

How many indricotheres would have lived in Helsinki?

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Received 1 Mar. 2024, final version received 20 June 2024, accepted 1 July 2024

Žliobaitė, I., Spiridonov, A. & Sinkkonen, V. 2024: How many indricotheres would have lived in Helsinki? — *Ann. Zool. Fennici* 61: 131–147.

Giant rhinoceroids were once named as the largest land mammals ever imagined. They lived in Eurasia during the Eocene and the Oligocene, and they could have potentially lived in the area of present-day Helsinki, Finland. We, however, may never know this with certainty because not only have no fossil remains of those animals been found in what is now Finland, but nearly no terrestrial sediments from the Eocene or the Oligocene are known to have been preserved in the area. Paleogene sediments, which formed in southern Finland, were destroyed by the local river systems in the Neogene and by the subsequent glaciations in the Late Pleistocene. Here, we present an analytical argument about whether giant rhinoceroses, known as indricotheres, could potentially have lived in Helsinki. From the continental palaeogeography and palaeoclimate estimates concerning the palaeoecology of indricotheres, we conclude that they could potentially have lived here in the Oligocene, even if climatically, they would have been on the margin of their environmental tolerances. Considering their metabolism, the Helsinki area could have accommodated 3–21 indricotheres. From a climatic perspective, perhaps closer to three individuals could have lived here at a time.

Introduction

The Oligocene was Björn Kurtén's favourite epoch. He called it the epoch of transition (Kurtén 1971). It was the epoch of mammals at the boundary of familiar and imaginary. Entelodonts, giant “pigs from Hell”, roamed North America and eastern Asia. Kurtén described them as “grotesque-looking animals with peculiar bony protuberants jutting out from the cheek region of the enormous head” (Kurtén 1971).

Cainotheres, rabbit-like ruminants, populated Europe. Bear-like dogs and sabre-toothed felids were around in the New and the Old World. Large arsinoitheres carrying a pair of enormous horns just above the nose lived in Africa along with small mastodonts and hyraxes of all sizes and kinds. To us, the most mysterious of all were the indricotheres, giant long-limbed hornless rhinoceroses (Fig. 1), the largest of all land mammals, that have been found across Eurasia between China and the Balkans. They originated

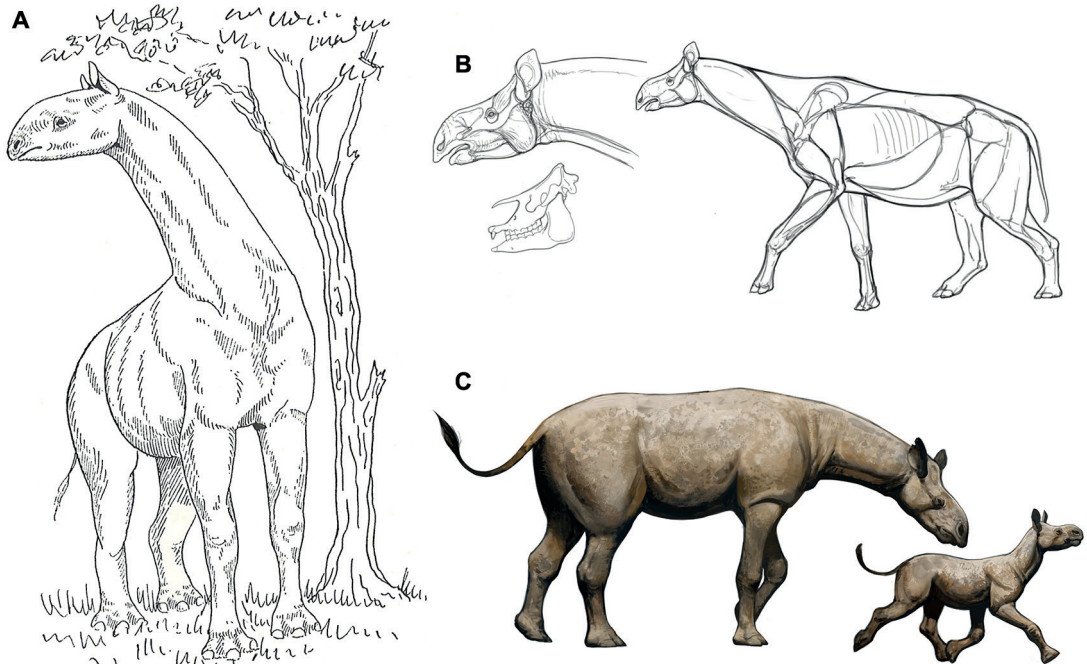


Fig. 1. *Paraceratherium* sp. (formerly *Indricotherium* sp.) drawn by (A) Margaret Lambert (from Kurtén 1971; reproduced with permission from Mikael Fortelius), which is likely based on Zdenek Burian's illustrations (Augusta & Burian 1958), and (B–C) Ville Sinkkonen made for this paper.

in the Eocene and flourished through the Oligocene and went extinct before the Miocene began (Prothero 2014).

Giant rhinoceroïds were first scientifically described at the beginning of the 20th century. Their remains were discovered nearly in parallel by expeditions representing the USA, United Kingdom and Russia (Prothero 2013). Initially the finds were allocated to different genera: *Paraceratherium* (Forster Cooper 1911) and *Baluchitherium* (Forster Cooper 1913) from Bugti Hills in present-day Pakistan, as well as *Indricotherium* (Borissiak 1915) from near the Aral Sea in present-day Kazakhstan. *Paraceratherium* translates from Greek as “near the hornless beast” in reference to *Aceratherium* (“the hornless beast”), the genus to which the species was initially assigned. *Baluchitherium* (currently considered a junior synonym of *Paraceratherium*) means “the beast from Baluchi(stan)”, a historical region in western and southern Asia where its fossil remains were found. *Indricotherium* (currently considered a junior synonym of *Paraceratherium*) was named for Indrik, a beast

from central-Asian mythology (Prothero 2013) who lives on a mountain where no other foot may trespass. When it walks, folklore says, the Earth trembles.

The genera *Indricotherium* and *Baluchitherium* were later synonymised under *Paraceratherium*, and this synonymy is broadly accepted (Lucas & Sobus 1989, Qiu & Wang 2007, Prothero 2013, Deng *et al.* 2022). The name of the subfamily including these taxa remains Indricotheriinae since its first mention takes precedence in time over Paraceratheriinae and Baluchitheriinae (Borissiak 1924). Throughout the text, we use the term ‘indricotheres’ in a generic sense, like ‘horses’ or ‘giraffes’, with reference to the subfamily.

Björn Kurtén spent most of his professional life in Helsinki, located on the shore of the Baltic Sea, on the tip of a peninsula, surrounded by more than 300 islands. Today, Helsinki (60°10'32.16" N, 24°56'3.12" E) is the capital and the largest city in Finland, its population slightly under 660 000. The current population density is 3034 people per km², and the population

is growing. The land area of Helsinki is 217 km², and the length of the shoreline is 131 km.

There are no sediments from the Eocene and almost no sediments from the Oligocene not only near Helsinki but in the whole of Finland. Most of the sediments of this age were removed by the local river systems during the Neogene, as well as glaciations of the Late Pleistocene. The only known sediment of the right age, the Akanvaara clay in northern Finland, is marine sediment deposited in the Early Cenozoic (Tynni 1982). The available Finnish geological cover mainly consists of Precambrian bedrock with some Palaeozoic rocks, stripped clean of younger layers by repeated glacial erosion during the Pleistocene (Ukkonen 2001, Donner 2014, Salonen *et al.* 2016). As a result, even if indricotheres did live in the region, no direct evidence of their presence in Helsinki remains.

Given that fossil evidence does not and cannot exist, we carried out a scientific thought experiment to analyse whether they could have lived in the present territory of Helsinki. We considered this question using three distinct approaches: continental palaeogeography, ecological niche modelling and metabolic scaling. First, we used palaeogeography and tectonics to answer whether there was terrestrial land in the territory of the present-day Helsinki at the time when indricotheres were widespread in Eurasia, and whether there was a terrestrial path connecting Helsinki with central Asia for them to potentially get here. Second, we used ecological niche modelling to answer whether the climatic conditions would have been suitable for indricotheres to establish a viable population here and feed all year round, and whether there would have been suitable vegetation for them to feed on. Finally, we applied the metabolic scaling theory of ecology to answer how many indricotheres could have lived in the Helsinki area at any time, and what would have been their population density.

The largest land mammals ever imagined: natural history of indricotheres

Giant rhinoceroses within the family Paraceratheriidae are known from Eurasia. Their remains

have been found in China, Mongolia, Kazakhstan, Pakistan, India, the Balkans, Anatolia, and the Caucasus. Before addressing the question of indricotheres potentially having lived in the Helsinki area, let us consider the natural history of indricotheres. Despite active ongoing research (Lucas & Sobus 1989, Qiu & Wang 2007, Prothero 2013, Deng *et al.* 2022), the taxonomy of the group remains uncertain (Antoine 2024), not least due to the fragmentation of their record, but the subfamily Indricotheriinae includes the largest taxa (Prothero *et al.* 2013).

Lucas and Sobus (1989) conservatively recognise only three genera under Indricotheriinae (*Juxia*, *Urtinotherium*, and *Paraceratherium*). Using their taxonomic approach, *Turpanotherium* would be a junior synonym of *Urtinotherium*; *Aralotherium* and *Dzungariotherium* would be junior synonyms of *Paraceratherium*. Of these genera, only *Paraceratherium* has been found in Europe (Antoine *et al.* 2008). Therefore, had there been indricotheres in the Helsinki area, most plausibly, they would have been representatives of *Paraceratherium* or closely related taxonomic lineages.

In the following analysis, we focus on the giant rhinoceroses that are currently included in the family Paraceratheriidae (following Deng *et al.* 2021, and the NOW database [NOW — Database of fossil mammals, <https://doi.org/10.5281/zenodo.4268068>, Žliobaite *et al.* 2023]) (Table 1) omitting forstercooperiine rhinoceroses from the middle Eocene in Asia.

Indricotheres are the largest known land mammals and were once called the largest land mammals ever imagined (Fortelius & Kappelman 1993). Prior to the synthesis by Fortelius and Kappelman (1993), the body sizes of indricotheres were often exaggerated, estimates sometimes exceeding 30 tonnes. This confusion came due to coarse extrapolation from the body size of the living mammals, while the body plan of indricotheres was quite far from any living mammals (Li *et al.* 2022). More recently, the estimates of the body mass of the largest indricotheres have settled around 10–20 tonnes (Li *et al.* 2022).

Not all indricotheres were as large as these estimates may indicate, as can be seen from the rough body mass estimates in Table 1. The smallest, *Juxia*, was comparable in its weight

to living rhinoceroses. *Urtinotherium* and *Turpanotherium* were comparable in body weight to living elephants. Only *Aralotherium*, *Paraceratherium* and *Dzungariotherium* were much larger than any present-day terrestrial mammals.

Body size is one of the primary traits characterizing the ecology of mammals (Schmidt-Nielsen 1984). We need body size estimates of indricotheres to reason about the metabolic scaling from which population density estimates derive. Estimating the body size of fossil mammals is challenging in many ways, particularly when there are no living analogues to their body build, as is the case for indricotheres. Recently Li *et al.* (2022) ran an association analysis of body builds of indricotheres with body builds of living mammals. It has long been clear that the body build of indricotheres is unlike any living mammal. They are not like their closest living relatives, rhinoceroses. Indricotheres had relatively longer limbs and longer necks. In the analysis of Li *et al.* (2022), the proportions of the limb bones of *Juxia* are closely similar to those of the limb bones of the living equids. However, in body proportions, *Dzungariotherium* was relatively unique. The closest analogues in the projection of Li *et al.* (2022) are rhinocerotids, bovids, and equids, but these three families are relatively distant in the morphological space. More than their generally longer limbs, it is the general proportions between limbs elements, as well as their shape, that make indricotheres unique (Mallet *et al.* 2022).

An additional challenge in interpreting the ecology of indricotheres is that the fossil record of indricotheres is highly fragmented. Indricotheres were large, so their population densities were small (Damuth 1981). As there were not many living individuals at a time, not many would fossilise, and of those fossilised the recovered remains typically represented only a small fragment of the whole animal. Only four complete or nearly complete skeletons are known: the type specimen of *Juxia sharamurenense* from Ula Usu (Chow & Chiu 1964), a skeleton of *Paraceratherium transouralicum* (formerly *Indricotherium transouralicum*) without the skull (Pavlova 2022), a skeleton of a large *Dzungariotherium* sp. from Lingwu (Li *et al.* 2022), and *Paraceratherium lepidum* from Turpan (Xu & Wang 1978, Qiu & Wang 2007).

Dzungariotherium is the largest known genus, with the estimate of its body mass around 19 000 kg (Table 1) following the analysis of Li *et al.* (2022). The estimates for *Paraceratherium*, the most likely candidate to have lived in Helsinki, come to around 11 000 kg (Fortelius & Kappelman 1993, Li *et al.* 2022). We used this value in our analysis of population densities.

Lucas and Sobus (1989) considered a possibility that all the indricotheriines belonged to a single genus, *Paraceratherium*. This argument was based on their large body sizes, because of which, due to metabolic scaling, associated population sizes are low (Damuth 1981). The question of the minimum population sizes needed to sus-

Table 1. Genera of Paraceratheriidae, Indricotheriinae. Body sizes estimates are approximate, mainly following Li *et al.* (2022) and Fortelius and Kappelman (1993).

Genus	Distribution	Age	Body mass (kg)	Species
<i>Juxia</i>	China	Middle–Late Eocene	1300	<i>J. sharamurense</i> , <i>J. micracis</i>
<i>Urtinotherium</i>	Inner Mongolia, northern China	Late Eocene–Early Oligocene	4000	<i>U. incisivum</i> , <i>U. parvum</i> , <i>U. intermedium</i>
<i>Turpanotherium</i>	China	Oligocene	5000	<i>T. yagouense</i> , <i>T. elegans</i>
<i>Aralotherium</i>	China, Kazakhstan	Oligocene	8000	<i>A. prohorovi</i> , <i>A. sui</i>
<i>Paraceratherium</i>	China, Kazakhstan, Mongolia, Pakistan, Turkey, the Balkans	Oligocene	11000	<i>P. bugtiense</i> , <i>P. transouralicum</i> , <i>P. grangeri</i> , <i>P. asiaticum</i> , <i>P. lepidum</i> , <i>P. huangheense</i> , <i>P. linxiaense</i>
<i>Dzungariotherium</i>	Northern China	Oligocene	19000	<i>D. orgosense</i> , <i>D. tienshanense</i> , <i>D. turfanense</i>

tain the diversity of species and genera are outside the scope of this study. The question what population size makes a population viable on geological time scales is even more complex, since different species of vertebrates, including our lineage (Hu *et al.* 2023), can experience fluctuations in their population sizes depending on climate (Nogués-Bravo *et al.* 2008, Spiridonov *et al.* 2020), trophic levels and other ecological characteristics besides body size (Santini *et al.* 2022).

For their size, their ecology must have been relatively straightforward. Based on their body build and dental morphology, they must have been browse-dominated herbivores, likely similar in their diet to deinotheres (Loponen 2020). From the functional-trait perspective (Žliobaitė *et al.* 2016) their molars are most similar to those of the living black rhinoceroses. Indricotheres would have fed on tree leaves, possibly twigs, tree bark, and perhaps occasionally fruits. During the Eocene–Oligocene, grasses were not yet widespread in Eurasia and grass-dominated ecosystems were not established until the middle Miocene (Jacobs 1999, Strömberg 2011). We estimated that an indricothere weighing ~11 000 kg should have consumed 200 kg or more of vegetation per day. This daily intake is our estimate based on the amount of food consumed by elephants (150–170 kg per day), as well as our prediction from the scaling of dry matter intake with body mass using a regression model fitted on the data from Müller *et al.* (2013). The resulting model is $DMI = 0.046M^{0.761}$, where M is the body mass in kilograms and DMI is the dry matter intake in kilograms per day. This model predicts 55 kg of dry mass intake per day for indricotheres. Pastures today contain roughly 15%–20% of dry matter (<https://ker.com/equine/understanding-dry-matter-forage-horses/>). If we assume a similar amount of dry matter in browse, indricotheres would require 275–367 kg of vegetation per day. Based on our estimates this is roughly the amount of vegetation that ten moose (*Alces alces*) would eat per day.

Their large body size and specialized anterior dentition suggest that indricotheres could have cropped vegetation from tree tops (Lucas & Sobus 1989, Biasatti *et al.* 2018). Bulk carbon and oxygen isotope compositions of tooth

enamel of paraceratheriids from Linxia Basin, China (Biasatti *et al.* 2018) suggest that they occupied relatively closed habitats and were unlikely to be migratory. Bulk carbon isotope values for paraceratheriids fall roughly in the middle of the value range for other East Asian fossil rhinoceroses. This can be interpreted as the middle ground between open and closed habitats. The most extreme negative bulk oxygen isotope values have been recorded for the East Asian fossil rhinoceroses, indicating the most extreme wet and cool habitats.

While no living analogues of indricotheres exist, their ecology at the margin of cool habitats could be compared to that of a moose at present day Finland. Moose are on the continuum between the facultative specialist and facultative generalist having a diet consisting mainly of one species during wintertime, but expanding to different species according to the availability of plants in other seasons (Shiple 2010, Nikula 2017). In summer, moose utilise tens of species of plants, but in winter, their diet consists mainly of woody species. Dwarf shrubs, blueberry and lingonberry make a substantial proportion of moose autumn diet before the snow cover becomes too thick (Cederlund *et al.* 1980). Moose consume only woody species when the depth of snow exceeds 30 cm. A moose's diet consists mostly of Scots pine, birches, willows, aspen, juniper and rowan during this period.

Our palaeoart reconstruction of Helsinki indricotheres (Fig. 1B) is largely based on the remains and proportions of *Paraceratherium transouralicum*, supplemented by the very well-preserved skull recently described by Deng *et al.* (2021) and assigned to a new species *Paraceratherium linxiaense*. The nose and lips were reconstructed after modern browsing rhinos aligning with estimated browsing dietary habits of *Paraceratherium*. The dull grey coloration in our reconstruction follows that seen in large extant land mammals.

Helsinki through time: the palaeogeographical context

Sediments pre-dating the Quaternary are almost entirely absent from present-day Finland. This

absence is due to multiple tectonic uplifts in Fennoscandia during the Paleogene and Neogene (Gibbard & Lewin 2016, Riis 1996), as well as the erosional impact of repeated Quaternary glaciations (Hall & van Boeckel 2020, Jansen *et al.* 2019). The mammalian record of Neogene Finland includes only an isolated, re-deposited proboscidean humerus fragment (Salonen *et al.* 2016, Saarinen & Salonen 2024).

A lack of the fossil record covering a specific period in a particular region is not uncommon. The modelling of modern vertebrate geographical distributions in conjunction with the distribution of modern sedimentary basins (Nyberg & Howell 2015) shows that a large area of terrestrial ecosystems today has little to no chance of being represented in the future fossil record (Krone *et al.* 2024, Mirsky 1998). The fact that there are gaps at different scales in time and space is a curse and a blessing for analysts (Plotnick 2017). The incompleteness of the record can bias the perception of biotic patterns through time (Benton *et al.* 2011), whereas it also gives us a structure to interpret those patterns (Holland 2017, Žliobaitė & Fortelius 2022). Thus, even though no direct fossil evidence for indricotheres ever living in Helsinki exists, we draw on multiple complementary pieces of evidence in the following analysis in the spirit of what Adrian Currie called a “methodological omnivory for historical sciences” (Currie 2018).

Our first analytical question was whether there was terrestrial land in the territory of present-day Helsinki at the time when indricotheres were widespread in Eurasia. We also asked, if there was a terrestrial path connecting Helsinki with central Asia for them to potentially get here.

Based on the distribution of sediments in northern and western Europe, during the Eocene the central part of the Baltic region was most probably covered by a shallow sea (Gibbard & Lewin 2016). Marine deposits of the late Early Eocene have been found in eastern Lapland (Paulamäki & Kuivamäki 2006, Tynni 1982), which indicates that the territory of present-day Finland would have been under a shallow sea during that time. Therefore, chances are very low that there would have been terrestrial lands for indricotheres to potentially inhabit this area during the Early Eocene. However, the setting

was changing during the Early Eocene period. As a result of an ongoing tectonic uplift, most of the central part of the Baltic region, or central-northern Europe, became dry, low-lying land (Gibbard & Lewin 2016), and a peneplain started forming during this period in the eastern Fennoscandia (Riis 1996). While it cannot be determined with certainty when the Helsinki region emerged from the sea, it is quite certain that it did before indricotheres went extinct, which happened before the transition from the Oligocene to the Miocene (23 Ma) (Prothero 2014).

In addition to the regional tectonics, the global sea level was changing. The boundary between the Eocene and the Oligocene is marked by a major glaciation of eastern Antarctica, which caused a relatively sudden drop in global sea levels by 50–60 m (Houben *et al.* 2012, Miller *et al.* 2020). The exact timing of the sea level decrease is still debated. The magnetostratigraphy of sections in North America (Prothero & Emry 1996) as well as the analysis of British mammalian assemblages (Hooker 1992) suggest that the sea level drop was in the earliest Oligocene. Integrated stratigraphical and sedimentological organic matter provenance studies suggest that the continent-level Antarctic glaciers, which presumably led to the global eustatic sea level drop, started developing in the latest Eocene (De Lira Mota *et al.* 2023). While the exact placement in time of the sea level drop associated with the Eocene–Oligocene transition is still debated (there are many factors which affect our knowledge of the timing of events) for most of its duration, the Oligocene was characterised by significantly lower sea levels than those during the Eocene. This is the most important palaeogeographic premise for our estimations of plausibility of the spread of rhinoceroids into northern Europe.

During the subsequent Neogene period and the Early Quaternary, a grand palaeoriver system (Eridanos) flowed from the east and north of the Baltic region shaping erosional geomorphic features preserved to this day and known as the Baltic Klint. Given that the major rivers of Fennoscandia discharged to the current Denmark and North Sea areas during the Oligocene (Gibbard & Lewin 2016), the presence of large and slowly meandering river systems flowing from the north and east, and crossing northern



Fig. 2. Reconstruction of palaeogeography of Europe. — **A:** Early Eocene. — **B:** Oligocene. Image from Palcu and Krijgsman (2023: fig. 1), reproduced with permission from the authors.

European plains in the territory of present-day Finland could be expected. Therefore, from a geological perspective, the region could have had potentially habitable terrestrial land during late Paleogene.

Was there a land bridge for indricotheres to potentially arrive in Helsinki? According to a reconstruction of the palaeogeography of Europe in the Early Eocene and the Oligocene (Fig. 2), during the Eocene, Europe and Asia were separated by seas. The continents docked around

the Eocene–Oligocene transition. The new land-bridge created opportunities for faunal and floral interchange between the continents. The turnover was so massive that it was termed *Grande Coupure* (French for “great cut”) (Stehlin 1910).

The Oligocene — during which indricotheres could have had a chance of dispersing and establishing a population in present-day Helsinki — was characterised by global cooling (Westerhold *et al.* 2020). Despite a notable global drop in temperatures by about $\sim 4\text{--}6^\circ\text{C}$ (Hren *et al.*

2013) during the Eocene–Oligocene transition, the general climate in Eurasia was subtropical (Li *et al.* 2018). The proximity of the Paratethys Ocean in the south and the North and Norwegian seas to the west (Palcu & Krijgsman 2023) additionally buffered northern Europe from low winter temperatures. We argue that from a continental perspective, the climatic conditions in the Helsinki area would not have been drastically different from the climates encountered by indricotheres in central and eastern Asia.

This set of gross palaeogeographic, tectonic, and palaeoclimatic evidence suggests that there would not have been indricotheres here in the Eocene, but indricotheres could have potentially arrived in Fennoscandia and consequently the Helsinki area during the Oligocene. Our next analytical question thus was whether the climatic conditions would have been suitable for indricotheres to establish a viable population here and feed all year round.

Climate in the Helsinki area during the Oligocene

To evaluate the climate in the Helsinki area during the Oligocene was suitable for indricotheres, we analysed temperature estimates from palaeoclimate model simulations of Valdes *et al.* (2021), using the palaeogeographical model of C. R. Scotese and N. M. Wright (<https://doi.org/10.5281/zenodo.5460860>). We used the results of model simulations of palaeoclimate presented and implemented in an online tool of Steinig *et al.* (2022), from which we queried the climatic conditions for the localities where Paraceratheriidae occurrences were reported in the NOW database of fossil mammals (NOW — Database of fossil mammals, <https://doi.org/10.5281/zenodo.4268068>, Žliobaite *et al.* 2023). We took these climatic conditions as a baseline for occurrence of Paraceratheriidae. We then analysed the estimates of conditions in Helsinki compared to those baselines.

Knowing that such an analysis comes with multiple layers of uncertainty, we aim at the coarsest-level analysis. These uncertainties relate to the reconstructions of tectonic movement, the robustness of proxies used to calibrate the cli-

matic models, and the accuracy of the modelled atmospheric processes, for example. Taxonomic identifications, as well as geographic locations of fossil finds, are also uncertain. Moreover, the Oligocene location of Helsinki lacks any direct palaeoclimatic information due to the absence of Paleogene sedimentary rocks. Thus, we broadly aim at rating the environmental conditions for indricotheres in Oligocene Helsinki on a scale from completely unsuitable to perfectly suitable as the first-order approximation of the actual bioclimatic relations. We focused on temperature, since primary productivity and plant food available for indricotheres throughout the year at these latitudes and this time was likely to have been primarily limited by temperature and availability of sunlight, and less so by precipitation (Lieth 1975).

We used surface temperatures coming from palaeoclimate simulations (Valdes *et al.* 2021) at indricothere localities during the Eocene–Oligocene transition along with the estimate for Helsinki (Fig. 3). The list of localities along with estimated climatic conditions are available at <https://github.com/zliobaite/indricotheres>. As a result of global cooling, indricothere localities are also found in cooler environments. This could have caused a change in climate envelope, and affected the shape of a realised climatic niche (Jackson & Overpeck 2000, Patzkowsky & Holland 2012). However, without observing the actual boundaries of their climatic niche through time, we do not know whether they would have shifted their climatic niche overall, or whether this is a result of sediments being available mostly over the same geographic region, which was getting cooler over time.

In terms of climatic conditions, Helsinki was consistent with our inferred climatic contexts for indricotheres. Sometimes temperatures in Helsinki were at the lower boundary of temperatures of the coldest indricothere locality, yet never below that.

A complementary perspective can be seen from the degree of seasonality at the same localities. We assessed the seasonality in two ways: (i) by analysing the maximal range of monthly average temperatures (difference between the temperature of the hottest and coldest months); and (ii) by estimating the standard deviation of monthly temperatures coming from the climate

model of Valdes *et al.* (2021). Both estimates show non-linear trends towards lower seasonality at higher average monthly temperatures (Fig. 4). This effect could be explained by high-latitude (and continentality) amplification of temperature variability — the tropical and subtropical locations are expected to have a smaller range of variability. Considering this pattern, indricotheres would have been a plastic group inhabiting climates of low and high seasonality, as well as could have lived in environments with high and moderate mean temperatures.

The mean \pm SD range temperature for all localities was 43 ± 10 °C, which is very close to the estimated annual temperature range in Helsinki during the Oligocene (44 °C) (Fig. 4A). The standard deviations of monthly temperatures are distributed in a very similar way as the temperature ranges (Fig. 4B). This supports our earlier interpretations that the climate in southern Finland in the Oligocene should have been suitable for indricotheres, even if it was colder and more seasonal than their estimated climatic niche.

Possible vegetation in the Helsinki area in the Oligocene

Given that the climate in the Helsinki area during the Oligocene was potentially suitable for indricotheres, would there also have been suitable vegetation for them to feed on? The record of plant macrofossils (Utescher *et al.* 2021) and pollen from the western and central Europe in the Oligocene show low prevalence of xeric plants, which implies that the conditions there were humid throughout the year. The closest fossil plant sites located in present-day Denmark, Poland, and other central European countries contain needleleaf cool temperate, and warm temperate trees, as well as broadleaved deciduous warm temperate, cool temperate, and warm temperate trees that would have been intolerant to droughts, as well as broadleaved evergreen warm temperate trees (Utescher *et al.* 2021). Meanwhile, in western Siberia there were also broadleaved evergreen tropical trees during the Early Oligocene, while C3 aquatic herbs and C3 mesic herbs dominated among the herbaceous plants. Southern Scandinavia and northern

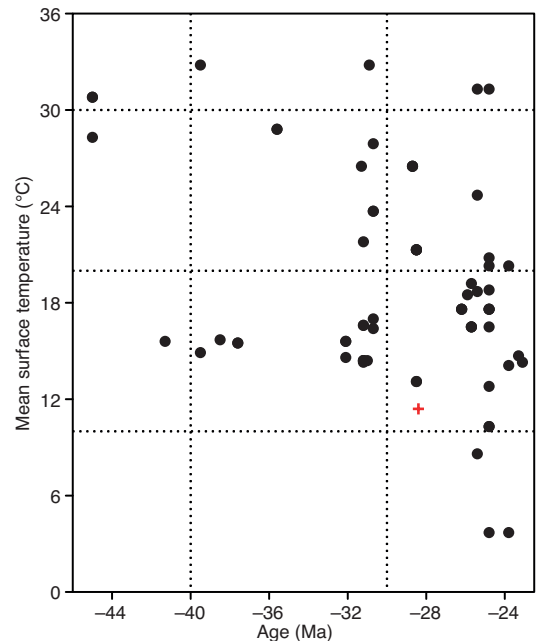


Fig. 3. Modelled surface temperatures at selected indricothere localities through time. Red cross shows averaged surface air temperature in Helsinki during the mid-Oligocene.

central Europe were dominated by broadleaved deciduous forests with moderately diverse shrubs and conifers (Utescher *et al.* 2021). Considering the evidence of all these plant functional types in a single floristic province with relatively weak physiographical barriers due to lack of orogenies in a stable cratonic environment (Paškevičius 1997), it is possible that all the listed floral components at one time or another could have been encountered in the Helsinki area during approximately 11 million years of the climatically variable Oligocene. Not all of them would have been edible for indricotheres. Our interpretation is that leaves of shrubs and young conifer shoots could have been good candidates for food for indricotheres and they would have been capable of reaching high branches of broad-leaved trees. Assuming these leaves were not too toxic, they could have made a major part of the diet.

While direct present day analogues of these Oligocene ecosystems do not exist, the closest analogues could be found in present day North America and East Asia which still host some taxonomic lineages that went extinct in

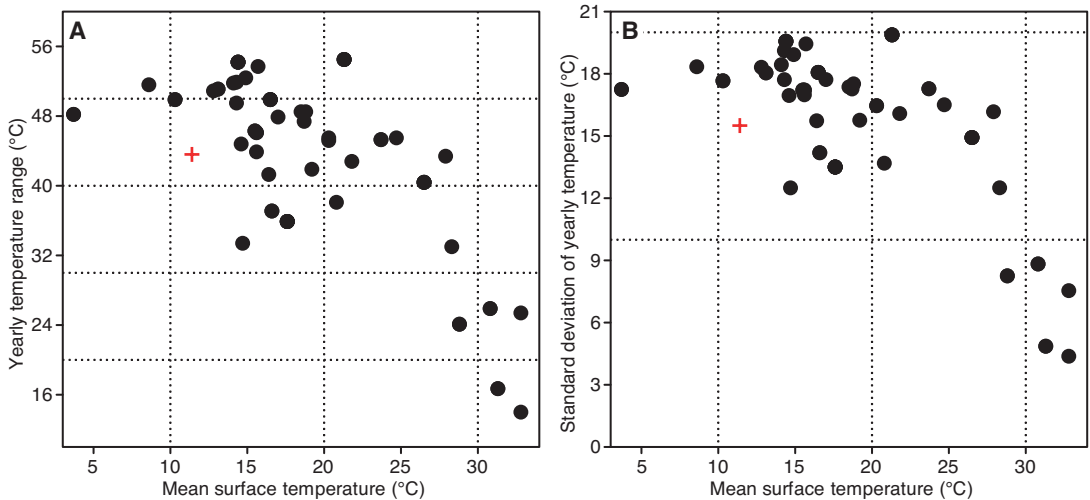


Fig. 4. Mean estimated temperatures vs. seasonality at the indricothere localities in Eurasia. — **A:** Mean temperature ranges (the mean temperature of the hottest month—the mean temperature of the coldest month). — **B:** Standard deviations of monthly temperatures. Red crosses represent Helsinki in the mid-Oligocene.

Europe during the Late Cenozoic cooling. It is possible that there was active plant dispersal between North America and Europe in the Oligocene (Hably *et al.* 2000). Some of the typical angiosperm tree genera which were found in central Europe were oaks, beeches (Denk *et al.* 2012), as well as maples, alders, hornbeams, and poplars. In addition, gymnosperms were present in much greater diversity than today. They would have included plum yews, golden larches, ginkgo trees, umbrella pines, China-firs, and swamp cypress, all of which are now endemic to East Asia, sequoia redwoods endemic to western North America, swamp cypresses now endemic to southern North America, firs and hemlocks now restricted to North America and Asia, and arars which are now endemic to North Africa, along with spruces and pines now that are still common in Europe today grew in central parts of Europe in the Oligocene (Gastaldo *et al.* 1998), and could possibly have reached the Helsinki area. These interpretations are supported by the palaeobotanical data from the east of the Fennoscandia, which shows that in the western Siberia ecosystems were co-dominated by angiosperms (such as oaks) and gymnosperms (Denk *et al.* 2021).

The evidence from palaeobotany and palynology thus suggests that there could very likely have been potentially suitable plant food

for indricotheres in the Oligocene in the Helsinki area. Southern Finland during the Oligocene must have had a unique vegetation landscape, combining features unseen in the present-day ecosystems and now possibly only observable in botanical gardens.

Metabolism, ecology, and population densities

Given that indricotheres likely would have lived in southern Finland in the Oligocene, our final analytical question was how many of them could have lived in what is now Helsinki at any time? What would have been their population density?

The population density of species directly competing for resources balances in such a way that the energy controlled by a species does not depend on the body size of its individuals (Damuth 1980). This goes back to the Red Queen's evolutionary theory (Van Valen 1973) and the pattern has been termed energy equivalence (Damuth 2007). While population densities of the same species can vary greatly depending on ecological circumstances (Santini *et al.* 2022), all else being equal the larger the individuals of a species, the lower the average population density.

Little is known regarding how metabolic scaling (Kleiber 1932) has changed through time but given that energy intake and processing is such a basic aspect of biophysics, even if it has changed, it should not have changed fast. In our predictive modelling of population densities, we assumed that the metabolic scaling has remained the same throughout the latter half of the Cenozoic. This allowed us to reason about population densities of extinct taxa, drawing analogies in terms of body mass with living mammals and their scaling (Kleiber 1932, Damuth 1981).

The energetic demands of individuals relate to their metabolic rate. Metabolism is a set of processes responsible for converting energy stored in food to energy required to keep organismal cells functioning, converting energy from food to building blocks, and disposing of waste. Even though physiological and ecological characteristics differ across organisms, the chemical reactions behind metabolism and metabolic pathways are strikingly similar across different organisms (Pace 2001).

Metabolic scaling strongly relates to body size, and the patterns span different ecologies (Kleiber 1932, Kolokotronis *et al.* 2010, Schmidt-Nielsen 1984). In line with evolutionary theory, population densities should scale inversely with this metabolic scaling (Damuth 1981, Žliobaitė & Fortelius 2020), and empirical evidence suggests that they do (Damuth 1981).

A recent analysis of empirically observed population densities showed that besides the body size (which is the strongest determinant of the metabolic rate), population densities can be explained by the trophic level as well as climatic factors, while climatic factors contribute very little to the explanation (Santini *et al.* 2022). Indeed, population densities are not uniform across the species' range (Brown 1984). For example, hunter-gatherer population densities depend on the net primary productivity; densities are lower at low productivity levels (Tallavaara *et al.* 2018, Zhu *et al.* 2021). Here we used density as a species level characteristic to the first approximation.

We produced population density estimates using seven alternative predictive models. We used present-day data to fit predictive models, which we then used to predict the expected population density of a species from an estimate

of the body mass of an individual of that species. We fitted ordinary least squares regression in the logarithm space. Population densities are known not to be uniform across the species' range (Brown 1984), scaling with the body size as the first approximation relates to the average population density of viable populations. The population density data for our modelling came from two sources: Damuth (1987) and Santini *et al.* (2018). We used the following mammalian orders for fitting the models, aiming to capture primary consumers: Artiodactyla, Hyracoidea, Proboscidea, Primates, Perissodactyla, Rodentia, and Lagomorpha.

The model variants we used differed in the data sources for model fitting, as well as in the subsets of mammalian species to be included in the model fitting. The model variants are encoded using two letters. The first letter stands for the data source: S = Santini *et al.* (2018), D = Damuth (1981), and B = both data sets combined. We used a single value of population density for each species. We took the median value if the data set reported more than one value per species. The second letter stands for the variant of species selection: A = model fitting is on all large herbivores, B = model fitting is on large herbivores that have acute lophs. We used the dental trait scheme defined in Žliobaitė *et al.* (2016) and scored acute lophs following the treatment for selenodonts as in Oksanen *et al.* (2019). Dental traits were not used as inputs for predictive modelling; they were only used for filtering the data for model training. The data set is given in the online repository accompanying this study (<https://github.com/zliobaite/indricotheres>). We included an additional model (D81) directly from the literature for comparison.

The models are summarised in Table 2 and fits are plotted in Fig. 5. Slopes of all seven models are similar to each other and close to -0.75 (Table 2) as expected from the metabolic theory (Brown *et al.* 2004, Damuth 1981). The results suggest that, from the metabolic perspective, Helsinki could have accommodated 3–21 indricotheres (Table 3). For comparison, from the energetic perspective, this would correspond to 200–900 humans. In comparison, the population density of present-day hunter-gatherers varies (depending on net primary productivity) from 0.03 to 1 km⁻²,

Table 2. Population density models for mammals. $D = aM^b$, where M is the body weight (kg) of an individual, a and b are the model coefficients, D is an estimate of the population density in individuals per km². SA = model fit on the population density data from Santini *et al.* (2018) for all large herbivores; SB = model fit on the population density data from Santini *et al.* (2018) for a subset of large herbivores that have specific dental characteristics (acute lophs), similar to those of indricotheres; DA = model fit on the population density data from Damuth (1987) for all large herbivores; DB = model fit on the population density data from Damuth (1987) for a subset of large herbivores that have specific dental characteristics (acute lophs); BA = model fit on the population density data from Santini *et al.* (2018) and Damuth (1987) combined for all large herbivores; BB = model fit on the population density data from Santini *et al.* (2018) and Damuth (1987) for a subset of large herbivores that have specific dental characteristics (acute lophs). D81 = model from Damuth (1981).

Model	Model fit	Density data source	Model scope	Number of species for model fit	a	b
SA	Our	Santini <i>et al.</i> 2018	All	547	34.1	-0.824
SB	Our	Santini <i>et al.</i> 2018	Acute lophs	107	64.2	-0.752
DA	Our	Damuth 1987	All	362	84.2	-0.726
DB	Our	Damuth 1987	Acute lophs	44	110.4	-0.789
BA	Our	Both	All	713	49.0	-0.782
BB	Our	Both	Acute lophs	118	78.4	-0.728
D81	Damuth (1981)		Primary consumers	307	68.7	-0.750

which would give 7–220 individuals in Helsinki (Zhu *et al.* 2021), which gives confidence that the estimates coming from the models are plausible. We report estimates for humans for comparison only and of course, humans would not have lived in Helsinki at the time of indricotheres. Early humans would have arrived in Helsinki in the Pleistocene at the earliest.

The estimates from different models are reassuringly close to each other. Models that are fit

Table 3. Estimates of how many indricotheres (11 000 kg) or early humans (70 kg) could have lived in the Helsinki area (217 km²).

Model	Estimated population density (indiv. km ⁻²)		Estimated number of individuals in Helsinki area	
	Indricotheres	Early humans	Indricotheres	Early humans
SA	0.0159	1.03	3	223
SB	0.0589	2.63	13	572
DA	0.0989	3.85	21	836
DB	0.0714	3.86	15	838
BA	0.0338	1.76	7	383
BB	0.0899	3.56	20	773
D81	0.0640	2.84	14	616

on Santini's *et al.* (2018) data compilation gave somewhat lower estimates than models that fit on Damuth's (1987) data compilation. This is consistent with Damuth's data generally having somewhat higher densities for the same species than Santini's *et al.* data (additional plots illustrating this are deposited in the online repository at <https://github.com/zliobaite/indricotheres>). It is possible that in his data collection, Damuth focused on well-documented populations at the centre of their ranges, while Santini's data is broader and more inclusive of the sources as well as observation circumstances. Models fit on species with similar functional dental traits to the indricotheres (acute lophs), gave tighter population density estimates for indricotheres, amounting to 13–15 individuals in the Helsinki area. Given that Helsinki in the Oligocene would have been at the colder and less productive boundary of the estimated climatic niche of indricotheres, the actual populations would probably have been closer to the lower limits of these estimates.

Concluding remarks

When we started this study, we did not know whether indricotheres may have ever lived in the present-day Helsinki territory. While doing so

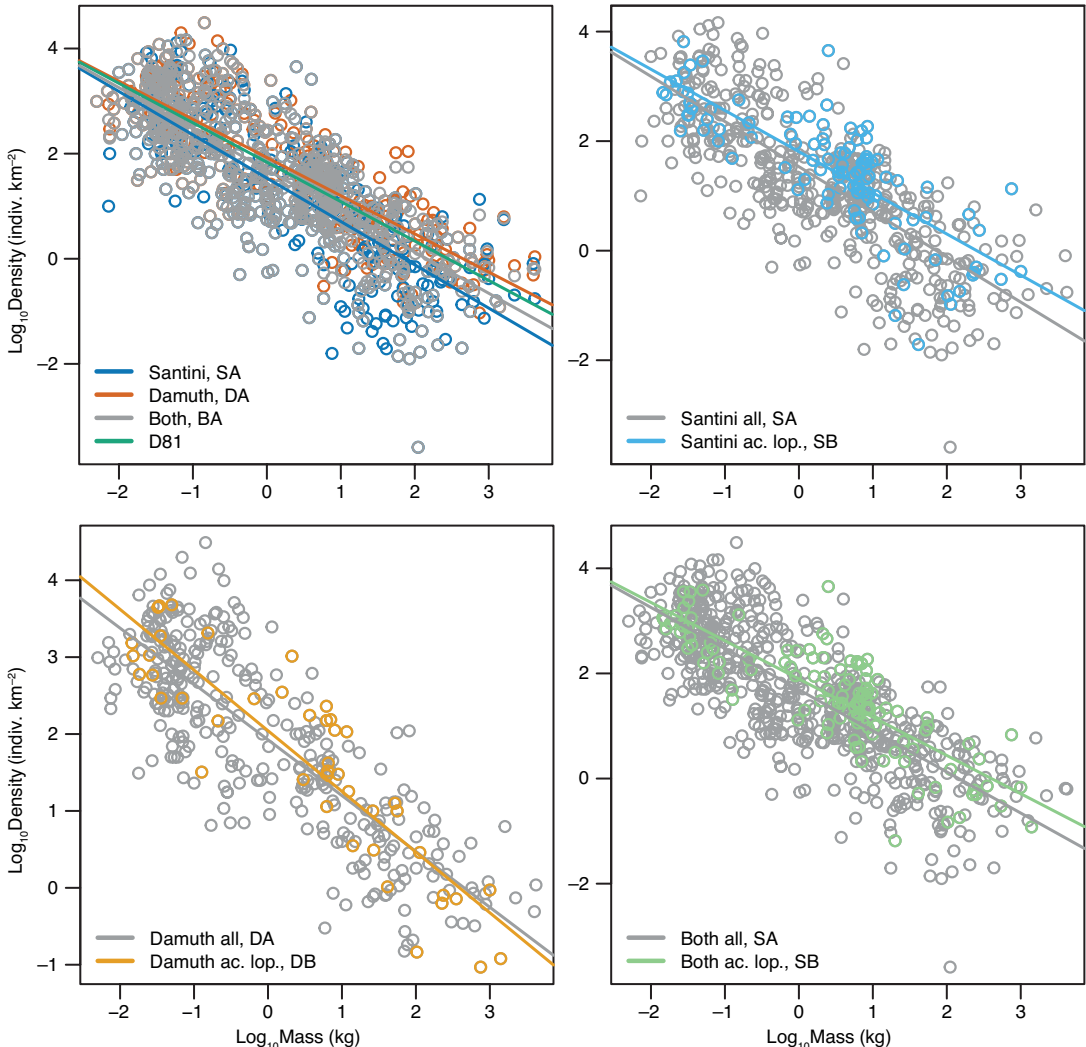


Fig. 5. Model fits. — **A:** SA, DA, BA and D81 and data sets used to fit them. — **B:** SA vs. SB. — **C:** DA vs. DB. — **D:** BA vs. BB. For model abbreviations see Table 2.

we constructed a methodology to investigate the ecology of animals in regions with very scarce or no fossil record at a given time. From the analytical results we are convinced that indricotheres could likely have lived here in the Oligocene. It is very likely that any possible direct evidence of the presence of indricotheres is forever gone, along with the sediments from the Eocene and the Oligocene that once overlaid present-day Finland. While not utterly impossible that terrestrial sediments of the right age may one day be found in Finland, we will probably not know, just as Björn Kurtén did not know when writing

the fictional novel, “Dance of the Tiger,” (Kurtén 1978) featuring interactions and interbreeding between the Neanderthals and the ancestors of modern humans, that his storylines would be scientifically backed up 40 years later (Mendez *et al.* 2016).

Björn Kurtén did not like mixing science and fiction, and we do not attempt it here. This is a scientific study, no matter how preliminary. It includes components of palaeoart, which Björn Kurtén liked a lot, and he often included collaborative palaeoart in his scientific work. To honour his legacy of art-science collaborations, we have

included here a tailor-made reconstruction of indricotheres (Fig. 1).

Björn Kurtén also worked a lot on palaeodemographics. The cave bear material he focused on (Kurtén 1971) presented a nearly natural experiment for demographics since fossils appeared in age cohorts, often due to deaths during hibernation. When starting this study, we knew that the fossil record of indricotheres itself does not leave much room for demographic analyses. Their record is fragmented, and even sorting out the taxonomy is a continuing challenge for the research community. Drawing on metabolic theory, however, we have provided here a glimpse into the ecology and the demographics of indricotheres.

Acknowledgements

We thank Pierre-Olivier Antoine for consultations regarding the taxonomy; any remaining misinterpretations are our own. The work of A.S. was supported by the project S-MIP-21-9 “The role of spatial structuring in major transitions in macroevolution”. This is a contribution from the Valio Armas Korvenkontio Unit of Dental Anatomy in Relation to Evolutionary Theory.

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