the same time range. Neither does it explain why the first speciation only led to an increase in plate number, but not to one in hypsodonty index. The second speciation, the one that produced *M. trogontherii*, was characterized by a marked increase in hypsodonty index as well as by an increase in plate number. The first of these changes led to mutually exclusive HI ranges for M^3, and the second almost did the same for the P values, were it not that mosaic specimens referred to *M. trogontherii* caused the modest overlap range 14-15. Morphologically the second speciation may be regarded as the biggest evolutionary step of the three, because in the final speciation, from *M. trogontherii* to *M. primigenius*, there was a further increase in hypsodonty index and plate number, but overlap was extensive. Although the average size of its individuals dropped, *M. primigenius* therefore much resembles *M. trogontherii* in its molars, especially when these happen to be big.

In essence the causes of the said variability in evolutionary change may have been stepped responses to the relative severity of the cold stages involved, as suggested in Part I, Section 3.2.2. Perhaps the (in-) availability of refugia also played a role, but for the time being these explanations must remain speculative.

All in all, the transitional stages (or punctuations) in the North-African / Eurasian mammoth lineage are still not or only partially known, but the situation regarding the parts that could represent the equilibrium phases is different. It was shown that the European *M. meridionalis* in its dental morphology remains a very recognizable species. Apart from some increase in individual size, little or no evolutionary change occurred throughout the Early Pleistocene and up to its extinction in the early Middle Pleistocene. Just a few stations along this time line are Khapry (c. 2.6-2.2 Ma), the Upper Valdarno (c. 2.0-1.9 Ma), Pietrafitta (c. 1.5 Ma), Saint-Prest (c. 1.0 Ma), Dorn-Dürkheim 3 (c. 0.8 Ma), and the Goldshöfe Sands (c. 0.8-?0.7 Ma). In retrospect, the historical subdivision of *M. meridionalis* into a number of subspecies is therefore of very limited practical use: these taxa - if still acknowledged as representing *M. meridionalis* - can hardly be separated on morphological grounds, especially when samples are small or comprise many fragmentary specimens. Larger samples are necessary for possible shifts in hypsodonty index and plate number to become visible, and even then these shifts may be statistically insignificant. This circumstance very much limits the possibilities of an accurate determination of the time level indicated by molars of *M. meridionalis*. In the fauna list of Dmanisi (Georgia), for example, the typical form of *M. meridionalis* together with *Pliocrocuta perrieri*, *Eucladoceros* aff. *tegulensis*, and other taxa was counted among the more primitive species that suggest a date near the transition from Middle to Late Villafranchian (Lordkipanidze *et al.*, 2007: Supplementary information, S2). In view of the above, however, it might as well have been listed as one of the more modern forms that would support a somewhat later age.

On the other hand, the morphological stability of the late Early to early Middle Pleistocene *M. meridionalis* functions as a steady background against which some contemporaneous elements of a rather incongruous nature stand out. Of the differences that exist between molars of *M. meridionalis* and its direct descendant, *M. trogontherii*, the hypsodonty index of the crown is of foremost importance and in diagrams leads to a clear separation of clusters. With regard to this character, more or less complete and relatively unworn dental remains of European mammoths from various time levels between 1.0 and 0.6 Ma are therefore morphologically separable with relative ease. The speciation of *M. trogontherii* apparently took place in northeastern Asia before or around 1.7 Ma, so that its advanced morphology entered Europe from the East, long after the species had actually come into existence. This can explain the gap between the hypsodonty index clusters of *M. meridionalis* and *M. trogontherii*. At the same time there is no evidence of any analogous European development within *M. meridionalis* that went further than the morphological level of Saint-Prest and Dorn-Dürkheim 3. This situation allowed the verdict that the subspecies *M. m. voigtstedtensis* (DIETRICH, 1958) does not exist: the dental material from Voigtstedt (c. 0.7 Ma), upon which this subspecies was based, in fact belongs to a comparatively primitive form of *M. trogontherii* that is dentally similar to the earliest representatives of this species in northeastern China, as well as to the 'primitive' part of the Süssenborn sample from Germany (c. 0.6 Ma). The same relatively primitive steppe mammoth now turns out to have been present at Üröm, Hungary, where it gave rise to another new subspecies of *M. meridionalis* in 1979. Although the Voigtstedt sample is not large, the absence of *M. meridionalis* at this site renders its persistence in Europe until c. 0.7 Ma less likely. Still the species' extinction before 0.7 Ma cannot be declared certain as long as its presence at the about contemporaneous site of West Runton (Cromer Forest-bed Formation, England) is still discussed. Reaching a decision in this matter is difficult because some of the material so far recovered from West Runton - although possibly referable to *M. meridionalis* - does not allow an unequivocal determination of relative crown height. It might therefore belong to the category of high-crowned mosaic molars rather than to the low-crowned *M. meridionalis*. An M^3 that certainly belongs to *M. meridionalis* is of uncertain stratigraphic origin (Lister and Stuart 2010: 203/204, 207 fig. 28de).

The so-called mosaic specimens - also present at Voigtstedt - are remarkable for their 'angular' combinations of meridionaloid and trogontherioid characteristics, which do not convince as the results of anagenetic evolution. These forms are here interpreted as the result of interbreeding between *M. meridionalis* and *M. trogontherii* and formally referred to *M. trogontherii* (*M. trogontherii* [POHLIG, 1885] x M. *meridionalis* [NESTI, 1825]). Even if Art. 23.8 of the ICZN should not be applicable, a transfer of the subspecific name *voigtstedtensis* from *M. meridionalis* to *M. trogontherii* is declined because of the partial morphological overlap between the samples from Voigtstedt and Süssenborn: material hypothetically referred to **M. trogontherii voigtstedtensis* would be indistinguishable from the relatively primitive specimens within samples traditionally referred to *M. trogontherii trogontherii* and would force an awkward division of the samples from Süssenborn and other sites at the subspecific level. It would also inappropriately confer a subspecific name of European geographical derivation upon the ancestral Chinese specimens, which would be an anachronism as well. Referral to the species *sensu lato* is therefore preferred.

Other subspecies of *M. meridionalis* that used to be called 'advanced' have already been doubted by other researchers or do not appear to have been erected on a firm footing:

- *M. m. vestinus* (AZZAROLI, 1972), Italian successor of the typical form, is now considered to differ very marginally from its direct ancestor in its dental characteristics, whereas evolutionary change is no longer regarded as the sole cause of cranial morphological differences observed between these taxa. In fact *M. m. vestinus* has therefore turned into a *nomen dubium*;
- *M. m. cromerensis* (DEPÉRET & MAYET, 1923), meant to characterize advanced southern mammoths from the supposedly rather late Cromer Forest-bed Formation in eastern England, was in part founded on specimens which are neither late nor advanced, and also on molars that belong to *M. trogontherii*. *M. m. cromerensis* was already declared a *nomen dubium* and should finally be rejected;
- *M. m. jockgrimensis* (DIETRICH, 1958) from SW Germany, conceived as the continental counterpart of *M. m. cromerensis*, has been in disuse for several decades now. The dental sample is stratigraphically composite and like that of *M. m. cromerensis* it comprises specimens referable to *M. meridionalis* and (sometimes even primigenioid) *M. trogontherii*, while the *M. meridionalis* part again cannot be shown to be either particularly advanced or contemporaneous with the steppe mammoth fossils. Nor were the latter all of the same age. Hence the taxon *M. m. jockgrimensis* should finally be rejected;
- *M. m. uromensis* (VÖRÖS, 1979) from Hungary is likewise in disuse, but its author rightly considered the holotype of this taxon to be very similar to specimens from Voigtstedt. The holotype (from Üröm near Budapest) is here accordingly considered as representing *M. trogontherii*. The taxon *M. m. uromensis* should be rejected;
- Pending the detailed comparison between dental remains of the typical form and *M. m. tamanensis* (DUBROVO, 1964), and also between the latter and *M. m. depereti* (COPPENS & BEDEN, 1982), it should be emphasized anew that *M. m. depereti* in most respects does not statistically differ from the typical form, but for its slightly higher average plate number in M^3. Given the size of the sample measured, this outcome is not necessarily final.

In summary: during the by far largest part of the Early Pleistocene, the only elephantine that inhabited Europe was the dentally hardly variable species *M. meridionalis*, the subdivision of which into subspecific units has inevitably failed to produce a workable set of distinctive morphological features that would enable one to accurately determine future finds according to taxon and age. Replacing the morphological argument by a characterization based on stratigraphical detail, palaeomagnetic data, palaeobiogeography, and accompanying fauna and flora would be inaccurate because this would not describe any biological or osteometric properties of the animals that would justify subspecific status. Generally speaking it is not the mere passing of time that leads to the evolution of subspecies, but a certain amount of inescapable environmental change.

The arrival of individuals or genes of *M. trogontherii* in Europe around 1.0 Ma introduced molars of a clearly different build - i.e., evolutionary level - and both species coexisted for some time until *M. meridionalis* finally became extinct in Europe as well. The nature of this coexistence is not known in any detail: so far the term has expressed contemporaneity in a wider sense because stratigraphical resolution is not so high that time averaging can be excluded where the presence of the two species may in fact have alternated in a certain rhythm. However, the presence of *M. trogontherii* at cold-stage sites such as Edersleben and Beeston, as well as at the temperate-stage sites of Dorst, West Runton, Voigtstedt, and Süssenborn suggests that correlations between climatic stages and the widths of ecological tolerance ranges in mammoths should not be oversimplified.

Further research in the fields of microwear analysis and stable isotope analysis is necessary especially to establish the relation between advanced and mosaic molars of the transitional episode between 1.0 and 0.6 Ma and the type of food they processed: is there a one-sided and stable relation between high crowns and grass-dominated diets, and if so, does this reduce the probability of *M. meridionalis* and *M. trogontherii* actually coexisting in one or more habitat types? While such questions for the time being remain unanswered, the occurrence of mosaic forms suggests that there were indeed occasions on which representatives of the two species met and crossbred. Where and when this could have happened is unclear: one could speculate that *M. meridionalis* and *M. trogontherii* from time to time or continually shared a certain European habitat, a contact zone where they produced fertile or infertile hybrids. Alternatively, the production of fertile hybrids occurred somewhere else, perhaps outside Europe, and at an earlier stage, but introduced a genetic instability that was regularly expressed in a variety of mosaic forms, possibly even after *M. meridionalis* had become extinct. At any rate, further selection apparently kept removing the meridionaloid detail from the dental variability ranges until the genetic disturbance had all but disappeared. From a certain time onward, probably since c. 0.8 Ma, *M. trogontherii* molars through selection developed characteristics that could be called primigenioid: hypsodonty indices above 200, plate numbers from 20 to 22, and enamel thickness values at or scarcely above 2.0 mm. Such values had already become fairly common at the time of Süssenborn (c. 0.6 Ma). With respect to enamel thickness this may have amounted to a restoration of ancestral values because 2.0 mm was recorded for one of the earliest Chinese representatives of the species. There are no indications yet that hybridization between *M. meridionalis* and *M. trogontherii* already took place in Early Pleistocene China, which might be explained by the regional eastern Asian extinction of the former around 1.8 Ma.

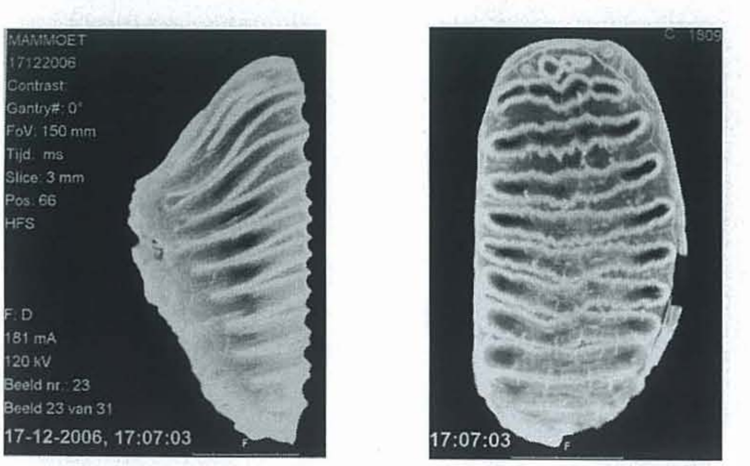
Evolutionary trends in *M. trogontherii* after Süssenborn and the problem of discerning between the last steppe mammoths and *M. primigenius* are well worth looking into, but are beyond the scope of the present volume.

Overlooking the field of evolutionary change in the Eurasian part of the mammoth lineage, one has to conclude that the amount of information obtained is far from being constant with respect to each stage. More data on *M. rumanus*, the various speciation processes, and especially also on the transitional episode that saw the decline and extinction of *M. meridionalis* in Europe would be more than welcome. As suggested above, a more active approach than waiting for the next chance recoveries could consist in a targeted series of microwear analyses, complemented by analyses of ratios between the proportions of various stable (i.e., non-radioactive) isotopes. Within the sphere of the biological sciences this mostly concerns elements such as carbon (C), nitrogen (N), and Oxygen (O). Fossil molar enamel, for instance, recorded the isotopic composition of the food matter it regularly came into contact with. Stable-isotope analysis is a technique that seems on its way to become an important tool with a chronologically wide applicability range (at least from the latest Miocene until today). In Africa, for example, proboscidean enamel may reveal which groups of plants were eaten because there are some basic differences in the ways in which the so-called C_3 and C_4 plants handle carbon dioxide in their photosynthesis, i. e., in their conversion of light energy to chemical energy. After the so-called light-dependent reactions through which pigments absorb the energy of the light, the second stage of photosynthesis - the light-independent reactions - can go two ways: the three-carbon (C_3) pathway or Calvin Cycle, or the four-carbon (C_4) or Hatch-Slack Pathway (Raven *et al.* 1992: 103ff), through which carbon is fixed in various compounds. The biochemical differences between C_3 and C_4 plants allow the distinction between molar enamel that belonged to animals whose staple diet was dominated by either type, which could provide a check on microwear analysis. Although there are still problems - such as the presumably different ways in which tropical grasses before the latest Miocene used carbon dioxide, the inconstancy of ratio values between different ecosystems, and the fluctuations in the isotopic composition of the atmosphere (Cerling *et al.* 2010) - the technique in principle and in practice allows statements on the composition of diets of recent and fossil animals.

Furthermore, the application of molecular techniques such as DNA sequencing remains promising. As remarked in Part I of this volume, it has already proved possible to identify the last populations of *M. primigenius* in northeastern Siberia as immigrants from North America (Debruyne *et al.* 2008), and one may wonder whether this result could ever have been reached by morphological analysis alone, or even be corroborated by it. Bridging greater distances in time will possibly increase the number of interpretations to choose from, because there may be more than one stage of evolutionary change that could be correlatable with the molecular results. It was, for instance, also discovered that Siberian woolly mammoths from the first half of the Last Glacial can be subdivided into two clades on the basis of mtDNA from hair shafts (Gilbert *et al.* 2007, 2008). This allowed the conclusion that the clades diverged between two and one million years ago, and that one of them disappeared earlier than the other. The existence of the two different mitochondrial genomes was believed to be interpretable either as evidence of two sympatric species that became extinct at different times, or as variation within a single species after an early maternal lineage split, in which case the shorter-lived clade would have disappeared because of genetic drift. The observation has so far not been linked with any subtle morphological differences between the two clades of Siberian woolly mammoths, and in fact physiological disparities that could have led to a selective advantage for the longer-lived clade were not expected. Yet it was not ruled out that some differences would be found later. Given this constellation of possibilities it would be very difficult indeed to determine exactly which known evolutionary change between 2.0 and 1.0 Ma could be correlatable with the clade divergence found. The split may even relate to an event hitherto not detected via the traditional methods used in the analysis of the fossil record. In spite of such difficulties, it is to be expected that molecular analysis will continue to alter many traditional concepts and allow fresh views on the complexity of evolutionary and populational processes.

Last but not least, morphological research - the age-old technique that still plays an important role in the palaeontological community's taxonomical endeavours - could much benefit from the non-destructive possibilities provided by the latest generation of CT scanners, for which even fully mineralised molars do not pose a problem (see images below). Detailed three-dimensional interiors of type specimens and other important and hitherto 'untouchable' fossils are now within reach and in some cases might lead to radical reinterpretations.

The above-mentioned techniques can be applied to existing collections of material, the sheer number and size of which will constitute a challenge to future generations of researchers and should warrant some unexpected results. In addition to this it is to be expected that further development of research methods in concert with the evolution of technical equipment during the 21st century will continue to enlarge our knowledge of fossil elephants, of palaeoecology, and, in a still wider sense, of life itself.



M. meridionalis, two CT scans from a series made of a near-complete M^2 sin. from the southern bight of the North Sea (arc 122; the right image is a horizontal section in dorsal view). The molar is heavily mineralized and an equivalent of the Pre-Pastonian specimens from the East Anglian coast, England (c. 1.9 Ma). Courtesy of Rijnstate Hospital, Arnhem, with special thanks to F. Wortel.

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Appendices

Map 1 - Africa and the Mediterranean Sea

SOUTH AFRICA
1 - Langebaanweg; 2 - Sydney-on-Vaal

KENYA
3- Lemudong'o; 4 - Lukeino (Tugen Hills); 5 - Lothagam/Nawata

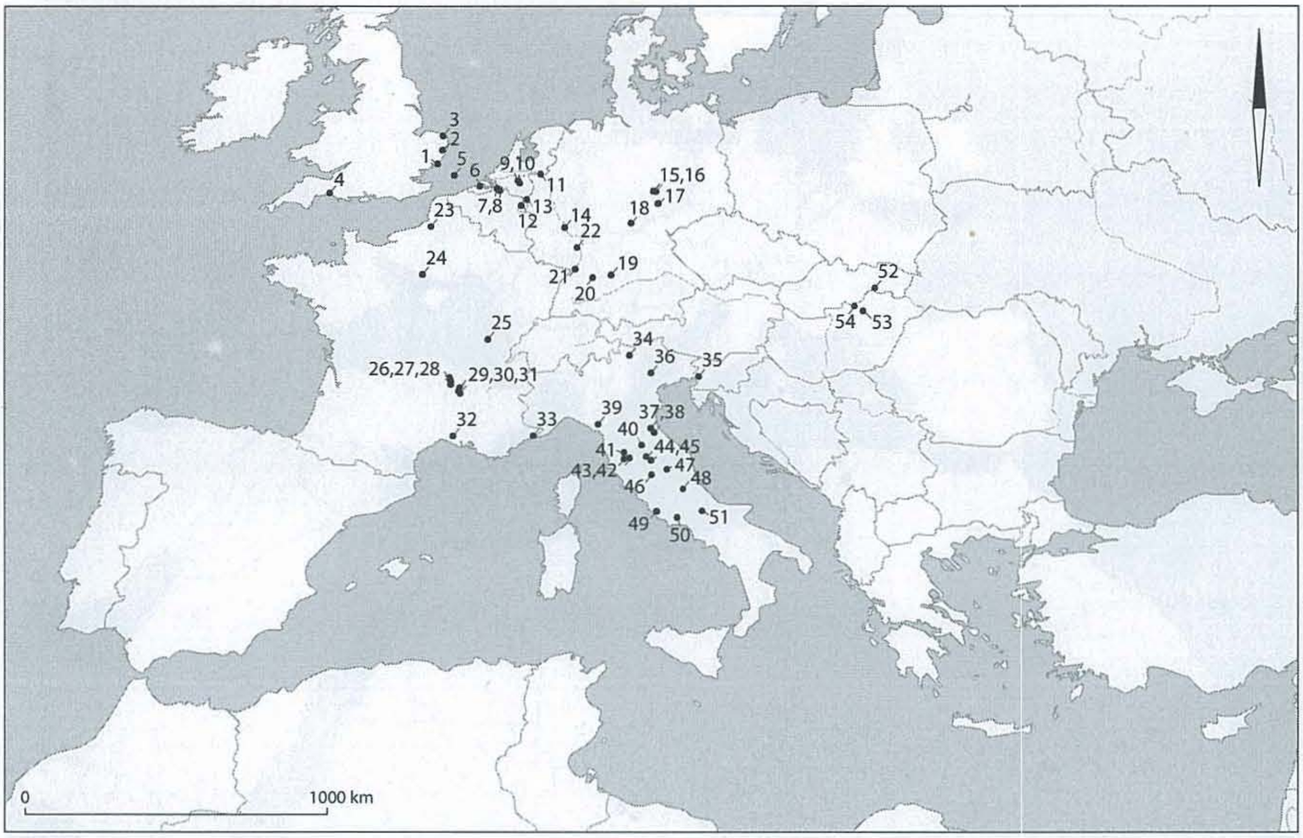
CHAD
6 - Kollé

TUNISIA
7 - Ichkeul; 8 - Aïn Brimba

ALGERIA
9 - Aïn Hanech; 10 - La Garet et Tir

MEDITERRANEAN
11- Malta; 12 - Sicily; 13 - Sardinia; 14 - Crete; 15 - Tilos; 16 - Cyprus

Map 2 - Western and Central Europe



ENGLAND
1 - Red Crag Formation; 2 - Norwich Crag Formation; 3 - Cromer Forest-bed Formation (a. o.: Beeston; W. Runton; Bacton; Corton; Kessingland); 4 - Dewlish

NORTH SEA
5 - Southern Bight

NETHERLANDS
6 - Eastern Scheldt; 7 - Dorst; 8 -Oosterhout; 9 - Deest; 10 - Groot Linden; 11 - Giesbeek; 12 - Wessem; 13 - Tegelen

GERMANY
14 - Kärlich; 15 -Edersleben; 16 - Voigtstedt; - Wendelstein (between 16 and 17, not plotted); 17 - Süssenborn; 18 - Untermassfeld; 19 - Goldshöfe Sands (Aalen); 20 - Stuttgart-Rosenstein; 21 - Jockgrim/Wörth am Rhein; 22 - Dorn-Dürkheim

FRANCE 23 - Abbeville; 24 - Saint-Prest; 25 - Bellecroix-Chagny; 26 - Malbattu; 27 - Senèze; 28 - Chilhac; 29 - Solilhac/Communac; 30 - Ceyssaguet; 31 - La Malouteyre; 32 - Durfort; 33 - Vallonet

ITALY (MAINLAND)
34 - Leffe; 35 - Slivia; 36 - Soave (Monte Tenda); 37 - Rio Pradella (Imola); 38 - La Salita di Oriolo; 39 - Olivola; 40 - Mugello Basin; 41 - Lower Valdarno (Montopoli; Laiatico; Le Strette near Péccioli); 42 - (St. Andrea in) Percussina (S. Casciano in Val di Pesa); 43 - San Giminiano; 44 - Upper Valdarno (Poggio Rosso; Matassino; Montevarchi; Tasso); 45 - Farneta; 46 - Pietrafitta; 47 - Colle Curti; 48 - Scoppito (L'Aquila); 49 - Roma (Monte Spaccato; Campo di Merlo); 50 - Campo del Conte (Frosinone); 51 - Isernia la Pineta

SLOVAKIA
52 - Gombasek (Hungarian: Gombaszög)

HUNGARY
53 - Üröm; 54 - Szomód-Csúcsoshegy

Map 3 - The Black Sea area

MOLDOVA
1 - Tiraspol

ROMANIA
2 - Tuluceşti; 3 - Cernăteşti; 4 - Orodelu, Dolj;
5 - Tetoiu; 6 - Slatina; 7 - Roşiorii de Vede

BULGARIA
8 - Bossilkovtsi; 9 - Russe

ARMENIA
10

GEORGIA
11 - Dmanisi; 12 - Taribana

RUSSIA & UKRAINE
13 - Georgievsk; 14 - Psekups; 15 - Saratovskaya;
16 - Bakinskaya; 17 - Taman' Peninsula (Sinyaya
Balka, a.o.); 18 - Nogaisk (Ukraine);
19 - Liventsovka; 20 - Khapry

Map 4 - Easternmost Europe and Asia

EASTERNMOST EUROPE
1 - Kvarkeno

ISRAEL
2 - Bethlehem

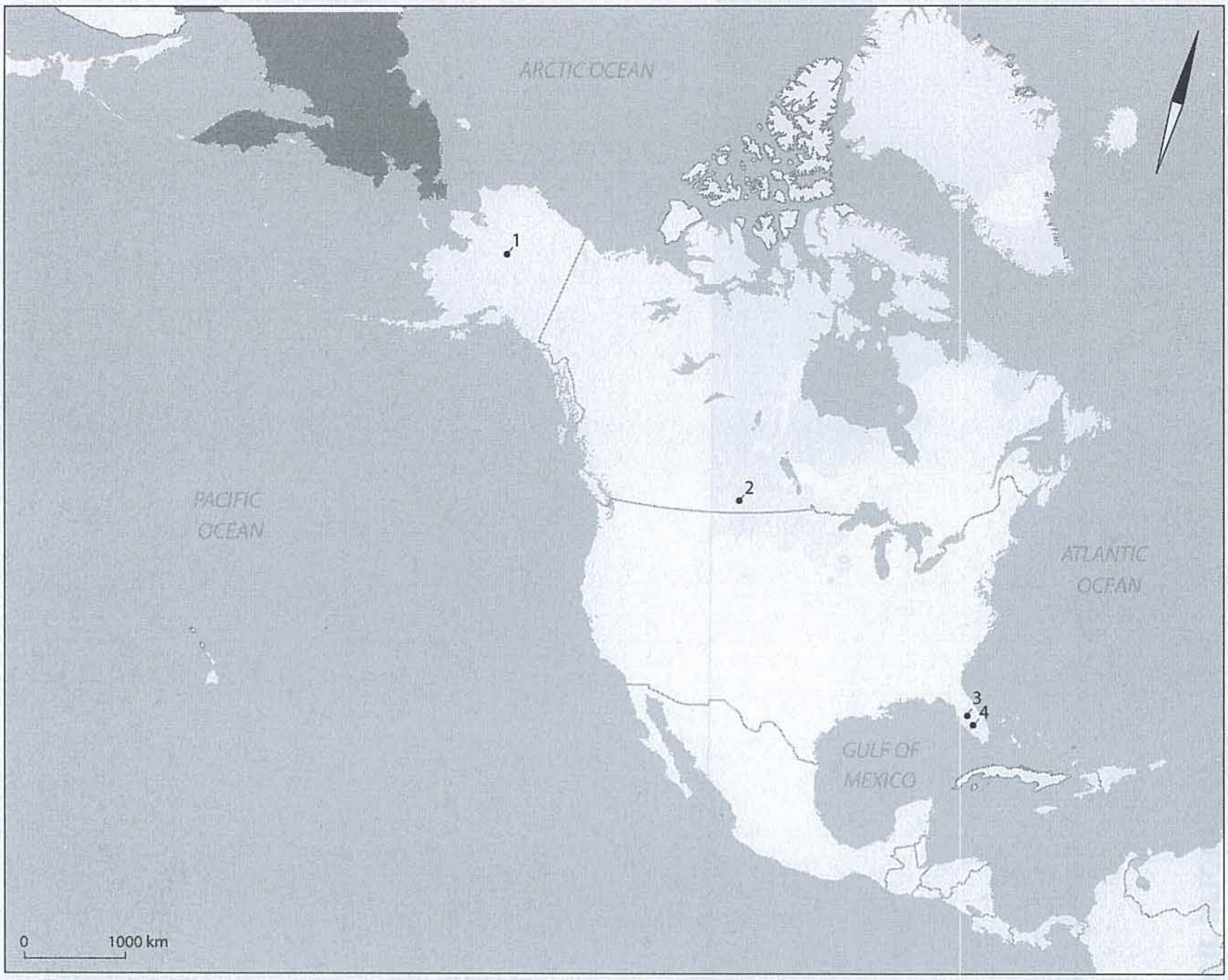
KAZACHSTAN
3 - River Ishim; 4 - River Irtysh (on both sides of the northern border); 5 - Podpusk; 6 - Ust'Talovka

ASIAN PART OF RUSSIAN FEDERATION
7 - Kuznetsk Basin (Mokhovo, Bachatsk, a.o.); 8 - Udunga (Transbaikalia, Buryatia);
9 - Viluisk (East Central Siberia, Sakha); 10 - Olyor (Sakha); 11 - Chukotka / 'Beringia'

INDIA
12 - Siwalik Hills, the southern foothills of the Himalayas. As originally indicated by Falconer (1868: Vol. I, Plate 2), they stretch from point 12 (on the Indus at c. 72.5° E) to the River Gandak at 84° E, c. 1200 km in southeastward direction)

CHINA
13 - Weinan (Shaanxi); 14 - Pinglu (Shanxi); 15 - Qinxian (Shanxi); 16 - Liyucun (Shanxi);
17 - Majuangou (Hebei)

Map 5 - North America



CANADA
2 - Wellsch Valley (Saskatchewan, Canada);

USA
1 - Alaska / 'Beringia'; 3 - Leisey Shell Pit (Hillsborough County, Florida); 4 - Punta Gorda (Florida)

Map 6 - Early Eurasian hominins (and/or their artefacts)

ENGLAND
1 - Happisburgh; 2 - Pakefield

ITALY
3 - Pirro Nord (Gargano Peninsula)

SPAIN
4 - Sierra de Atapuerca (incl. Sima del Elefante);
5 -Barranco León; 6 - Fuente Nueva

GEORGIA
7 - Dmanisi

ISRAEL
8 - Ubeidiya

PAKISTAN
9 - Riwat

CHINA
10 - Majuangou

Appendix III Abbreviations (in texts and appendices)

AEY - African Equivalent Years
App - Appendix / Appendices
appr(ox) - appoximate(ly)
arc - author's reference collection
c - circa, approximately
CF-bF - Cromer Forest-bed Formation (East Anglia, England)
CIS - Commonwealth of Independent States (Russian Federation)
coll - collection
DD 3 - Dorn-Dürkheim 3 (Germany)
Dt - Dorst (the Netherlands)
Edl - Edersleben (Germany)
e g - *exempli gratia* (for example)
FAD - first appearance date
FSFM - Forschungsinstitut Senckenberg, Frankfurt am Main
FSFQ(W) - Forschungsinstitut Senckenberg, Forschungsstelle für Quartärpaläontologie, Weimar
FU - Faunal Unit
GB - Great Britain
GIN - Geological Institute of the Russian Academy of Sciences, Moscow
GPIAU - Geological and Palaeontological Institute of Athens University
GPIUH - Geologisches und Paläontologisches Institut der Universität Heidelberg
GS - Goldshöfe Sands (Germany)
Hfs - Hauptfundschicht: main fossiliferous layer
HNHM - Hungarian Natural History Museum, Budapest
hypoth - hypothetical
ibid - *ibidem* (at the same place, in the publication last mentioned)
i e - *id est* (that is, which means)
IGF - Museo di Geologia e Paleontologia dell'Università degli Studi di Firenze
IGR - National Museum of Natural History, Bucharest
in litt - *in litteris* (in a written message)
ISER - Speleological Institute 'Emil Racoviţă', Bucharest, Romania
IUGS/ICS - International Union of Geological Sciences / International Commission on Stratigraphy
K - Kärlich (Germany)
ka - *kilo-annum* (accusative): 1 000 years (as a date before present)
KNM - Kenya National Museum
kyr - 1 000 years (as a time span)
l / lat - lateral
Ma - *mega-annum* (accusative): 1 000 000 years (as a date before present)
mand - mandible / mandibular
MAT - mean annual temperature
MCI (Sc) - Musei Civici di Imola (collezione Scarabelli)
MCSNM - Museo Civico di Storia Naturale di Milano
MEPP - Museum of the ENEL Power Plant at Pietrafitta (Perugia)
MEW - Museum of the Earth, Polish Academy of Sciences, Warszawa
mmts - measurements
MNHN - Muséum National d'Histoire Naturelle, Paris
MPM - Museo Paleontologico di Montevarchi (L'Accademia Valdarnese del Poggio di Montevarchi)
Msnp(C) - Muséum des sciences naturelles et de préhistoire, Chartres
myr - 1 000 000 years (as a time span)
NAT - Naturalis, Leiden
NCM - Norwich Castle Museum (Norwich, Norfolk, England)
n - number of specimens
NBM - Noordbrabants Museum, 's-Hertogenbosch
n m - not measured / not measurable
NMB - Naturhistorisches Museum, Basel
no - number

Ot - Oosterhout (the Netherlands)
par - paragraph
pers obs - personal observation
pp - *pro parte* (in part)
prob - probably
resp - respectively
RP - Rio Pradella (Italy)
SA - South Africa
SAM - South African Museum
SB/Sb - Süssenborn (Germany)
SP - Saint-Prest (France)
SMNS - Staatliches Museum für Naturkunde, Stuttgart
SMNK - Staatliches Museum für Naturkunde, Karlsruhe
SMS - Spengler Museum, Sangerhausen
s s - *sensu stricto* (in the narrow sense)
stat - statistics
SR - Stuttgart-Rosenstein (Germany)
umd - unspecialized mammalian dentition
Umf - Untermassfeld (Germany)
UMT - Universitätsmuseum Tübingen
viz - *videlicet* (namely, that is to say, to wit)
VM - Vicchio di Mugello (Italy)
Voi - Voigtstedt (Germany)
WCK - Würges collection, Kärlich
ZIN - Zoological Institute of the Russian Academy of Sciences, St. Petersburg

Morphology-related symbols and abbreviations (in texts and appendices)

∞ - dentine platform; worn root dentine beyond furthest rootward extent of enamel sheaths (in crowns that show advanced wear)
~ - less secure value approximation because of damage or sediment cover; result in [square brackets].
+/(+) - the measured value is not /(possibly not) the true maximum
-/(-) - the measured value is higher/(possibly higher) than the crown value (e.g., LF values found in molar fragments)
\- - in plate formulae: part of the molar was lost through breakage
- not measured
$\frac{1}{2}$ - plate vertically/medio-laterally split through dentine core (e.g.,- $\frac{1}{2}$ 3 $\frac{1}{2}$-)
1/2 - laterally inserted half plate (e.g., ∞ 8 1/2 4 p); not counted when single or counted as one lamella per pair
8 etc. - 8th etc. lamella counted from the front in any anteriorly complete molar
VIII etc. - 8th etc. lamella counted from the rear in any posteriorly complete molar
[8] etc. - 8th etc. lamella counted from the front in a both anteriorly and posteriorly incomplete molar
(-$\frac{1}{2}$ / $\frac{1}{2}$-here counts as the first and/or last lamella of the fragment)
α - (statistics:) the probability that the null hypothesis is unduly rejected
φ - eruption angle (between plane of occlusal surface and base of the crown as measured along the lateral basal enamel extremes of the lamellae)
A - the angle A (between plane of occlusal surface and apical outline of the unworn lamellae in a crown in early wear)
ann - annular (ring-shaped; description of round wear figure on a single digitation)
all pr - all present
a-m/ant-med - antero-medially
ant - anterior(ly)
C - complete
C - *caninus* (canine)
cf - *confer* (compare)
cc - cover cement
CR - complete remains
crown (App) - crown value (quotient of maximal values, usually at different lamellae)

d - dex(t)./dexter, right
DI - Divergence Index (ratio apical LF : basal LF)
el grp - element group
ET - enamel thickness
F - fragment
F - *F* value/Fisher's value (quotient of sample variances)
FCR - fragment of complete remains
H - height
HI - hypsodonty index
I - *incisivus* (incisor)
ind(et) - indeterminable
inf - inferior, lower
L - length
lam - lamella(e)/lamellar (description of oblong, band-shaped wear figure)
lat - lateral(ly)
LF - lamellar frequency (n lam. x 100 : L in mm, or 100 : LLQ)
LFi - LF based on Pi (for which see below); used in dP2 descriptions and analyses
LHI - length-height index
LLQ - length-lamellae quotient (L in mm : n lam., or 100 : LF)
LWI - length-width index
$\mathbf{M}^{x}$ - *dens molaris superior* (upper molar, with indication of rank)
$\mathbf{M}_{x}$ - *dens molaris inferior* (lower molar, with indication of rank)
Mx - *dens molaris / dentes molares*
(both upper and lower molar(s)/either upper or lower molar(s), according to context)
max - maximum, maximal, maximum value
m/med - median value
min - minimum value
MNI - minimum number of individuals
mod - modal value
n m - not measured / not measurable
P (upper case) - *dens praemolaris* (premolar)
P (upper case) - number of true lamellae
p (lower case) - posteriormost platelet, not a talon(id) (in M3) /
probability, according to context
Pi - total number of plates (including talons/talonids);
used in dP2 descriptions and analyses
pl - plate(s)
plate form - plate formula
post - posterior(ly)
r(ec) - reconstruction, reconstructed
r - coefficient of correlation
r^2 - coefficient of determination
S - semi-lamella: a plate that has the morphological properties of a talon on one side of the crown, and those of a true lamella on the other
s - sin./sinister, = left
s - standard deviation of the sample
s p - single-plate value
sublam - sublamellar; slightly oblong or oval wear figure
(between 'annular' and 'lamellar')
sup - superior, upper
t - *t* value (Student's *t*-test)
V - coefficient of variation
W - width
x - talon(id)
x! - large talon(id)
(x) - small talon(id)

(Bibliographical) usage in text, references and reference list

88 fig. 2 -	page 88 is quoted for fig. 2
88, fig. 2 -	page 88 is quoted for text and figure 2
^{2}1900 -	second edition or impression, published in 1900
[1880] ^{2}1900 -	first publication 1880, reprinted/re-edited in 1900, which is the version consulted
A. b **X, 1847/ -** ***B. b*** **(X, 1847)**	only proboscidean taxa, when first mentioned, are followed by the name(s) of the first author(s) and the year of publication
NESTI, 1825/ - Nesti 1825: 8	only when it immediately follows the name of a taxon, the name of the author of this taxon is rendered in Capital/Small Capital and followed by a comma and the year of publication. If this publication is just referred to in the text, with or without a page number, Small Capital and comma are not used. In the majority of cases the publications indicated by the Capital/Small Capital versions will not be found in the references list
100ff -	page 100 and following
Fig -	refers to a figure in a present text
fig -	refers to a figure in quoted text
ibid -	*ibidem* (at the same place, in the publication last mentioned)
id -	*idem* (the same)
in litt -	*in litteris* (in a written message)
passim -	throughout the text
pr vol 80 -	page 80 in the present volume
recte -	correctly
Section -	indicates a section of a present text
section	indicates a text section in another text or a stratigraphical section; hence: Section 2.1.6 above; Part I, section 2.2; sections I, II, etc. respectively.
Table/table -	analogous to *Fig/fig* and *Section/section*
"xyz" -	quoted text
'xyz' -	translation of quoted text, or metaphor
* -	placed before a taxon indicates that this taxon is hypothetical only

Curriculum Vitae

Johan Albert (Hans) van Essen werd op 8 oktober 1950 geboren te Dieren, waar hij al snel (vanaf 1957) zijn blijvende belangstelling voor zwerfstenen, geologie en paleontologie ontwikkelde. Van 1963 tot 1969 volgde hij middelbaar onderwijs aan het Baudartius Lyceum - later College - te Zutphen. Deze opleiding werd afgesloten met het aan het pré-mammoetwetprogramma verbonden diploma Gymnasium A.

In de jaren 1969 - 1972 begon hij met de studies Engelse Taal- en Letterkunde en Kunstgeschiedenis aan de Rijksuniversiteit Utrecht.

Van 1972 - 1974 was hij 18 maanden dienstplichtig militair bij de Koninklijke Luchtmacht en was na het behalen van het diploma Assistent Verkeersleiding achtereenvolgens gestationeerd op de vliegbasis Deelen en in het vluchtleidingscentrum bij Nieuw Milligen.

Van 1974 - 1976 volgde hij - naast een werkkring in het bankwezen te Amsterdam en Nijmegen - de avondopleiding Duits M.O. A aan de Gelderse Leergangen te Arnhem en sloot die af met het diploma. Het jaar 1974 markeert tevens het begin van zijn zelfstudie en collectievorming op het gebied van Pleistocene zoogdieren, met de nadruk op de gebitsmorfologie van fossiele olifanten.

In de jaren 1977 - 1983 studeerde hij Duitse taal- en letterkunde aan de Katholieke Universiteit - later Radboud Universiteit - te Nijmegen en sloot deze studie *cum laude* af met het doctoraalexamen, omvattend het verzwaarde hoofdvak met scripties op het gebied van de Moderne Letterkunde (de eerste roman van Robert Musil) en de Oude Taal- en Letterkunde (de functie van het Gotische prefix *ga-*), alsmede een kunsthistorisch bijvak: de sacrale architectuur van Armenië van de vierde tot de veertiende eeuw).

Vanaf 1984 was hij o.a. bestuurslid van de landelijke Werkgroep Pleistocene Zoogdieren, redacteur en samensteller van het door de W.P.Z. uitgegeven tijdschrift Cranium (tot 1989 en van 2001-2003), freelance vertaler, en (co-) auteur van een aantal publicaties, met name over fossiele olifanten.

In 1992 was hij met een beurs van de National Environment Research Council in Engeland werkzaam als onderzoeksassistent van Dr. A. M. Lister (Cambridge University en University College London) ten behoeve van hernieuwd onderzoek aan de fossiele olifanten uit de Cromer Forest-bed Formation en de Crags van East Anglia.

Van mei tot november 1997 was hij in het Natuurmuseum West-Overijssel/Ecodrome te Zwolle assistent van conservator Dr. T. Kemperman voor een revisie van de collecties fossiele zoogdieren en kristallijne zwerfstenen.

Vanaf 2001 was hij extern promovendus binnen de Archeologische Faculteit van de Universiteit Leiden en was sindsdien regelmatig gastmedewerker, c.q. medewerker onderzoek en onderwijs van het zoölogisch laboratorium van de Faculteit. De gedurende deze jaren gegroeide dissertatie is in 2011 afgesloten.