

# Miocene of Finland? Discoveries of Neogene microfossil assemblages and mammal fossils from northern Europe

Juha Saarinen\* & J. Sakari Salonen

*Department of Geosciences and Geography, P.O. Box 64, FI-00014 University of Helsinki, Finland  
(\*corresponding author's e-mail: juha.saarinen@helsinki.fi)*

*Received 2 Mar. 2024, final version received 2 Apr. 2024, accepted 2 Apr. 2024*

Saarinen, J. & Salonen, J. S. 2024: Miocene of Finland? Discoveries of Neogene microfossil assemblages and mammal fossils from northern Europe. — *Ann. Zool. Fennici* 61: 119–129.

While there is a rich Miocene fossil record from Europe, it is heavily biased to areas south of 50°N, and Miocene records from northern Europe are very scarce. Especially Fennoscandia has traditionally been considered to lack practically all evidence from the Neogene mainly due to heavy glacial erosion during the Pleistocene. However, during recent years, a few isolated, re-deposited finds of Miocene mammal fossils from Finland and Sweden have somewhat changed the situation. While the original provenance of these finds is uncertain, they most likely originate from eroded Miocene sediments within the Fennoscandian shield itself, in any case broadly representing northern Europe. A proboscidean humerus fragment from Suomusjärvi, Finland, is considered Miocene in age because of microfossil contents of the attached sediment remnant, and it has been tentatively identified as *Deinotherium* sp. Microfossils from the Suomusjärvi specimen indicate a warm, humid freshwater shore environment, broadly similar to the swamp-forest dominated plant communities from Miocene deposits of Denmark and Iceland. Molars of a tetraconodontine suid and a gomphothere from Sweden add to the Miocene finds from Fennoscandia, although the provenance of the latter is still uncertain.

## Introduction

Much of the Nordic countries, especially Fennoscandia, are almost fully devoid of any Miocene sediments, due to drastic glacial erosion during the Pleistocene. However, locally weak glacial erosion is suggested by the preservation of Mesozoic to Cenozoic palaeosurfaces and saprolites in parts of Sweden and Finland (Söderman 1985, Lidmar-Bergström 1995, Lidmar-Bergström *et al.* 1997, 2000, Gilg *et al.* 2013, Hall *et al.* 2024), indicating that such landforms have survived several glacial events

during the Pleistocene, and thus finding erratic pre-Quaternary fossils from eroded local sources within Fennoscandia is not impossible. In general, relatively little is understood about the climatic and palaeoenvironmental conditions of northern Europe during the Miocene. However, some erratic and fragmentary discoveries of Miocene fossil materials revealed by glacial erosion and transport have brought to attention modest but tantalizing clues about the palaeoenvironmental conditions in northern Europe, including in Finland, during the Miocene. The problem with all these cases is that these isolated

finds are not *in situ* and assessing their provenance is often problematic. However, considering the extent of the Late Pleistocene continental glaciation in northern Europe, and considering that the Miocene materials can only have been carried and re-deposited by glacial processes within this area, it can be argued that these materials broadly represent northern Europe. Furthermore, considering the relatively modest erosion and lack of distortion of the mammal fossils discovered from Fennoscandia (even including attached sediment remnant in the fossil proboscidean humerus from Suomusjärvi, Finland) and the prevalent last glacial maximum (LGM) palaeo-ice stream directions from Gulf of Bothnia towards southeast in southern Finland and south to southwest in Sweden (Punkari 1997), it is likely that all these finds originate from eroded Miocene deposits within the Fennoscandian shield itself and are not likely to have been transported from much further south or east as has been suggested before. We believe Björn Kurtén himself would have been interested in any possibility to evaluate environmental conditions in Finland during the “Tertiary” based on fossil evidence. Here we provide a brief review of Miocene finds from Finland and elsewhere in northern Europe.

Our review centers around one key find: a fragment of a proboscidean humerus (Finnish Museum of Natural History (MZF), specimen KS.KN47425) found in the garden of a lake-shore summerhouse in the village of Salittu on the shore of Enäjärvi in the municipality of Suomusjärvi, southern Finland, and considered to be Miocene in age based on microfossil contents of sediment remnant attached to the fossil (Salonen *et al.* 2016). The story of the discovery of this specimen is as unexpected as the find itself, but we have no reason to doubt it based on the information available to us. The fossil was discovered in about 1960 by a young biology student Marja Sorsa (1939–2018), who identified it as a fragment of a large bone, which at the time was speculated to be perhaps a piece of bone of a mammoth or maybe just a plowing ox. The find was then stored in a cardboard box in a garden shelter and nearly forgotten for decades until the finder, who would later become an esteemed geneticist herself, presented it to professor

Mikael Fortelius at the meeting of the Finnish Academy of Science and Letters in 2006. Fortelius immediately confirmed that it was a piece of a fossil proboscidean humerus, perhaps indeed a mammoth bone. However, the heaviness and re-mineralized appearance of the piece drew attention and raised the intriguing possibility of an older chronological age of the fossil. This was confirmed in 2015 by microfossil analyses from the sediment remnant attached to the fossil, performed by Sakari Salonen (pollen and spores) and Arto Miettinen (diatoms) from the University of Helsinki, and further supported by the analysis of the bone itself by Juha Saarinen, who at the time was working as a visiting researcher at the Natural History Museum, London. The find was published as the northernmost discovery of a Miocene proboscidean fossil by Salonen *et al.* (2016). Björn Kurtén would undoubtedly have been fascinated by this discovery, which together with a couple of other *ex situ* Miocene finds from Sweden, as well as more extensive Miocene deposits in Denmark and Iceland, offers a rare glimpse into the environmental conditions and mammals of northern Europe during the Miocene.

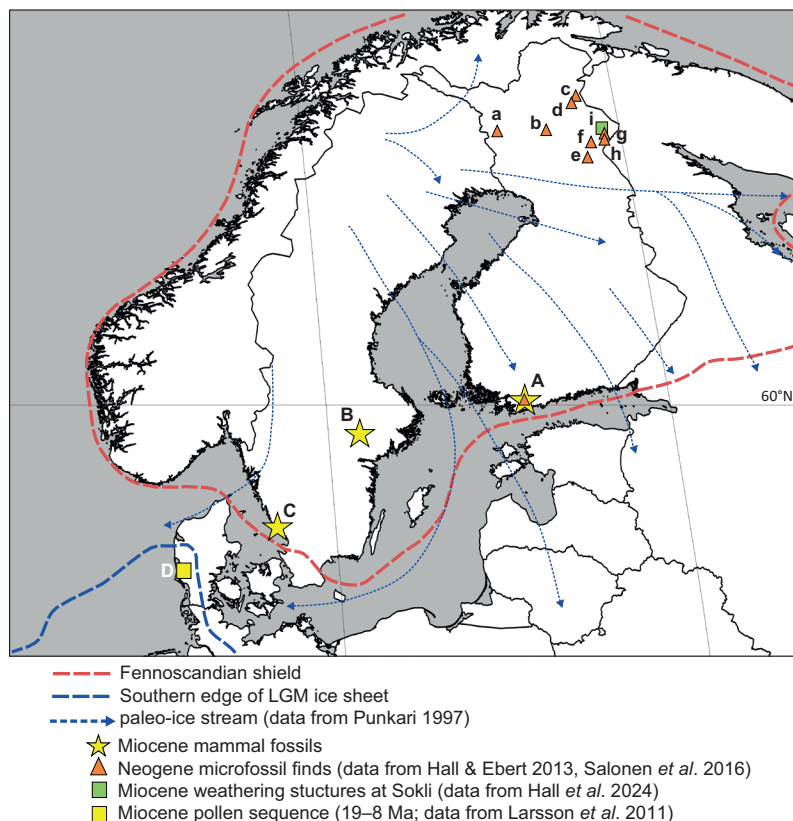
## **Vegetation, palaeoenvironments and climate in northern Europe during the Miocene**

Here, we discuss climate and vegetation in Finland or at least the near surroundings at some point during the Miocene (probably between ca. 16 and 5 Ma) based mainly on a single discovery, a fossilized fragment of a proboscidean humerus with remnants of sediment containing pollen and other microfossils discovered in Suomusjärvi, southern Finland (KS.KN47425, <http://id.luomus.fi/KS.KN47425>), having been re-deposited in early Holocene marine sandy clay by glacial transport (Salonen *et al.* 2016). While pockets of diatomite sediment of Neogene age were discovered in Naruskajärvi, Salla, and smaller concentrations of reworked Neogene diatoms also in other localities in northern Finland (Hirvas & Tynni 1976, Tynni 1982, Saarnisto *et al.* 1999, Hall & Ebert 2013), their palaeoenvironmental implications have to our knowledge not been

discussed, except for demonstrating the presence of freshwater environments in the region during the Neogene. In addition to Neogene freshwater diatoms, some erratic finds of redeposited pre-Quaternary Cenozoic palynomorph types were also discovered, including *Ephedra* and *Stereisporites* from Akanvaara, Savukoski (Hirvas & Tynni 1976), and *Podocarpus* from Tepsankumpu, Kittilä (Saarnisto *et al.* 1999), but their age as well as whether they come from locally reworked material or from a longer distance via wind transport are uncertain (Hall & Ebert 2013). Thus, we consider the Suomusjärvi find to represent the only confirmed case of a local palynomorph sample of Miocene age identified from Fennoscandia. We also discuss other discoveries from the Nordic countries that provide clues as to the climate and environmental conditions in northern Europe during the Miocene.

The brownish silty sediment remnant in the proboscidean humerus fragment from Suomusjärvi (clearly different from the Holocene clay in which the fossil was found) contained microfossils that originally led to the establishment of Miocene age for the fossil (Salonen *et al.* 2016). Of particular importance in this regard was the presence of fossils of freshwater diatoms of the genus *Alveolophora*, which existed primarily from the Late Eocene to the end of the Miocene, although a single find was considered Early Pliocene in age by Kozyrenko *et al.* (2008). Further clues about the age of the find came from tentative identification of the proboscidean as *Deinotherium*, a genus found in Eurasia from the Middle to the Late Miocene (Göhlich 1999, Vislobokova 2005, Cantalapiedra *et al.* 2021, and NOW — Database of fossil mammals, <https://doi.org/10.5281/zenodo.4268068>, Žliobaite *et al.* 2023). Although a more precise age estimate was not possible, it was tentatively discussed that a relatively early, possibly Middle Miocene, age is plausible, because there are subtropical elements in the fossil pollen sample (*see below*) that suggest warm climatic conditions, tentatively supported by the relatively modest size of the humerus itself, which is morphometrically closer to the Middle Miocene *Deinotherium levius* than the on average larger Late Miocene *Deinotherium giganteum* and *D. proavum* (Salonen *et al.* 2016).

Although the Suomusjärvi proboscidean fossil was not *in situ*, we argue that it is likely to originate from a relatively local source area within Fennoscandia, although Salonen *et al.* (2016) discussed a possibility of it originating from the Russian plain towards the east based on alkalinity of the sediment remnant. This interpretation is supported by several observations. First, considering the extent of the Late Pleistocene continental ice sheets, it is likely that the fossil had been transported from approximately the same latitude or even further north, thus making it possibly the northernmost terrestrial Miocene mammal fossil known from anywhere (Salonen *et al.* 2016). Second, considering the northwest-to-southeast direction of the LGM palaeo-ice streams originating from the Scandinavian mountains (Punkari 1997; *see Fig. 1*) and similarly oriented glaciofluvial transport directions during the melting phase, the most likely source of the Suomusjärvi fossil is towards the north-west or north from where it was discovered. Despite being transported by ice-rafting and re-deposited in shallow marine clay during the melting phase of the last glacial ice sheet, it is likely that the fossil was transported following the flow direction of the ice and meltwaters. Glaciofluvial transport distances of clasts in southwestern Finland were typically short (Kaitanen *et al.* 1978), although ice rafting could have carried the Suomusjärvi fossil from further away (but perhaps unlikely against the main meltwater flow directions). Hall and Ebert (2013) considered local reworking the likely source of Neogene freshwater diatoms in Lapland. Furthermore, a relatively local origin from eroded material within Fennoscandia is supported by relatively weak erosion of the specimen, even containing remnants of the compacted Miocene sediment exposed on its surface. No Miocene mammal fossils have been reported from northwestern Russia near Finland (*see* NOW — Database of fossil mammals, <https://doi.org/10.5281/zenodo.4268068>, Žliobaite *et al.* 2023), which was proposed by Salonen *et al.* (2016) as a possible source area for the Suomusjärvi find, further making origin from that area unlikely. A possible local source for the alkalinity of the sediment remnant in the Suomusjärvi fossil could be the metamorphic calcite deposits of southern Finland (Saranpää *et al.* 2001). Thus, we suggest that a



**Fig. 1.** Miocene finds in Fennoscandia and Denmark. — **A:** Salittu, Enäjärvi, Suomusjärvi (data from Salonen *et al.* 2016). — **B:** Eskilstuna (data from Mörs & Tütken 2008). — **C:** Falkenberg (data from Mörs *et al.* 2019). — **D:** Sønder Vium (data from Larsson *et al.* 2011). — **a:** Sivakkapalo. — **b:** Siurunmaa. — **c:** Riukuselkä. — **d:** Kopsujärvi. — **e:** Kankaanlampi. — **f:** Akanvaara. — **g:** Värriöjoki. — **h:** Naruskajärvi. — **i:** Sokli.

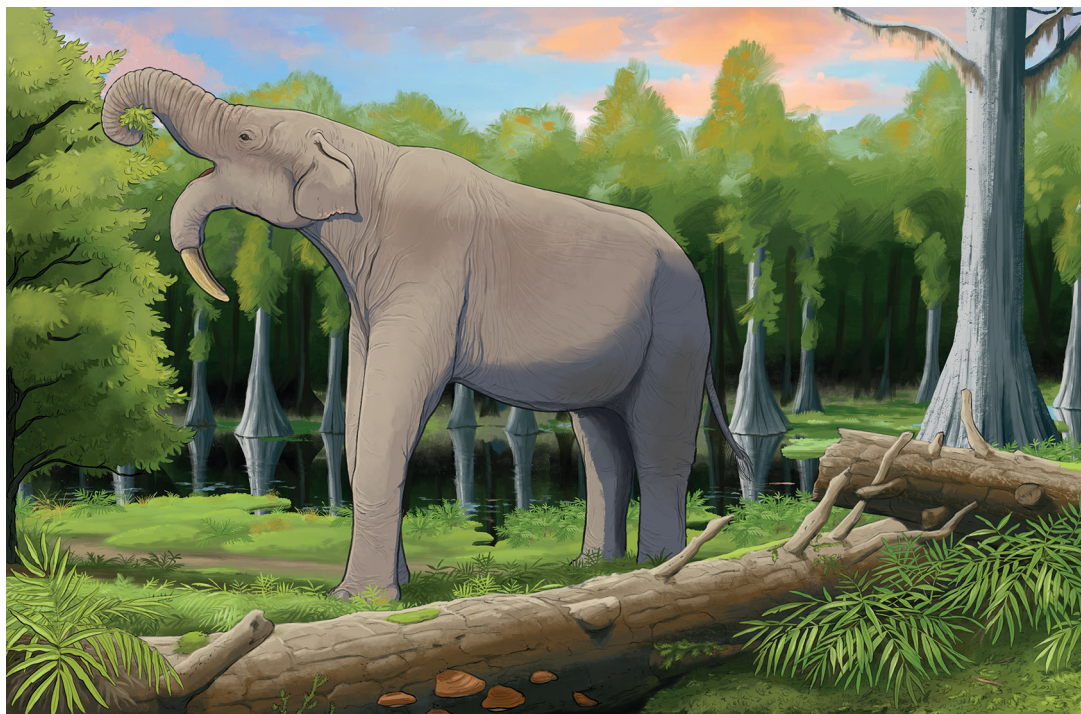
local origin of the Suomusjärvi fossil within Fennoscandia is most likely.

Some interpretation of the climate and palaeoenvironment associated with the Suomusjärvi fossil was possible based on the analysis of fossil palynomorph contents of the associated sediment remnant (Salonen *et al.* 2016). Particularly informative in this regard was the presence of spores of the fern *Pteridacidites variabilis*, which is considered ancestral to the modern Cretan brake fern (*Pteris cretica*). In fact, *P. variabilis* was the dominant palynomorph in the sample from the Suomusjärvi specimen. The second most common palynomorph type was the spores of spike mosses of the genus *Selaginella*. In addition to these, the Miocene palynomorph assemblage includes pollen of coniferous trees of the family Cupressaceae (other than *Juniperus*, which has been the common Quaternary

taxon in the region) and *Dryopteris*-type spores. These clear pre-Quaternary types occurred mixed with pollen types that were considered possibly Quaternary in origin (Salonen *et al.* 2016), such as *Pinus* and *Betula*, although all of those taxa are also known from Miocene pollen assemblages from other northern European locations (for example Iceland; Denk *et al.* 2011) making this determination inconclusive. Further, because pollen can be carried by long-distance wind transport (e.g., Hall & Ebert 2013), some of the pollen occurring along the relatively more abundant pteridophyte spores may not be indicative of the local vegetation at site of deposition of the Suomusjärvi bone.

The microfossil community from the Miocene proboscidean fossil from Suomusjärvi indicates at least a warm-temperate or subtropical climate. Moreover, based on the exceptional





**Fig. 2.** Tentative reconstruction of a Miocene environment in northern Europe, based mainly on the fossil proboscidean humerus fragment (Finnish Museum of Natural History, specimen KS.KN47425), and associated palynomorph sample from Suomusjärvi, Finland. The ground-level vegetation of the moist shoreline environment is dominated by *Pteris*-type ferns and spike mosses (*Selaginella*). Wetland with swamp cypresses is shown in the background, based on abundant evidence of the presence of such environments in northern Europe as demonstrated by palynological evidence from the Miocene deposits in Denmark and Iceland. Pre-Quaternary Cupressaceae were also present in the Suomusjärvi microfossil sample, although their preservation did not allow them to be determined more precisely than to the family level. *Deinotherium* (of a late Middle to early Late Miocene European morphotype) is shown browsing on an alder. Artwork by Maija Karala.

number of fern spores (over 50%) in the pollen sample, it was judged that the bone must have been deposited close to the shore of a freshwater lake or a stream, which resulted in strong representation of the local riparian plant assemblage in the pollen sample (Salonen *et al.* 2016). *Pteris cretica*, the closest modern analogue to the dominant palynomorph *Pteridacidites variabilis*, is today associated with warm and humid climate and shoreline habitats in forest environments, suggesting broadly similar conditions for the Suomusjärvi find, although it should be kept in mind that the ecology of the fossil *Pteridacidites* may not be fully analogous to the present *Pteris*. However, also *Selaginella* is found today in warm, humid forest environments, further supporting the interpretation of such palaeoenvironmental conditions. A reconstruction of a

palaeoenvironment in northern Europe during the Miocene, based mainly on an interpretation of the palynomorphs from the Suomusjärvi fossil find and the proboscidean fossil itself, is shown in Fig. 2.

The palynology-based climatic and palaeoenvironmental interpretations of the Suomusjärvi find are broadly similar to those from other Miocene records in northern Europe, both those coming from further south (Jylland, Denmark (Larsson *et al.* 2011) and those coming from even further north (Iceland; Grímsson *et al.* 2007, Denk *et al.* 2011). A common feature of all these records is the prevalence of warm-temperate to subtropical humid swamp forest elements, such as swamp cypresses (*Taxodium* and *Glyptostrobus*), or the *Pteridacidites* ferns. Remarkably, the long palynological record from Jylland, Den-

mark, ranging from the Early Miocene ca. 19 Ma to the Late Miocene ca. 8 Ma, indicates mostly relatively warm and humid climatic conditions throughout the sequence, with some brief cooling events in late Early Miocene and late Middle Miocene, suggesting a persistence of a shallow temperature gradient and mostly warm-temperate climatic conditions in northern Europe during the Miocene, at least until ca. 8 Ma (Larsson *et al.* 2011). Estimated mean annual temperatures were between 15 °C and 20 °C throughout the Miocene sequence from Jylland, with consistently high estimated mean annual precipitation ranging from 1200 to 1600 mm (Larsson *et al.* 2011). The largest change from the Middle to the Late Miocene in Jylland seems to have been gradual loss of subtropical swamp forest plants starting between 10 and 9 Ma. Thus, the interpreted warm, humid forest and freshwater shoreline environment from Suomusjärvi could be representative of much of the Miocene in northern Europe. However, due to the fact that the Suomusjärvi fossil is likely to have originated from much further north than the Danish records, it is perhaps more likely to be representative of a relatively warm phase of the Miocene, perhaps close to the temperature optimum during the Middle Miocene (Steinhorsdottir *et al.* 2021), as Larsson *et al.* (2011) considered Fennoscandia to be a source of cool-temperate pollen types in the record from Denmark during most of the Miocene. In fact, during the globally warm Middle Miocene, warm-temperate swamp forests with such “exotic” elements as water pines (*Glyptostrobus europaeus*, Cupressaceae) and magnolia trees (*Magnolia* sp., Magnoliaceae) existed as far north as Iceland (Grimsson *et al.* 2007).

## Geological and geochemical evidence of climate and landscapes in Fennoscandia during the Miocene

An important additional clue about climatic conditions in Finland during the Miocene comes from chemical weathering structures (saprolites) formed during the Middle Miocene Climatic Optimum (MMCO) in Palaeozoic deposits of the westernmost member of the Kola Alkaline Prov-

ince in Sokli in Savukoski, northeastern Lapland (Hall *et al.* 2024). The formation of apatite-francolite in Sokli, as the result of carbonatite weathering under warm, humid climate, started during the Palaeogene. However, later cryptomelane (K-Mn oxide) crusts formed on top of these weathering structures, and  $^{40}\text{Ar}/^{39}\text{Ar}$  dating indicated that they formed during the MMCO, ca. 16.9–14.7 Ma (Hall *et al.* 2024). This finding demonstrates that the MMCO triggered intensified weathering under warm and humid climatic conditions as high north as in the Arctic, and the mean annual temperature in Sokli was probably about 12–14 °C higher than the current ca. 1 °C (Hall *et al.* 2024).

Cenozoic uplift of the Fennoscandian shield led to exposure of Phanerozoic peneplains as well as deep weathering of the exposed lowland landforms in large parts of Fennoscandia, from northern Finland towards southwest to Sweden and southern Norway (Söderman 1985, Lidmar-Bergström 1995, Lidmar-Bergström *et al.* 1997, 2000, Lidmar-Bergström & Näslund 2002, Gilg *et al.* 2013). The Baltic Sea Basin was characterized by the Baltic (Eridanos) River system and subsequent fluvial erosion and deposition during the Miocene (Gibbard & Lewin 2016). These features of the landscape of Fennoscandia during the Miocene set a broader framework for the erratic large mammal fossil and microfossil discoveries, which would have originated either from lowland terrestrial landscapes characterized by chemical weathering under relatively warm and humid climatic conditions in Sweden and Finland, or from the fluvial realm of the Baltic River system in the Baltic Sea basin between Sweden and Finland.

Gilg *et al.* (2013) studied several kaolin formations from northern and southeastern Finland (Eteläkylä and Litmanen (Virtasalmi) SE Finland; and Siurunmaa (Sodankylä), and Vittajänkä (Salla), N Finland), suggesting based on oxygen and hydrogen isotope ratios that they formed under lower temperatures than have been usually assumed (mean annual temperatures between 13 °C and 15 °C). Kaolins are mostly assumed to form under tropical climatic conditions, but Gilg *et al.* (2013) argued that the kaolins from Finland formed in lower temperatures, nonetheless as a result of long-term exposure to

high humidity. However, it should be noted that the mean annual temperatures of 13–15 °C are much higher than the mean annual temperatures in central and northern Finland today (ca. –3 to +3 °C), being instead characteristic of the cooler end of the modern-world subtropical climate belt, for example in the southeastern United States. Gilg *et al.* (2013) considered such mild climatic conditions in Finland to suggest either Palaeocene–Eocene or alternatively Early to Middle Miocene age for the Finnish kaolins. The suggested warm-temperate, humid climatic conditions interpreted for these kaolins are similar to those interpreted for the Middle Miocene weathering structures at Sokli (Hall *et al.* 2024), and also align with the aforementioned palaeobotanical evidence from the Suomusjärvi bone as well as other northern European localities.

## Miocene terrestrial mammal fossils from northern Europe

While Neogene mammal assemblages are not known from northern Europe, a few fascinating but isolated finds of Miocene terrestrial mammal fossil specimens have been discovered. We again begin with discussing the only such find from Finland, the humerus fragment of a proboscidean (probably deinothere) from Suomusjärvi, mentioned above (specimen KS.KN47425). We then discuss a couple of other finds from Fennoscandia, which include a tetraconodontine suid molar and a gomphotheriid proboscidean molar from Sweden (although the latter having a more uncertain provenance) (for locations *see* Fig. 1).

The proboscidean fossil from Suomusjärvi is a fragment from the middle of the diaphysis of a left humerus, preserving the narrowest section of the bone. Although it is fragmentary and somewhat weathered, there does not appear to be any obviously heavy distortion to the overall morphology. It was tentatively identified as belonging to a deinothere of the genus *Deinotherium* by J. Saarinen (*see* Salonen *et al.* 2016), mainly based on the lack of prominent crista humeri that tends to be strong in most kinds of proboscideans but is reduced in *Deinotherium*, resulting in a rounded rather than triangular cross-section of the mid-diaphysis (*see* Huttunen 2002). Morpho-

metrically the Suomusjärvi humerus (assuming it comes from an adult individual, which is impossible to assess with certainty) represents the smallest end of the size range of *Deinotherium*, similar to some specimens of *D. levius* from the Middle Miocene of Europe, and possibly some individuals of the early Late Miocene *D. giganteum* (Salonen *et al.* 2016).

Estimated body mass for this specimen, calculated using the regression equations from Christiansen (2004) based on relationships between body mass and postcranial bone measurements in extant elephants, ranges from 4700 kg (based on mid-shaft least circumference) to 5020 kg (based on mid-shaft least width). As compared with the other *Deinotherium* species, it is closest in estimated size to the *D. levius* vel *giganteum* (body mass 4878 kg calculated based on radius length using the equations from Christiansen (2004)) whose fragmentary skeleton was discovered from the Middle Miocene locality of Gratkorn, Austria (Aiglstorfer *et al.* 2014). Also, a partial deinotheres skeleton from Munich, Germany, assigned to *D. giganteum* by Stromer (1938), allowed for estimation of similar body mass (5200 kg) based on humerus mid-shaft width. Other specimens of *Deinotherium* tend to be larger on average. For example, a *D. levius* from Gusyatin, Ukraine, described by Svistun (1974), has an average estimated body mass of ca. 8600 kg based on several postcranial bone measurements using the equations from Christiansen (2004), and the late Miocene *D. giganteum* and *D. proavum* body mass estimates typically range from ca. 6000 to ca. 15 000 kg, averaging around 11 000 kg (Christiansen 2004, Saarinen 2009, Larramendi 2016).

Assuming the identification of the Suomusjärvi humerus as *Deinotherium* is correct, the presence of this taxon in northern Europe during the Miocene further corroborates the interpretation of the presence of predominantly wooded vegetation in the region. Palaeodietary analyses have consistently demonstrated purely browsing diets, probably mostly folivory, for the deinotheres across their range in time and on different continents (e.g. Cerling *et al.* 1999, Calandra *et al.* 2008, Lopenon 2020, Xafis *et al.* 2020, Saarinen & Lister 2023, Konidaris *et al.* 2023).



Furthermore, a specialized canopy-level browsing ecology has been suggested for the deinotheres based on a combination of their traits, including tapir-like bilophodont molar morphology, tall stature due to relatively long limb elements, and downturned lower tusks and lack of upper tusks in combination with a probably quite short proboscis to facilitate browsing among canopy thickets (Harris 1975, Markov *et al.* 2001).

Besides the palaeoenvironmental implications, the Suomusjärvi humerus is remarkable in representing possibly the northernmost Miocene find of a fully terrestrial mammal globally (although semi-aquatic carnivoran fossils from the Miocene are known from further north, from Arctic Canada; Rybczynski *et al.* 2009). The Suomusjärvi humerus demonstrates the presence of proboscideans in northern Europe, although a gomphothere molar from south of Lake Mälär in Sweden was found just a little bit southward (but has a somewhat uncertain provenance, as discussed below). Interestingly, Osborn (1936) mentioned another comparatively northern proboscidean find from the western side of the Ural Mountains, Russia, which was named “*Dinotherium uralense*” by Eichwald (1831). However, this taxon has not been revised since then, the current location of the material seems to be unknown and its validity is questionable (e.g., Markov 2004).

A lower third molar of a tetraconodontine suid (NRM-PZ-M8135) was discovered in Falkenberg, Halland, southern Sweden and described by Mörs *et al.* (2019). The location of this find is considerably more southern than that of the Suomusjärvi find, and although it was discovered as an *ex situ* find on a beach, it was located near the Miocene deposits of Denmark to the south-west. Mörs *et al.* (2019) discussed three possible source areas for the find, one of which was the Miocene deposits in Denmark, another one could be eroded and lost Miocene sediments from central or northern Sweden or the Baltic Sea (which could also be the provenance of the gomphothere molar found south of Lake Mälär in Sweden), and the third possibly the Miocene deposits further east in the Russian Plain. The provenance was left uncertain, although the Miocene sediments of Denmark were considered the closest possible source (Mörs *et al.* 2019). How-

ever, transport from Denmark seems unlikely, because it would be against the east-to-west-oriented palaeo-ice stream in that area during the LGM (Fig. 1). Similarly, transport from as far east as western Russia seems highly unlikely, also being against the prevalent LGM ice flow and meltwater flow directions that are oriented from northwest towards southeast in eastern Fennoscandia (Fig. 1). Furthermore, the Miocene deposits in Denmark are located south-west from the southern edge of the maximum extent of LGM north-European ice sheets (Fig. 1). Thus, a more local source area, probably north from where the Falkenberg fossil was found, seems like the most likely source area. Tetraconodontine suids were present in Europe between ca. 16 and 10 Ma, suggesting that the Falkenberg specimen comes from within this age range (Mörs *et al.* 2019). Morphometrically the Falkenberg tetraconodontine molar falls within the range of *Conohyus simorreensis*, a common Middle Miocene tetraconodontine known from France, Spain and central Europe. However, Mörs *et al.* (2019) considered several morphological traits of the Falkenberg specimen to be non-analogous to other European Miocene tetraconodontines, including relatively high tooth crown and a prominent hypoconulid. The tetraconodontines had a wide distribution and they seem to have occupied various habitats (Fortelius *et al.* 1996), making it difficult to say anything more about the palaeo-environment based on their presence in northern Europe during the Miocene.

Finally, a third intriguing Miocene mammal fossil discovery from Fennoscandia is a specimen of a first or second lower molar of a gomphotheriid proboscidean found in a conglomeratic sandstone cobble redeposited in Pleistocene glaciofluvial deposits south of Lake Mälär in Eskilstuna, central Sweden (Mörs & Tütken 2008, Tütken & Mörs 2008, Mörs *et al.* 2019). A comprehensive description of this specimen is, however, not yet published so we mention it provisionally as a possible additional find of a Miocene mammal fossil from northern Europe, noting that the provenance of this specimen is currently considered uncertain (Mörs *et al.* 2019). Based on analysis of C, O, Sr and Nd isotope composition of the specimen, Mörs and Tütken (2008) and Tütken and Mörs (2008)



suggested that the likely provenance of the specimen is within the Fennoscandian shield, as they reflect the isotopic ratio of old crustal rocks. However, the provenance of the specimen was later considered unproven (Mörs *et al.* 2019). Nonetheless, as with the Suomusjärvi and Falkenberg fossils, a local source area within Fennoscandia seems plausible considering that the Eskilstuna fossil is in good condition and was found in glaciofluvial deposits which extend a short distance northward (A. Hall pers. comm.). Mörs and Tütken (2008) mentioned *Gomphotherium* or *Amebelodon* as possible taxonomic identifications of the specimen, although the latter is known primarily from North America and is the less likely identification. From available photographs of the specimen, the identity as *Gomphotherium* seems plausible because of the relatively simple morphology and cusp alignment in relatively straight transverse rows. *Gomphotherium* was an ecologically versatile and widespread genus in Europe during the Early and Middle Miocene, and it occupied a wide range of environments from open and dry savannas and semi-deserts in Spain (Menéndez *et al.* 2017) to warm-temperate forests, woodlands and wetlands in central Europe (e.g., Eronen & Rössner 2007). Dietary analyses of Miocene European *Gomphotherium* indicate mixed-feeding in more open environments, for example in Spain and France, and browse-dominated feeding in more forested areas in central and eastern Europe (Calandra *et al.* 2008, Lopenen 2020, Xafis *et al.* 2020, and first author's unpubl. data). Thus, the presence of this taxon constitutes a typical faunal element in Early to Middle Miocene Europe rather than being associated with a particular type of palaeoenvironment. Further description of the fossil is needed to evaluate its potential palaeoenvironmental implications.

## Conclusions

Although there is no direct evidence of environmental and climatic conditions in Finland during the Miocene, a single *ex situ* Miocene mammal find from Finland, the partial proboscidean humerus from Suomusjärvi, southern Finland, brought by glacial transport from the vicinity,

and a couple of other finds from Fennoscandia, as well as microfossil evidence from *in situ* Miocene sediments from Denmark and Iceland, allow bracketing of environmental conditions of Finland during parts of the Miocene with reasonable confidence. The palynomorph assemblage from the Suomusjärvi specimen is dominated by *Pteridacidites* and *Selaginella* spores and pollen of cypress trees, which by modern analogue indicate the presence of a warm-climate wooded shoreline environment, while pollen assemblages from Denmark and Iceland also demonstrate prominent presence of warm-climate swamp forest plants such as swamp cypresses (Taxodiaceae). Lowland landscapes with prominent chemical weathering under relatively warm and humid climatic conditions prevailed in Finland at least during the Middle Miocene Climatic Optimum, as evidenced by saprolite formations. Combining these lines of evidence suggest that conditions in Finland were warm-temperate and environments were characterized by warm, relatively humid forests and wetlands, at least during the warmest stages of the Miocene. Isolated, allochthonous finds of Miocene proboscidean and suid fossils from Fennoscandia demonstrate similarity to Miocene mammals from central Europe. The tentative identification of the humerus fragment of a proboscidean from Suomusjärvi as *Deinotherium* secondarily supports the interpretation of wooded environmental conditions in northern Europe during the Miocene.

## Acknowledgements

We thank the Finnish Museum of Natural History for providing access to the proboscidean humerus from Suomusjärvi. We thank Marja Sorsa, Arto Miettinen, Heikki Hirvas, Maria Uusoltseva and Mikael Fortelius, who participated in the study of the Suomusjärvi specimen, as well as Thomas Mörs and Lars Werdelin from the Naturhistoriska Riksmuseet, Stockholm, for discussions on the Miocene mammal fossils from Sweden. Finally, we hold special gratitude to the late Marja Sorsa for bringing the Suomusjärvi specimen to the attention of University of Helsinki palaeontologists, as well as for her participation in its later study. We thank the reviewers Thomas Mörs and Adrian Hall for their positive and constructive feedback that helped us improve this work. We owe special thanks to Maija Karala for the insightful reconstruction of a Miocene environment from Fennoscandia based on careful interpretation of the palaeobotanical, fossil mammal and climatic evidence from the Suomusjärvi fossil find from

Finland. This work was supported by the Research Council of Finland projects 331426 and 340775/346292.

## References

- Aiglstorfer, M., Göhlich, U. B., Böhme, M. & Gross, M., 2014: A partial skeleton of *Deinotherium* (Proboscidea, Mammalia) from the late middle Miocene Gratkorn locality (Austria). — *Palaeobiodiversity and Palaeoenvironments* 94: 49–70.
- Calandra, I., Göhlich, U. B. & Merceron, G. 2008: How could sympatric megaherbivores coexist? Example of niche partitioning within a proboscidean community from the Miocene of Europe. — *Naturwissenschaften* 95: 831–838.
- Cantalapiedra, J. L., Sanisidro, O., Zhang, H., Alberdi, M. T., Prado, J. L., Blanco, F. & Saarinen, J. 2021: The rise and fall of proboscidean ecological diversity. — *Nature Ecology & Evolution* 5: 1266–1272.
- Cerling, T., Harris, J. & Leakey, M. 1999: Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. — *Oecologia* 120: 364–374.
- Christiansen, P. 2004: Body size in proboscideans, with notes on elephant metabolism. — *Zoological Journal of the Linnean Society* 140: 523–549.
- Denk, T., Grimsson, F., Zetter, R. & Simonarson, L. A. 2011: *Late Cainozoic floras of Iceland*. — Springer, Dordrecht.
- Eichwald, E. (ed.) 1831: *Zoologia Specialis quam expositis animalibus tum vivam, tum fossilibus potissimum Rossiae in universum, et Poloniae in specie*. — Zoologia Specialis, Pars Prior, typis Josephi Zawadzki, Vilnae.
- Eronen, J. & Rössner, G. E. 2007: Wetland paradise lost: Miocene community dynamics in large herbivorous mammals from the German Molasse Basin. — *Evolutionary Ecology Research* 9: 471–494.
- Fortelius, M., van der Made, J. & Bernor, R. L. 1996: Middle and late Miocene Suoidea of central Europe and the eastern Mediterranean: evolution, biogeography, and paleoecology. — In: Bernor, R. L., Fahlbusch, V. & Mittmann H.-W. (eds.), *The evolution of western Eurasian Neogene mammal faunas*: 348–377. Columbia University Press.
- Gibbard, P. L. & Lewin, J. 2016: Filling the North Sea Basin: Cenozoic sediment sources and river styles (André Dumont medallist lecture 2014). — *Geologica Belgica* 19: 201–217.
- Gilg, H. A., Hall, A. M., Ebert, K. & Fallick, A. E. 2013: Cool kaolins in Finland. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 392: 454–462.
- Grimsson, F., Denk, T. & Simonarson, L. A. 2007: Middle Miocene floras of Iceland — the early colonization of an island? — *Review of Palaeobotany and Palynology* 144: 181–219.
- Göhlich, U. B. 1999: Order Proboscidea. — In: Rössner, G. E. & Heissig, K. (eds.), *The Miocene land mammals of Europe*: 57–75. — Pfeil, München.
- Hall, A. M. & Ebert, K. 2013: Cenozoic microfossils in northern Finland: local reworking or distant wind transport? — *Palaeogeography, Palaeoclimatology, Palaeoecology* 388: 1–14.
- Hall, A. M., Barfod, D. N., Gilg, H. A., Stuart, F. M., Sarala, P. & Al-Ani, T. 2024: Intensive chemical weathering in the Arctic during the Miocene Climatic Optimum. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 634, 111927, <https://doi.org/10.1016/j.palaeo.2023.111927>.
- Harris, J. M. 1975: Evolution of feeding mechanisms in the family Deinotheriidae (Mammalia: Proboscidea). — *Zoological Journal of the Linnean Society* 56: 331–362.
- Hirvas, H. & Tynni, R. 1976: Tertiary clay deposits at Savukoski, Finnish Lapland, and observations of Tertiary microfossils, preliminary report. — *Geologi* 28: 33–40. [In Finnish with English summary].
- Huttunen, K. 2002: Systematics and taxonomy of the European Deinotheriidae (Proboscidea, Mammalia). — *Annalen des Naturhistorischen Museums in Wien A* 103: 237–250.
- Kaitanen, V. & Ström, O. 1978: Shape development of sandstone cobbles associated with the Säkylä-Mellilä esker, southwest Finland. — *Fennia — International Journal of Geography* 155: 23–66.
- Konidaris, G., Lechner, T., Kampouridis, P. & Böhme, M. 2023: *Deinotherium levius* and *Tetralophodon longirostris* (Proboscidea, Mammalia) from the Late Miocene hominid locality Hammerschmiede (Bavaria, Germany), and their biostratigraphic significance for the terrestrial faunas of the European Miocene. — *Journal of Mammalian Evolution* 30: 923–961.
- Kozyrenko, T. F., Strelnikova, N. I., Khursevich, G. K., Tsoy, I. B., Yakovschikov, T. K., Mukhina, V. V., Olshynskaja, A. P. & Semina, G. I. [Козыренко, Т. Ф., Стрельникова, Н. И., Хурсевич, Г. К., Цой, И. Б., Жаковщикова, Т. К., Мухина, В. В. & Семина, Г. И.] 2008: *[The diatoms of Russia and adjacent countries, vol. II(5): fossil and recent]*. — St. Petersburg University Press, St. Petersburg. [In Russian].
- Larramendi, A. 2016: Shoulder height, body mass, and shape of proboscideans. — *Acta Palaeontologica Polonica* 61: 537–574.
- Larsson, L. M., Dybkjær, K., Rasmussen, E.S., Piasecki, S., Utescher, T. & Vajda, V. 2011: Miocene climate evolution of northern Europe: a palynological investigation from Denmark. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 309: 161–171.
- Lidmar-Bergsröm, K. 1995: Relief and saprolites through time on the Baltic Shield. — *Geomorphology* 12: 45–61.
- Lidmar-Bergsröm, K., Olsson, S. & Olvmo, M. 1997: Palaeosurfaces and associated saprolites in southern Sweden. — *Geological Society of London, Special Publication* 120: 95–124.
- Lidmar-Bergström, K. & Näslund, J. O. 2002: Landforms and uplift in Scandinavia. — *Geological Society of London, Special Publication* 196: 103–116.
- Lidmar-Bergström, K., Ollier, C. D. & Sulebak, J. R. 2000: Landforms and uplift history of southern Norway. — *Global and Planetary Change* 24: 211–231.
- Loponen, L. 2020: *Diets of Miocene proboscideans from Eurasia, and their connection to environments and vegetation*. — M.Sc. thesis, University of Helsinki, <http://hdl.handle.net/10138/318862>.
- Markov, G. N. 2004: The fossil proboscideans of Bulgaria

- and the importance of some Bulgarian finds — a brief review. — *Historia naturalis bulgarica* 16: 139–150.
- Markov, G. N., Spassov, N., Simeonovski, V. 2001: A reconstruction of the facial morphology and feeding behaviour of the deinotheres. — In: Cavaretta, G., Gioia, P., Mussi, M., Palombo, M. R. (eds.), *The world of elephants*: 652–655. Consiglio Nazionale delle Ricerche, Roma.
- Menéndez, I., Gómez Cano, A. R., García Yelo, B. A., Domingo, L., Domingo, M.S., Cantalapiedra, J. L., Blanco, F. & Hernández Fernández, M. 2017: Body-size structure of central Iberian mammal fauna reveals semi-desertic conditions during the middle Miocene Global Cooling Event. — *PLoS ONE* 12(10), e0186762, <https://doi.org/10.1371/journal.pone.0186762>.
- Mörs, T. & Tütken, T. 2008: First Tertiary land mammal from Scandinavia: paleontology and isotope fingerprinting. — *Journal of Vertebrate Paleontology* 28: 118A.
- Mörs, T., Liu, L. & Hagström, J. 2019: A Miocene tetracondontine (Suidae, Mammalia) from Falkenberg (Halland, Sweden). — *GFF* 141(1): 77–81.
- Osborn, H. F. 1936: *Proboscidea*, vol. 1. — American Museum Press, New York.
- Punkari, M. 1997: Glacial and glaciofluvial deposits in the interlobate areas of the Scandinavian Ice Sheet. — *Quaternary Science Reviews* 16: 741–753.
- Rybczynski, N., Dawson, M. R. & Tedford, R. H. 2009: A semi-aquatic Arctic mammalian carnivore from the Miocene epoch and origin of Pinnipedia. — *Nature* 458: 1021–1024.
- Saarinen, J. 2009: *Body mass patterns of Eurasian Miocene large land mammals and their connections to environment and climate*. — M.Sc. thesis, University of Helsinki.
- Saarinen, J. & Lister, A. M. 2023: Fluctuating climate and dietary innovation drove ratcheted evolution of proboscidean dental traits. — *Nature Ecology & Evolution* 7: 1490–1502.
- Saarnisto, M., Eriksson, B. & Hirvas, H. 1999: Tepsankumpu revisited — pollen evidence of stable Eemian climates in Finnish Lapland. — *Boreas* 28: 12–22.
- Salonen, J. S., Saarinen, J., Miettinen, A., Hirvas, H., Usoltseva, M., Fortelius, M. & Sorsa, M. 2016: The northernmost discovery of a Miocene proboscidean bone in Europe. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 454: 202–211.
- Saranpää, O., Reinikainen, J., Seppänen, H., Kärkkäinen, N. & Ahtola, T. 2001: Industrial minerals exploration in southwestern and western Finland. — *Geological Survey of Finland, Special Paper* 31: 31–40.
- Steinthorsdottir, M., Coxall, H. K., de Boer, A. M., Huber, M., Barbolini, N., Bradshaw, C. D., Burls, N. J., Feakins, S. J., Gasson, E., Hendriks, J., Holbourn, A. E., Kiel, S., Kohn, M.J., Knorr, G., Kürschner, W. M., Lear, C. H., Liebrand, D., Lunt, D. J., Mörs, T., Pearson, P. N., Pound, M. J., Stoll, H. & Strömberg, C. A. E. 2021: The Miocene: the future of the past. — *Paleoceanography and Paleoclimatology* 36, e2020PA004037, <https://doi.org/10.1029/2020PA004037>.
- Stromer, E. 1938: Huftier-Reste aus dem unterstpliocänen Flinzsande Münchens. — *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung* 44: 1–39.
- Söderman, G. 1985: Planation and weathering in eastern Fennoscandia. — *Fennia* 163(2): 347–352.
- Svistun, V. I. [Свистун, В. И.] 1974: [*Deinotherium of Ukraine*]. — Izdatel'stvo "Naukova dumka", Kiev. [In Russian].
- Tynni, R. 1982: The reflection of geological evolution in tertiary and interglacial diatoms and silicoflagellates in Finnish Lapland. — *Geological Survey of Finland, Bulletin* 320: 1–40.
- Tütken, T. & Mörs, T. 2008: Isotope fingerprinting of the first Tertiary land mammal from Scandinavia. — *Geochimica et Cosmochimica Acta* 72: 12.
- Vislobokova, I. 2005: On Pliocene faunas with proboscideans in the territory of the former Soviet Union. — *Quaternary International* 126–128: 93–105.
- Xafis, A., Saarinen J., Nagel, D. & Grimsson, F. 2020: Palaeodietary traits of large mammals from the middle Miocene of Gračanica (Bugojno Basin, Bosnia-Herzegovina). — *Palaeobiodiversity and Palaeoenvironments* 100: 457–477.
- Žliobaite, I., Fortelius, M., Bernor, R. L., van den Hoek Ostende, L., Janis, C. M., Lintulaakso, K., Sällä, L. K., Werdelin, L., Casanovas-Vilar, I., Croft, D., Flynn, L., Hopkins, S. S. B., Kaakinen, A., Kordos, L., Kostopoulos, D. S., Pandolfi, L., Rowan, J., Tesakov, A., Vislobokova, I., Zhang, Z., Aiglstorfer, M., Alba, D. M., Arnal, M., Antoine, P. O., Belmaker, M., Bilgin, M., Boisserie, J.-R., Borths, M., Cooke, S. B., Dam, J. van, Delson, E., Eronen, J. T., Fox, D., Furió, A. F. M., Giaourtsakis, I. X., Holbrook, L., Hunter, J., López-Torres, S., Ludtke, J., Minwer-Barakat, R., van der Made, J., Mennecart, B., Pushkina, D., Rook, L., Saarinen, J., Samuels, J. X., Sanders, W., Silcox, M. & Vepsäläinen, J. 2023: The NOW Database of Fossil Mammals. — In: Casanovas-Vilar, I., van den Hoek Ostende, L. W., Janis, C. M. & Saarinen, J. (eds.), *Evolution of Cenozoic land mammal faunas and ecosystems*: 33–42. Vertebrate Paleobiology and Paleoanthropology, Springer, Cham, [https://doi.org/10.1007/978-3-031-17491-9\\_3](https://doi.org/10.1007/978-3-031-17491-9_3).