The Late Pliocene vertebrate fauna of Vatera (Lesvos Island, Greece)

George A. Lyras and Alexandra A.E. van der Geer

Samenvatting

Vatera is een laat-pliocene (ongeveer twee miljoen jaar geleden) vindplaats in het zuidelijk deel van het Griekse eiland Lesbos, waar een vastelandsfauna van grote vertebraten is gevonden en systematisch is opgegraven. De fauna bestaat uit de typische Europese zoogdieren van die tijd: paarden (*Equus*), giraffes (*Mitilanotherium*), gazelles (*Gazella*), antilopen (*Gazellospira*), runderen (*Leptobos*), wasbeerhonden (*Nyctereutes*), dassen (*Meles*), sabeltandkatten (*Homotherium*), neushoorns (*Stephanorhinus*), mastodonten (*Anancus*) en mammoeten (*Mammuthus*). Bovendien zijn er ook resten van een zeldzame soort makaak (*Paradolichopithecus*) en van een soort reuzenschildpad (*Cheirogaster*) ontdekt.

Summary

Vatera is a Late Pliocene (~2 Ma) locality in the southern part of Lesvos Island, Greece, in which a mainland fauna of large vertebrates has been found and systematically excavated. The fauna is composed of the typical European mammals of that time: horses (*Equus*), giraffes (*Mitilanotherium*), gazelles (*Gazella*), antelopes (*Gazellospira*), oxes (*Leptobos*), raccoon dogs (*Nyctereutes*), badgers (*Meles*), dirk-toothed cats (*Homotherium*), rhinoceroses (*Stephanorhinus*), mastodonts (*Anancus*) and mammoths (*Mammuthus*). In addition, the remains of a rare species of macaque (*Paradolichopithecus*) and a species of a giant tortoise (*Cheirogaster*) were also discovered.

Introduction

Vatera is a holiday resort at the south part of Lesvos Island (Greece), famous for its long sandy beach. But the area is known for yet anther reason: in the nearby sedimentary rocks there are several sites with fossil vertebrates (Dermitzakis *et al*. 1991; De Vos *et al*., 2002). Although they all belong to the typical Late Pliocene fauna, which is common in many European localities, Vatera is a very special one, as it is there, that the remains of two rare and extraordinary creatures have been found. The first is the primate *Paradolichopithecus*, a large sized macaque, known only from Senèze (France) and Valea Grauneanu (Romania). Vatera is now the third locality in the world with this primate. The second is the giant tortoise *Cheirogaster,* one of the largest tortoises of the world and the last of its kind in Europe.

The scope of this paper is to present an illustrated overview of the Vatera locality, which is often missed within the details of the studies published so far (Dermitzakis *et al*., 1991; Athanassiou, 2002; Eisenmann, 2002; De Lapparent de Broin, 2002; De Vos *et al*., 2002; Drinia *et al*., 2002; Van der Geer & Sondaar, 2002; Sondaar *et al*., 2006). The animal illustrations, used here, have been prepared by Alexis Vlachos under the guidance of the authors. The photographs of specimens have been shot by Kyriakos Sykas. The fossils from Vatera are now part of the collections of the Museum of Paleontology and Geology of the University of Athens and are housed in the Vrissa Natural History Collection on Lesvos Island.

The fossil sites and their age

All the vertebrate fossils were found in exposures within the upper unit of the Vatera Formation. This unit is represented by fluvial deposits consisting of alternations of breccia-conglomerates, sandy clays, sandy conglomerates and silt (Drinia *et al*., 2002). In total, 630 fossils have been recovered from 7 sites (Fig. 1). All fossils were found within the sandy clay layers, with the exception of the proboscidean remains (sites H and U), which were found within the conglomerates. This seems to be related to the size of the proboscidean remains, which large as they are, require, just like pebbles, a faster stream flow to be transported.

F-Site

This is the richest site of the Formation . It has been named after the discovery of **F**unny fragments of bones at the initial stages of the research. The site was systematically excavated for 4 continues seasons (1997-2000), yielding 550 fossils belonging to 15 different species of mammals, one bird and one reptile (the giant

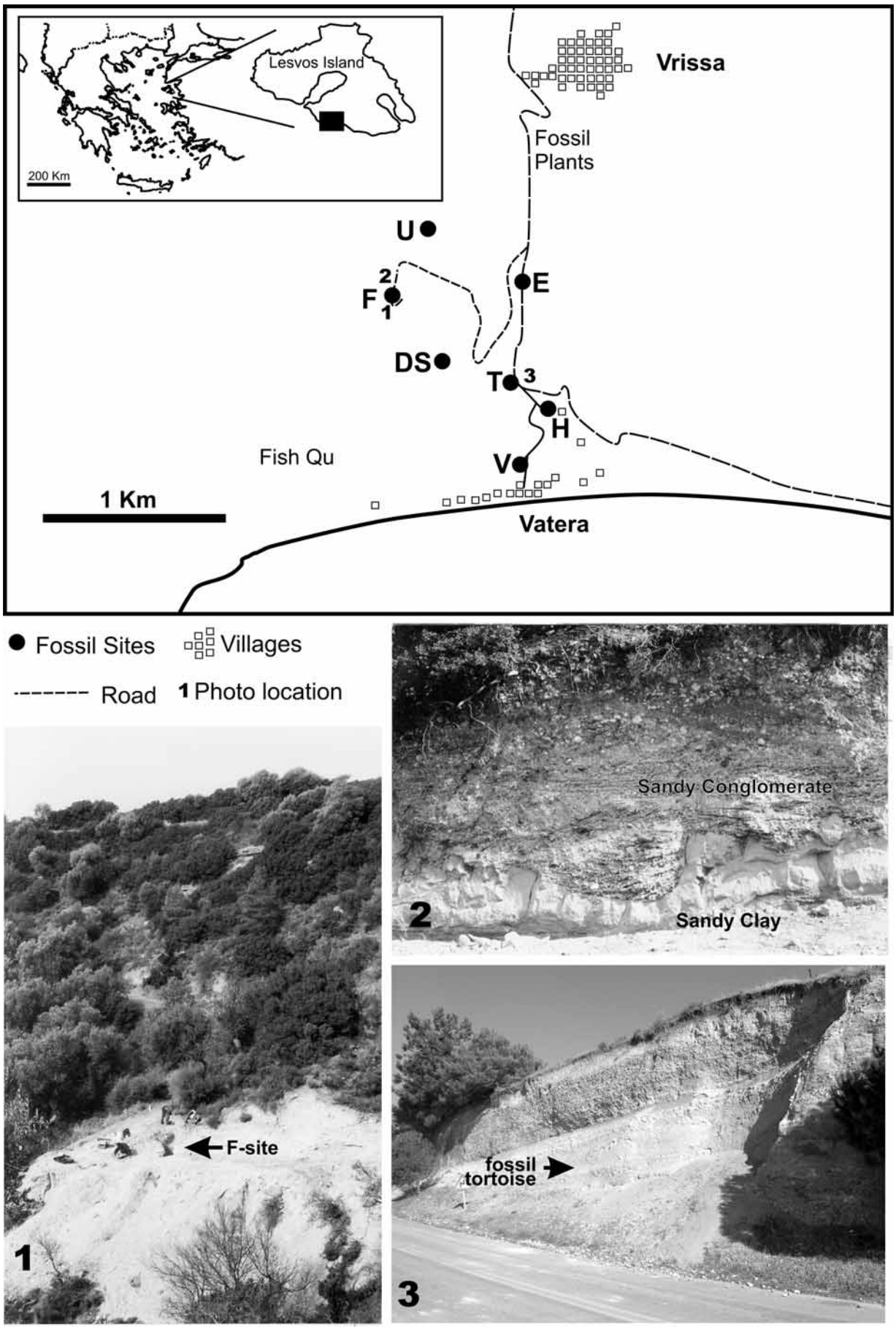


Fig 1 Location of the fossil sites and photos showing some sections of the Vatera Formation

Locatie van de vindplaatsen van de fossielen en fotos met enkele secties van de Vatera Formatie.

tortoise). Based on the fauna composition the site has been attributed to the MN 17 (about 2 Ma) at the Late Pliocene (De Vos *et al*., 2002).

DS-Site

It was called after the names (**D**aniela and **S**andra) of the ones who found the site. It has been excavated in the autumn of 2000. From this site sixty fossils were collected, belonging to one bird and at least ten different mammalian species. Its age is probably Late Pliocene (De Vos *et al*., 2002).

E-site

This was the first site to be discovered in Vatera. It was named after a nearby building, which was thought to belong to the **E**lectric Company. The only remains that have been found are two bovid teeth, material of a large horse, a raccoon dog mandible and a femur fragment of a large felid. Originally, this site was considered to be of Late Pleistocene age (Dermitzakis *et al*. 1991; and see bellow, under the section of horses). Later, due to the presence of the raccoon dog, a Late Pliocene age was considered as more realistic (De Vos *et al*., 2002).

U, H, T and V-site

From each one of these sites (**U** for **U**nknown, **H** for **H**ouse, **T** for **T**ortoise and **V** for **V**atera), only one species is known. In the U-site, a tusk fragment and two molars of a mammoth (*Mammuthus meridionalis*) were found. The H-site was discovered while digging a trench for the construction of a house. In that trench heavily fragmentated tusks and molars of a mastodont (*Anancus arvernesis*) were found. From the T- and V-sites, only the carapax of 2 small tortoises were excavated. The small tortoises from the T- and V-sites are of little stratigraphic value. The same is valid for the mammoth, because the stratigraphic range of this mammoth species is from the Late Pliocene till the early Middle Pleistocene. The mastodont *A. arvernensis* lived from the Late Miocene till the end of the Late Pliocene.

Other fossiliferous sites

The lower part of the Vatera Formation consists of lacustrine and brackish deposits (Drinia *et al*., 2002). Within this part of the formation and close to Vatera, there is a quarry (Fig. 1) of claystone that contains plant and fish fossils. On a higher stratigraphic level, close to the village of Vrissa, there is a second clay quarry, in which fossil plants were discovered (Fig. 1). Till now, no further study has been carried out in these two sites.

The fauna of Vatera 2 million years ago

The terrestrial macaque

Two million years ago, a kind of giant macaque (*Paradolichopithecus arvernensis*). lived around Vatera Remains of this primate have been found only in the F-site, and consist of two mandibles (one attributed to an adult female, the other to a juvenile male), some postcranials and some isolated teeth (Fig. 2). The size and morphology of the material is similar to that from Senèze (holotype of the species) and Valea Graunceanului in Romania.

Paradolichopithecus was as big as the largest baboons (*Papio ursinus*) of today. However, what makes this macaque so special is not its size, even if it is too large for a macaque, but its way of life. According to Van der Geer & Sondaar (2002), Postcranial material from *Paradolichopithecus* suggests a highly terrestrial way of locomotion. It has also been suggested that this large monkey occupied a similar ecological niche as *Australopithecus*, and had a similar way of locomotion (Sondaar *et al*., 2006). The same authors demonstrated that *Australopithecus* was not a perfect biped as modern humans (*Homo sapiens*), but employed a more all-round locomotion, somewhat comparable to a trained chimpanzee or macaque, which can walk bipedally for quite a distance, but are also good at climbing trees. On the ground of the similarities in the postcranial material, it has been suggested that the locomotion of *Paradolichopithecus* was comparable to that of early hominids like *Australopithecus.* Finally, Sondaar *et al*. (2006) concluded that *Paradolichopithecus* lived at the forest edge bordering the savannah.

One of the two *Paradolichopithecus* mandibles found in Vatera belongs to a juvenile male (Van der Geer & Dermitzakis, unpublished data). It was concluded that, based on eruption pattern, this animal died during his puberty. For male baboon-like monkeys this is a very stressful episode of their lives. During this life stage, they leave their natal group and become peripheral. Social behaviour like grooming and playing now decreases, while aggressive encounters and fighting with other males

Fig 2 Two mandibles and a humerus from the baboon-like *Paradolichopithecus arvernesis* from Vatera. The mandible on the left belongs to a juvenile male and the mandible on the right to an adult female.

Twee onderkaken en een dijbeen van baviaan-achtige *Paradolichopithecus arvernensis* van Vatera. De onderkaak links is van een jong mannetje en de onderkaak rechts van een volwassen vrouwtje.

Fig 3 Hans Brinkerink standing next to a full sized replica of the Vatera giant tortoise. The giant tortoise, named "Lolita" by France De Lapparent de Broin, was sculptured by Hans Brinkerink in Baarn (The Netherlands) and transported to Lesvos for opening of the Vrissa Natural History Collection in September of 1999. It is now standing in the backyard of the building, which houses the collection.

Hans Brinkerink staande naast een levensgrote replica van de reuzenschildpad van Vatera. De reuzenschildpad, genaamd "Lolita" door France De Lapparent de Broin, was door Hans gemaakt in Baarn (Nederland) en toen naar Lesvos getransporteerd voor de opening van de Vrissa Natuurhistorische Collectie in september 1999. Ze staat nu in de achtertuin van het gebouw waarin zich de collectie bevindt.

Fig 4 Life appearance of the spiral-horned antelope *Gazellospira,* based on the fossils from Vatera, Sesklo and Pyrgos (Museum of Paleontology and Geology of the University of Athens, Greece). The animal's coloration and posture has been adapted from the living *Tragelaphus* of Africa.

Reconstructie van de spiraalhoornige antilope *Gazellospira*, gebaseerd op de fossielen van Vatera, Sesklo en Pyrgos (Museum van Paleontologie en Geologie van de Universiteit van Athene, Griekenland). De vachtkleur van het dier en de lichaamshouding zijn afgeleid van dat van de nu levende *Tragelaphus* van Afrika.

increase. About half the male mandrills die at this age, and also for *Paradolichopithecus* this was true, with nearly half having died before the third molars erupted (Szalay & Delson 1979: 369)

The giant tortoise

Remains of a giant tortoise were found only in the F-site (De Vos *et al.,* 2002). The material consists of a femur, a tibia, carpal bones, phalanges and osteoderms, which probably all belong to a partial left hind limb of a single individual.

In the past, the large terrestrial tortoises were attributed to the genera *Testudo* and *Geochelone*. These genera are phylogeneticaly unrelated to the large terrestrial forms and therefore, today these taxonomies are considered inappropriate.

The material from Vatera has been studied by De Lapparent de Broin (2002), who determinated it as cf. *Cheirogaster* aff. *schafferi.* The reason that she was not able to give a more firm determination (she preferred to use the abbreviations cf. and aff.) is that she was missing the bones on which the diagnosis of the species and the genus is based. The tortoises can be distinguished by morphological features of the plastron and anterior and posterior part of the carapax. Since the Vatera tortoise consists only of a partial left hind limb, these features could not be used. Therefore, De Lapparent de Broin (2002) based her determination on similarities on size and morphology of the Vatera material with those of an almost complete skeleton of a *Cheirogaster* from Perpignan (Early Pliocene of France) and the limb elements of other giant tortoises from the Mediterranean.

On the ground of these comparisons De Lapparent de Broin was able to estimate the size of the Vatera tortoise. According to her, the length of its carapax could be maximal 186 cm long, an estimation, which brings the *Cheirogaster* from Vatera as the largest individual of this genus (Fig. 3).

Fig 5 Reconstruction of the small *Gazella* of Vatera, based on the fossil material from the F-site and the living *G. thomsonii* of Africa.

Reconstructie van de kleine *Gazella* van Vatera, gebaseerd op fossiel materiaal van de F-site en de nu levende *G. thomsonii* van Afrika.

The antilopes

The true antilopes are among the most common fossils in Vatera. In total, five species of antelopes were recognized: one species of *Gazellospira*, three species of *Gazella* and one, yet unidentified, species of a very small antelope, probably belonging to the neotragini (De Vos *et al*., 2002).

The largest of the three antelopes is *Gazellospira* (Fig. 4). It is an antelope with very characteristic morphology, which had a wide geographic distribution (from Europe till China) during the Plio-Pleistocene (Duvernois & Guèrin, 1989). The most typical features of this animal are the rather elongated metapodials and the robust and anti-corkscrew torsion of the horn cores. There is only one species of *Gazellospira* in Europe (*G. torticornis*), however De Vos *et al*. (2002) attributed the Vatera specimens to *G.* cf. *torticornis,* due to their slightly smaller size.

The presence of three species of gazelles has been suggested by Athanassiou (in De Vos *et al*., 2002 and Athanassiou, 2002). He attributed the Vatera material to *G. agaea* (the largest), *G.* cf. *bouvrainae* (the medium size) and *G.* aff. *borbonica* (the smallest, Fig. 5). For the determination of the two smaller gazelles, the abbreviations aff. and cf. were used, because their identification is unsure: There are only a few and badly preserved medium sized horn cores and the smaller horn cores are shorter that the minimum sizes for *G. borbonica.* This is not the only problem concerning the gazelles from Vatera. Van der Made (in De Vos *et al*., 2002) gave a different interpretation of the material. He suggested that there are only two species of *Gazella* (*G.* aff. *bouvrainae* and *G.* cf. *borbonica*), that the differences is size are due to sexual dimorphism and that the neotragine is in reality a female individual of the small gazelle species. Contrary to only one species of *Gazella* (*G.borbonica*) in Western Europe, there is a larger diversity of Pliocene gazelles in South Eastern Europe (Kostopoulos & Athanassiou 1997; Athanassiou, 2002). Therefore, the presence of three species of *Gazella* in one locality is considered by us as the most probable scenario. A more definite conclusion however, can de drawn only after a more extensive study of the material.

The giraffe, the deer and the ox

Some postcranial remains, consisting of phalanges, carpals, an astragalus and an articulated distal humerus and proximal radius

Fig 6 Reconstruction of the giraffe *Mitilanotherium* based on the material from Vatera and Volax (Museum of Paleontology and Geology of the University of Athens, Greece).

Reconstructie van de giraf *Mitilanotherium* gebaseerd op materiaal van Vatera en Volax (Museum van Paleontologie en Geologie van de Universiteit van Athene, Griekenland).

(F-site) belong to a giraffid (Fig. 6). The size and morphology of this postcranial material is very similar to material from other Plio-Pleistocene sites, such as Valea Graunceanului (Romania), Vólax and Sésklo (Greece), which favors attribution to *Mitilanotherium inexpectatum* (De Vos *et al*. (2002) attributed it to *Mitilanotherium* cf. *Inexpectatum*). Giraffid material from Vólax has been named *Macedonitherium martinii* (Sickenberg, 1967), and that from Kuruk Say (Tajikisthan) Sogdianotherium kuruksaense (Sharapov, 1974), but metrical and morphological differences between these two genera and *Mitilanotherium* are small, and they are to be considered synonyms; most likely all medium sized Plio-Pleistocene giraffids belong to one species only.

Mitilanotherium inexpectatum is a medium sized giraffid, probably belonging to the subfamily Palaeotraginae. The skull is elongated with a flat cranial roof. The ossicones are long, and are

Fig 7 Reconstruction of *Metacervoceros rhenanus* (the small deer from Tegelen), based on a complete skeleton from Senèze (Natural History Museum of Basel, Switzerland).

Reconstructie van *Metacervoceros rhenanus* (het klein Tegelse hert), gebaseerd op een compleet skelet van Senèze (Natuurhistorisch Museum van Basel, Zwitserland).

situated exactly above the orbits, inclined towards the front and bent towards the rear. The limb bones are elongated and moderately slender, with a size in between that of *Palaeotragus* and *Samotherium*. In Europe giraffids seem to occur only in Greece, Romania, and Ukraine; they are missing in the other European Plio-Pleistocene sites, although recently (Arribas *et al*., 2001) refer to a cf. *Mitilanotherium* found at the Spanish locality Fonelas (Late Pliocene).

A fragmentary male skull with shed antlers and its maxillaries, a partial skull, a left maxillary and some postcranial elements (F-site) are ascribed to the *Dama*-like deer (Fig. 7) *Metacervoceros* cf. *rhenanus* (*Dama* cf. *rhenana* in De Vos *et al*., 2002). The size of the maxillaries and the metapodials is similar to that of the material from Tegelen (type locality of the species). *Dama*-like deer occur in Europe from the Late Pliocene until today, and show a gradual morphological and metrical transition from the earlier to the later forms. Cladistic analysis indicates that they actually all belong to the genus *Dama* (Van der Made 1999), in contrast to the study of Azzaroli (1953;1992), in which a separate genus *Pseudodama* is proposed

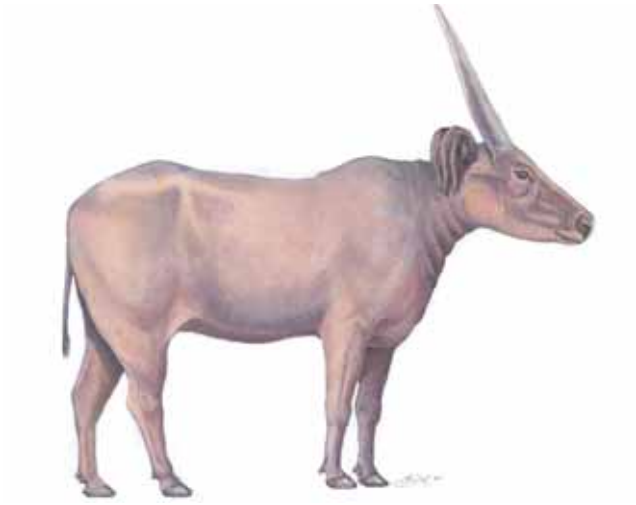


Fig 8 Life appearance of *Leptobos*, based on a reconstructed partial skeleton from Valdarno (Museo di Storia Naturale, Firenze, Italy). The head is based on a drawing by Adrie and Alfons Kennis; the body is adapted after the living Indian bison, *Bos gaurus*.

Reconstructie van *Leptobos*, gebaseerd op een gereconstrueerd gedeeltelijk skelet van Valdarno (Natuurhistorisch Museum van Florence, Italië). De kop is gebaseerd op een schildering door Adrie en Alfons Kennis; het lichaam is afgeleid van dat van de nu levende Indiase bison, *Bos gaurus*.

Fig 9 Life appearance of the rhino *Stephanorhinus etruscus*. Redrawn from a painting by Mauricio Antón (Agusti & Antón, 1997).

Reconstructie van de neushoorn *Stephanorhinus etruscus*. Nagetekend van een schildering door Mauricio Antón (Agusti & Antón, 1997).

for the early forms. However, at present, the generic name *Metacervoceros* is in use for the earlier *Dama*-like forms.

Remains of yet another small deer were found (F-site). They may belong to *Croizetoceros ramosus*, but this is by no means certain at present. *C. ramosus* has more or less the same size as *M. rhenanus* (Valli 2004: *C. philisi*), but has a more complicated antler. It is tempting to assume that this deer preferred the plains (Valli 2004), contrary to *M. rhenanus*, which is a forest deer.

A distal part of a metacarpal from the F-site might be attributed to the larger bovid *Leptobos* sp (Fig. 8). If so, then it is slightly larger than the *Leptobos* metacarpals from St. Vallier. Another metacarpal (DS-site) is very similar. Other elements are a distal radius and a phalanx (DS-site). Due to these uncertainties, De Vos *et al*. (2002) attributed the material to cf. *Leptobos* sp.

The rhinoceros

The rhino remains (a vertebra and some limb bones) have been found in the DS- site. The material is attributed by De Vos *et al*. (2002) to *Stephanorhinus* cf. *etruscus* (Fig. 9). The Etruscan rhinoceros (*Stephanorhinus etruscus*) was an inhabitant of the forests. This rhinoceros was small and had relatively long limbs. It bore two horns: one larger horn on its nose and one much smaller horn on its forehead.

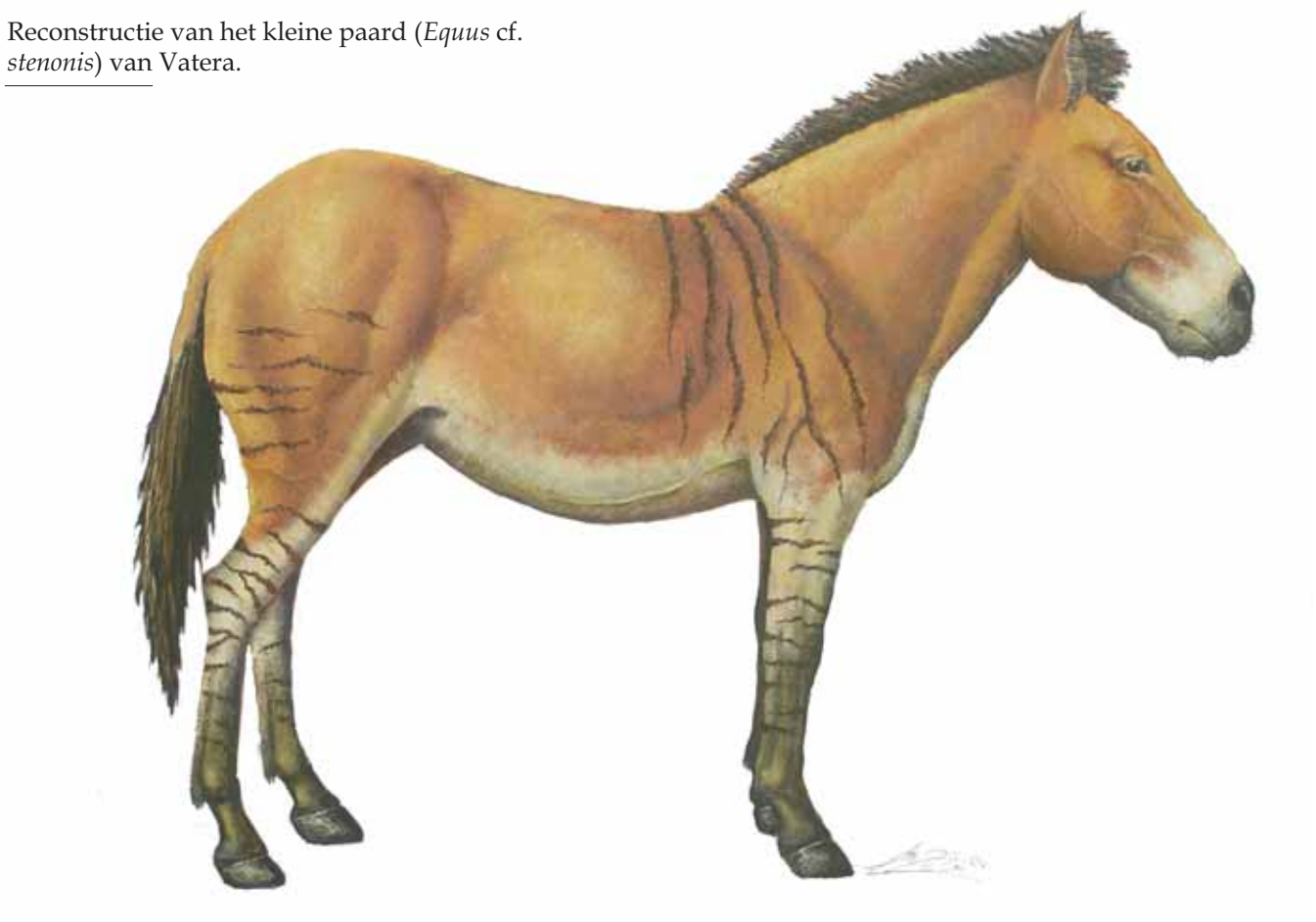
The horses

There are two kinds of horses in Vatera. A large and very robust one (Dermitzakis *et al*., 1991; Eisenmann, 2002) and smaller and more slender one (Eisenmann, 2002).

The slender horse (Fig. 10) is represented by some teeth and several postcranial remains (Fig. 11). Its limb bones are very long and slender and morphologically comparable to those of *Equus stenonis* (De Vos *et al*., 2002). *E. stenonis* is the typical horse of the Plio-Pleistocene of Eurasia. Therefore, its morphology is very well known. However, because of its large temporal and geographical occurrence it developed a

Fig 10 Life reconstruction of the small horse (*Equus* cf. *stenonis*) from Vatera.

Reconstructie van het kleine paard (*Equus* cf. *stenonis*) van Vatera.



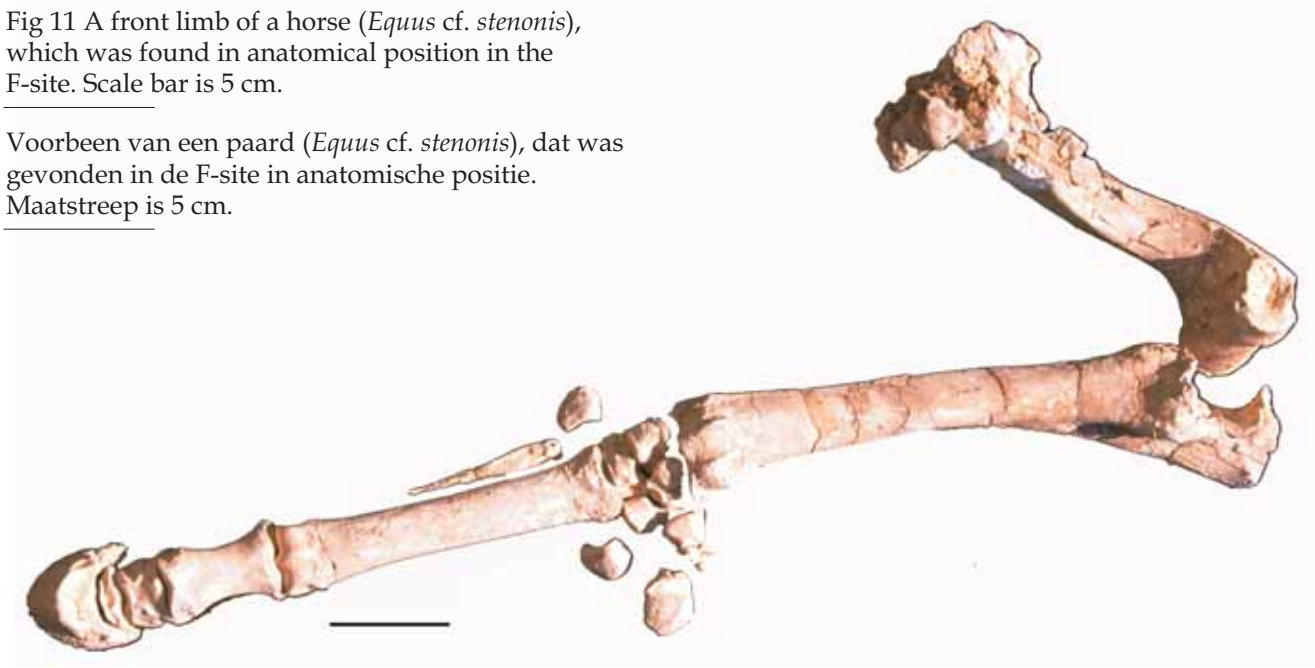


Fig 11 A front limb of a horse (*Equus* cf. *stenonis*), which was found in anatomical position in the F-site. Scale bar is 5 cm.

Voorbeen van een paard (*Equus* cf. *stenonis*), dat was gevonden in de F-site in anatomische positie. Maatstreep is 5 cm.

very large morphological variation, complicating in this way, the views about its taxonomy and exact phylogenetic position, which still remain unclear.

Eisenmann (2002) estimated that the size of the small Vatera horse is comparable with a Grevy's zebra (more the 400 Kg) and that its withers height should be 157 cm. Because its metapodials and phalanges are very slender, she concluded that it was an animal adapted to dry conditions and open landscapes.

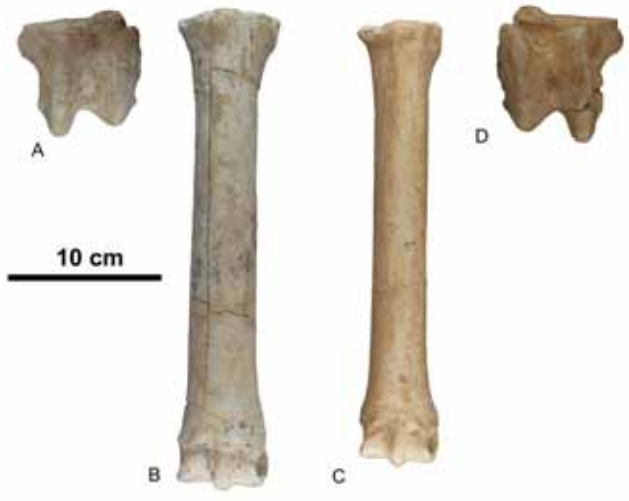


Fig 12 Astragals and metatarsals from the robust horse of the E-site (A and B) and the slender horse of the F-site (C and D).

Enkelbeenderen en middenvoetsbeenderen van het robuste paard van de E-site (A en B) en van het slankere paard van de F-site (C en D).

The second horse is a more puzzling one. Its remains have been found only in the E-site (Fig.12). There are only three fossils known, an astragal, a metatarsus and a tibia. The astragal was the first fossil to be found in Vatera, about twenty years ago. Although its proportions are comparable to *E. stenonis* (see Dermitzakis *et al.*, 1991), it is far more robust than that of the F-site (Eisenmann, 2002). The body size of this horse has been estimated up to 605 Kg (Eisenmann, 2002).

The presence of two different kinds of horses in Vatera can not be easily explained, as there are only a few Pliocene localities in the world with coexistence of two types of horses (Eisenmann, 2002). One possibility is that the horse from the E-site is of a later age than that of the F-site (originally, Dermitzakis *et al.*, 1991, thought that the E-site was Late Pleistocene). There are many faults cutting the Vatera Formation and, at least, one unconformity is present within the formation. Therefore, it is possible that there is a considerable time difference between the two sites. Such a possibility was not supported by De Vos *et al.* (2002), because of the presence of raccoon dog remains in both sites (Fig. 13). Raccoon dogs went extinct from Europe at the end of the Pliocene and that was sufficient evidence for them to suggest that the E- and F-sites are of the same age. It should be noted here that the raccoon dog from the E-site is much smaller from the one from the F-site (see bellow, under the section of carnivora), so

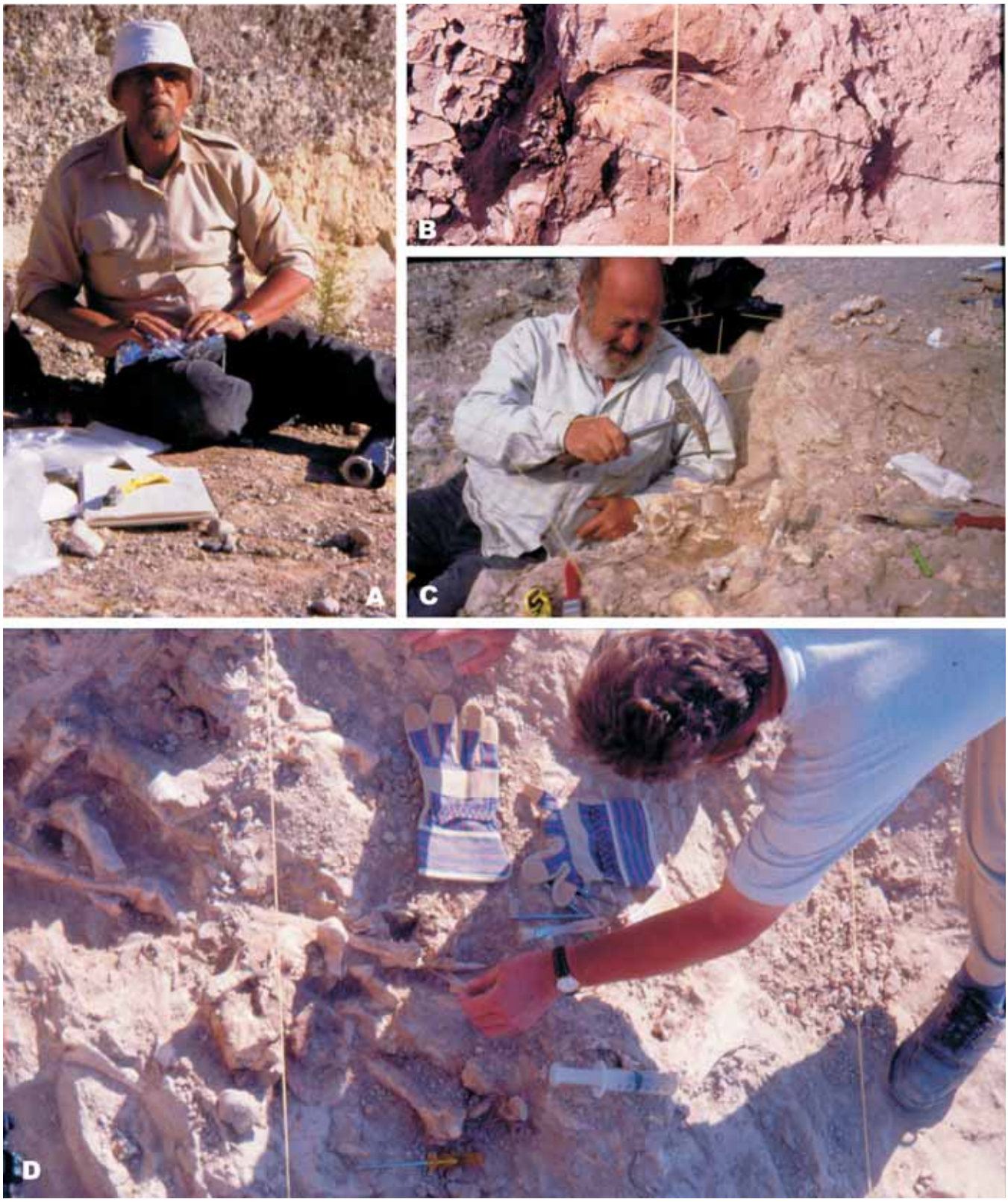


Fig 13 Most of the biostratigraphic data come from the F-site. The site was systematically excavated for 4 seasons by a Greek-Dutch team. A. John De Vos supervising the cataloging and packing of the fossils. B. The mandible of the female *Paradolichopithecus*, as it was found in situ. C. Although the presence of fossils around the site was known for a long time, the actual location of the site was discovered only after Paul Sondaar surveyed the area in 1997. D. Jan Van der Made taking a photo of the site.

De meeste biostratigrafische gegevens komen van de F-site. De site was systematisch opgegraven voor vier seizoenen door een Grieks-Nederlands team. A. John de Vos houdt toezicht op het catalogiseren en inpakken van de fossielen. B. De onderkaak van het *Paradolichopithecus* vrouwtje, in situ gevonden. C. Hoewel de aanwezigheid van fossielen rond de site al langer bekend was, werd de juiste locatie van de site pas ontdekt toen Paul Sondaar het gebied in 1997 af zocht. D. Jan van der Made neemt een foto van de site.

Fig 14 Life reconstruction of the raccoon-dog *Nyctereutes megamastoides* based on cranial and postcranial remains from Sesklo (Museum of Paleontology and Geology of the University of Athens, Greece).

Reconstructie van de wasbeerhond *Nyctereutes megamastoides* gebaseerd op schedel- en skeletresten van Sesklo (Museum van Paleontologie en Geologie van de Universiteit van Athene, Griekenland.

maybe indeed there is some small time difference between the two sites or, as an alternative hypothesis, the E-site fauna represents a migration from a different ecological niche or landscape.

The carnivores

The remains of a canid (*Nyctereutes*), a mustelis (*Meles*) and felids have been found in the sites E, F and DS of Vatera.

The raccoon dog (*Nyctereutes*) has been found in the E- and F-sites (Fig. 14). Their remains are limited to a hemi-mandible with preserved c-m3 (F-site) and a right toothrow c-m2 (E-site). Their morphology is characteristic for *Nyctereutes megamastoides,* a canid which went extinct at the end of the Pliocene from Europe (Tedford & Qiu, 1991). The *Nyctereutes* from the E-site is much smaller that the one from the F-site and actually one of the smallest fossil *Nyctereutes* ever found.

The badger (*Meles thorali*; Fig. 15) of Vatera is represented in the F-site by a front part of a skull and a mandible (De Vos *et al*., 2002). The upper and lower dentition are both complete. Measurements of the lower carnassial show that the species is the same as that from St. Vallier (France).

The only fossils of larger representatives of the cat family (Felidae; Machairodontinae) from Vatera are a left femur fragment from the E-site (Dermitzakis *et al*. , 1991), another left femur, missing the distal condyles (F-site), a damaged ulna (DS-site; olecranon and distal end missing), a distal tibia (DS-site), and a complete tibia (DS-site) (De Vos *et al*., 2002).

The proximal femur fragment might belong to a dirk-toothed cat (cf. *Homotherium latidens*; Fig. 16); the same is true for the ulna and the distal tibia. The complete tibia is somewhat smaller and could belong to the dirk-toothed cat (cf. *Meganterion cultridens*). The almost complete left femur is again smaller; its morphology is similar to that of *Lynx issiodorensis*, but is somewhat smaller.

Fig 15 The badger of Vatera, *Meles thorali*, based on the appearance of the living European badger.

De das van Vatera, *Meles thorali*, gebaseerd op het uiterlijk van de nu levende Europese das.

The small tortoises and birds

In Vatera the remains of small tortoises and birds have been found as well. At the beginning, only the remains of one individual, consisting of a partial carapax and a plastron (T-site) of a *Testudo graeca ibera* have been identified (De Lapparent de Broin, 2002). Later, in the year 2003, a second partial carapax of *Testudo graeca* was found in a site very close to Vatera beach (V-site). Morphologically they do not differ from the living tortoise of the region.

The bird remains have not been determined on genus and species level (Aves gen. et sp. indet., in De Vos *et al*., 2002). The material is restricted to a radius fragment and a humerus (F-site) and two associated thoracic vertebrae (DS-site). The size of the humerus approaches that of an eagle (*Aquila*).

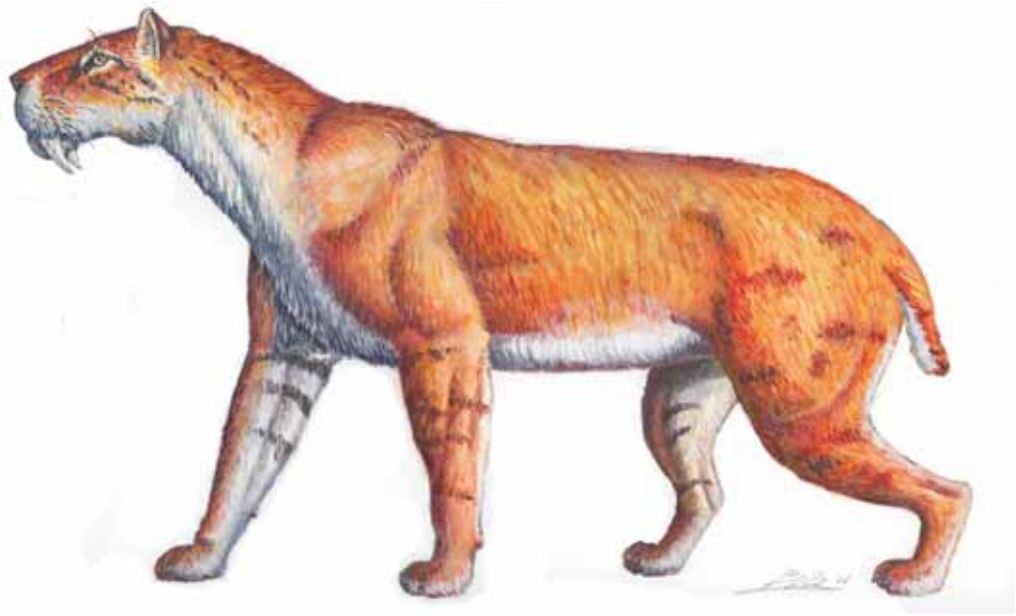


Fig 16 Life appearance of the dirk-toothed cat *Homotherium*. Based upon a painting by Mauricio Antón (Turner & Antón, 1997).

Reconstructie van de sabeltandkat *Homotherium*. Gebaseerd op schildering door Mauricio Antón (Turner & Antón, 1997).

The proboscideans

In Vatera two kinds of proboscians were found: a mastodont and a mammoth.

The remains of mastodonts consist of a complete, very worn left molar, a fragment of a right molar, two tusks (all from H-site) and a fragmentary metapodial (F-site). The dental elements belong without doubt to the gomphothere *Anancus arvernensis* (Fig. 17); the size of the metapodial is suggestive for the same species.

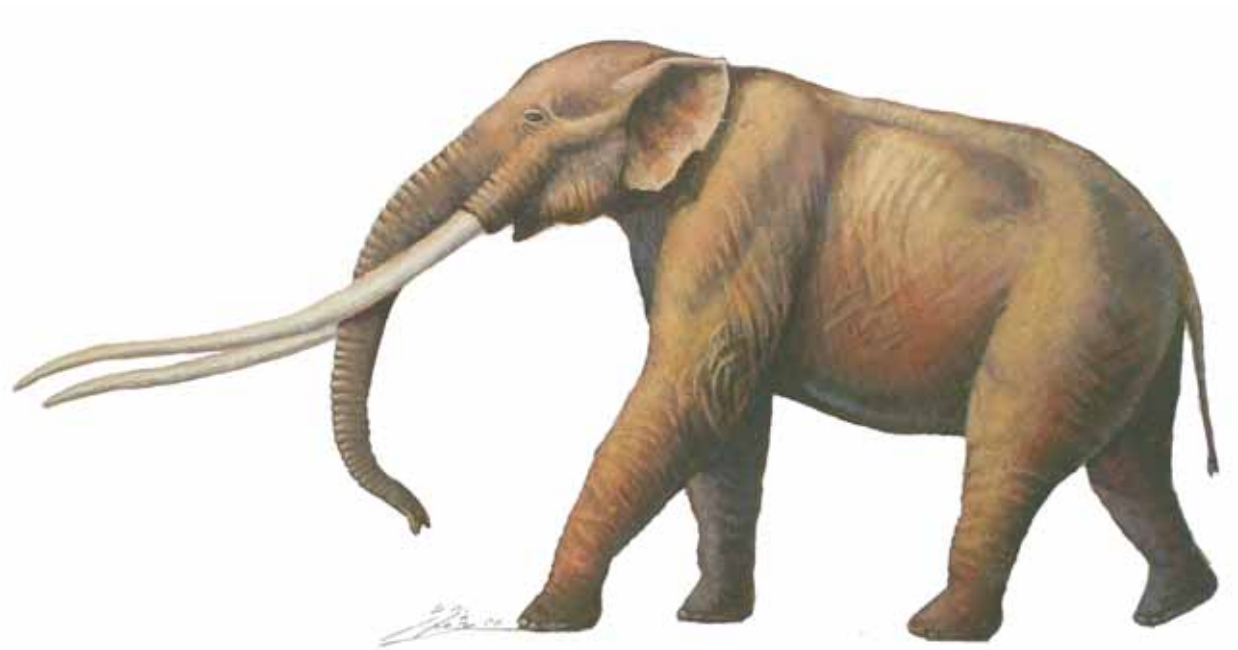


Fig 17 The mastodont *Anancus arvernensis*, based on a complete skeleton from Valdarno, Italy (Museo di Storia Naturale, Firenze, Italy).

De mastodont *Anancus arvernensis*, gebaseerd op een compleet skelet van Valdarno, Italië (Natuurhistorisch Museum van Florence, Italië).

The southern mammoth (*Mammuthus meridionalis*; Fig. 18) is represented only by a tusk and two molar fragments (U-site) and some molar fragments (DS-site). The attribution to *M. meridionalis* is likely, but not decisive at present (De Vos *et al*., 2002 determinate it as cf. *Mammuthus meridionalis*).

The gomphothere mastodont *Anancus* and the elephantine *Mammuthus meridionalis* seem to have coexisted in Europe for some time during the Late Pliocene, although their fossils have so far not been found at exactly the same site. *Anancus* became extinct in the Early Pleistocene, whereas the southern mammoth *Mammuthus meridionalis* persisted, and gave rise to the steppe mammoth (*M. trogontherii*, Middle Pleistocene) and eventually to the woolly mammoth *(M. primigenius*, latest Pleistocene) in Eurasia.

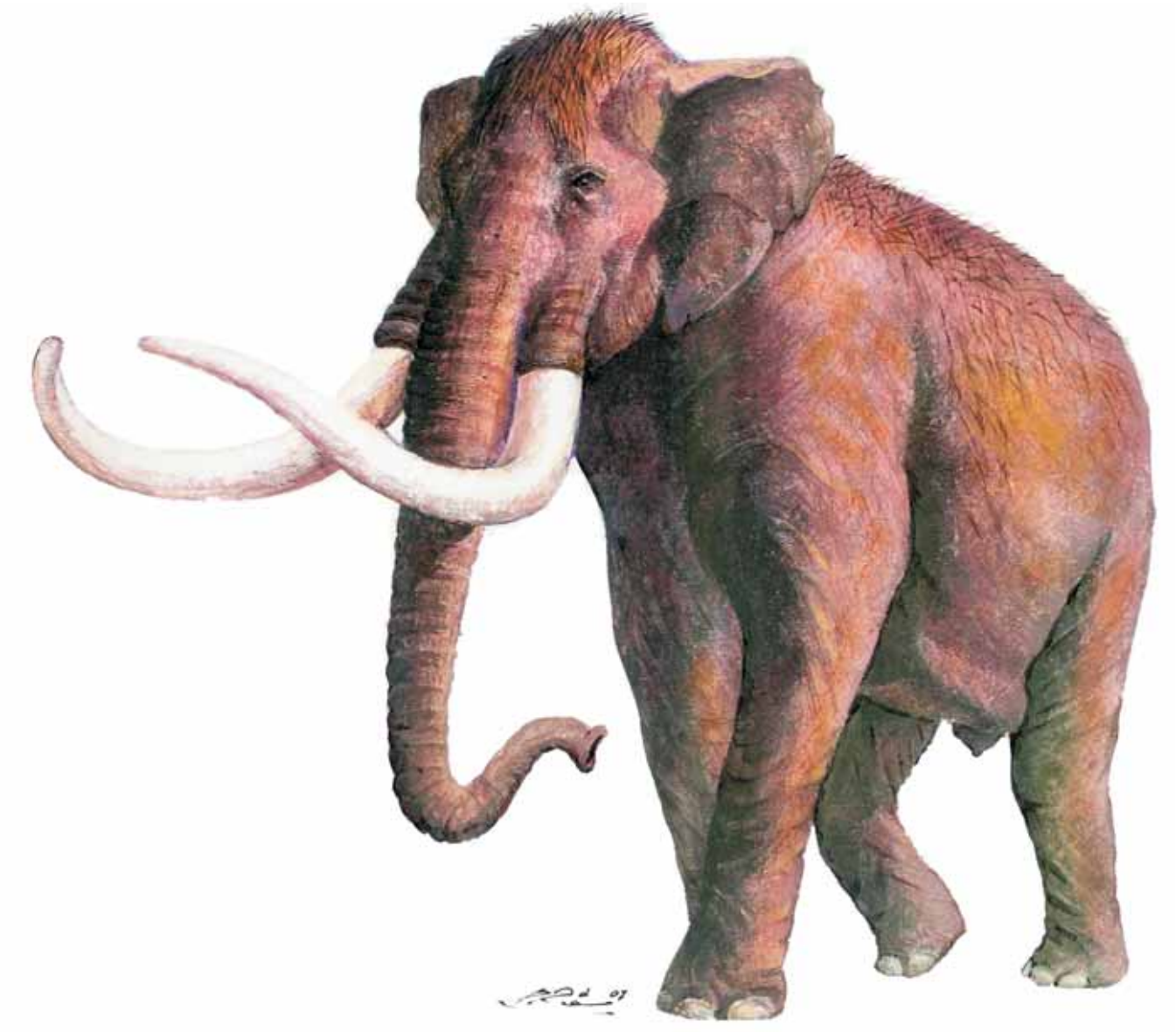


Fig 18 The southern mammoth *Mammuthus meridionalis*, based on a complete skeleton from Valdarno, Italy (Museo di Storia Naturale, Firenze, Italy). The southern mammoth is the ancestor of the woolly mammoth and is the largest proboscidean of all times.

De zuidelijke mammoet *Mammuthus meridionalis*, gebaseerd op een compleet skelet van Valdarno, Italië (Natuurhistorisch Museum van Florence, Italië). De zuidelijke mammoet is de voorouder van de wolharige mammoet en is de grootste slurfdrager die ooit geleefd heeft.

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Addresses of the authors

George Lyras and Alexandra van der Geer
Museum of Palaeontology and Geology
Faculty of Geology
Panepistimiopolis
15784 Zografou
Athens, Greece
E-mail glyras@geol.uoa.gr, geeraae@geol.uoa.gr