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Paleodiet reconstructions and human utilization of middle Holocene *Equus ferus* in northwest Europe

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ABSTRACT

This study uses tooth meso- and microwear together with bone collagen stable isotope ratios (carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulphur ($\delta^{34}\text{S}$)) to investigate diet and human utilization of two middle Holocene (~5 ka cal B.P.) populations of wild horses, *Equus ferus* from northwest Europe. The results of the mesowear analysis places one population (Ginnerup, Denmark) amongst extreme grazers and the other (Hüde I, NW Germany) amongst less-abrasion dominated grazers. These are contrasted by microwear, which suggest that both populations were killed, when browsing. The low microwear scratch variation in the Ginnerup population suggests that the duration of the mortality event(s) was short and confined to the same season. The mesowear analysis further suggests that the horses at Hüde I included more browse in their diet than at Ginnerup. This is supported by depleted $\delta^{13}\text{C}$ values in the Hüde I population. The $\delta^{34}\text{S}$ values also differ between the two sites. The higher values at Ginnerup (a coastal site) compared to Hüde I (an inland site) is interpreted as an effect of marine-influenced sulphur-enriched rainfall. Furthermore, the rather consistent $\delta^{34}\text{S}$ values at the two sites respectively suggest that the horses killed were from locally available herds. In general, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of horses and other animals from Ginnerup and contemporary nearby sites show tendencies towards more depleted values in the horses and other wild herbivores than in livestock. We suggest that this is a result of niche partitioning and hunting pressure. The results presented here further our understanding of some of the youngest known never-domesticated populations of wild horses *Equus ferus* in northwest Europe.

1. Introduction

The success of monodactyl horses of the genus *Equus* throughout Pleistocene Europe is evident as shown by their abundance in the archaeological and palaeontological records. However, during the Pleistocene the number of *Equus* species declined, and at the end of the

Pleistocene the dominance of *Equus ferus* (*E. ferus*) together with the European wild ass *Equus hydruntinus* was absolute (Boulbes and van Asperen, 2019; Cirilli et al., 2022). Although horses are habitual grazers (Ackermans, 2020: Fig. 1), Middle and Late Pleistocene *E. ferus* have been found in various environmental and climatic settings through time indicating that the species adapted to highly varied environments.

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Further, while generally viewed as a dedicated grazer, the fossil record shows that *E. ferus* was able to include a substantial amount of browse in its diet (van Asperen, 2010; Rivals, 2012; Rivals et al., 2015b; Rivals and Lister, 2016; Saarinen et al., 2016, 2021; Boulbes and van Asperen, 2019; Uzunidis, 2021; Cirilli et al., 2022). Nonetheless, during the Holocene the *E. ferus* population in Europe saw a significant reduction and fragmentation, and the population size was probably at its lowest during the early Atlantic period (~9–7.5 ka B.P.) in which *E. ferus* seems to have partially withdrawn to more peripheral parts of Europe including southwestern Atlantic Europe (including Iberia) and the eastern Baltic zone, with only scattered records in Central Europe (Sommer et al., 2011; Bendrey, 2012; Librado et al., 2021). The apparent scarcity of *E. ferus* in most parts of the European lowlands during the early Atlantic has been suggested to be a consequence of increasing forest cover and loss of open grasslands, scattering the *E. ferus* population into small, isolated relict populations (Sommer et al., 2011, 2018; Leonardi et al., 2018). This explanatory model contrasts pollen evidence for substantial open and semi-open vegetation in the region throughout this period (Nielsen et al., 2012; Trondman et al., 2015).

Throughout the Holocene, southern Scandinavia formed part of the northwestern-most boundary of *E. ferus*' biogeographical range and its occurrence here may have involved several episodes of local extinctions and reimmigrations (Aaris-Sørensen, 2009, 2016). The dynamic history of *E. ferus* in the region has likely involved responses to climatic and other environment fluctuations, with both population size and biogeographical range being linked to the amount of suitable habitat (Leonardi et al., 2018). To this we may add hunting and other human impacts as likely important factors as seen in both horses and other megafauna species (Lorenzen et al., 2011; Bergman et al., 2023). At a local scale, this is especially obvious at the beginning of agriculture and the introduction of domesticates, which brought changes in wild herbivore diet and habitat and may be associated with increasing human niche construction (Noe-Nygaard et al., 2005; Schulz and Kaiser, 2007).

During the late Atlantic and early Subboreal period (~7.5–4.65 ka cal B.P.) and after an almost total absence of horse bones in the archaeological record in Northwestern Europe since the Boreal period (~9.6 ka cal B.P.) a final and substantial population increase is evident in this region and beyond (Benecke, 2002; Aaris-Sørensen, 2009; Sommer et al., 2011; Leonardi et al., 2018; Librado et al., 2021; Klassen et al., 2023). In the central part of the European lowlands this coincides with the spread of agriculture. The repopulation of *E. ferus* in many parts of Europe during the late Atlantic and early Subboreal period may therefore be linked to human activities and a gradual opening of the landscape (Sommer et al., 2011, 2018).

The wild horse lineage(s) in Europe appears to have occupied a wider range of ecosystems than the Asiatic in the Holocene (Leonardi et al., 2018) and as an alternative to the above hypothesis it has been suggested that the survival and subsequent recovery and spread of *E. ferus* in Holocene Europe was a result of increasing adaptability to woodlands including changes in coat colours (Saarinen et al., 2016; Sandoval-Castellanos et al., 2017). Whatever the cause, one might, however, also argue that the continued opening of the landscape during the Subboreal period, as part of humanity's intensifying sociocultural niche construction and associated biosphere transformation (Ellis, 2015), represents one of the main factors that ended the era of the original wild horse *E. ferus*, despite its preference for open landscapes and its initial success.

To test the different explanatory models of the late Atlantic/early Subboreal population increase in or reappearance of *E. ferus* in northwestern continental Europe, this study presents the results of combined isotope (carbon, nitrogen, and sulphur) and tooth meso- and microwear analyses as proxies for paleoenvironmental reconstructions and human utility including seasonality of middle Holocene (~5 ka cal B.P.) horses in the northwestern European lowland (Fig. 1). The study is the first detailed dietary study of Neolithic *E. ferus*, and the populations under study may represent some of the last known western Eurasian never-domesticated populations of wild horses. As such, and although out of

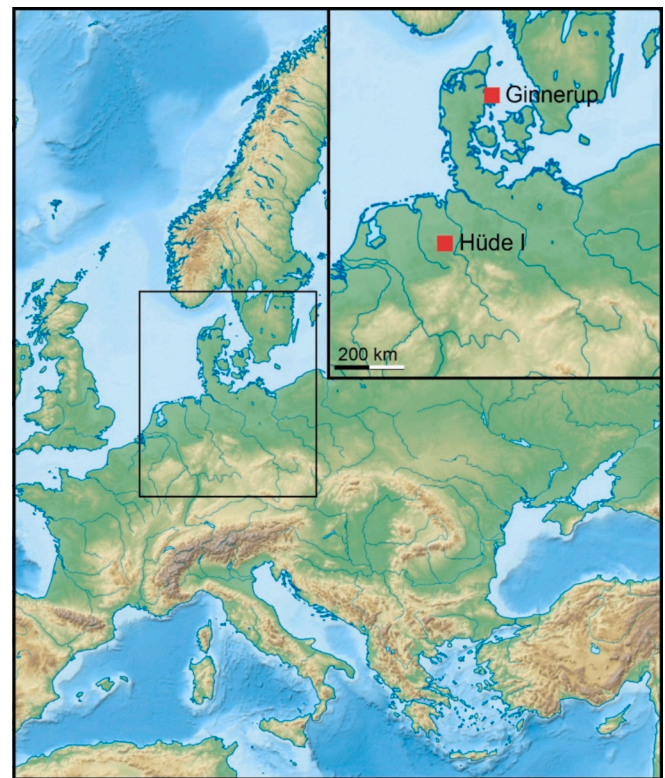


Fig. 1. Map of Europe showing the location of the two main sites used in the study. The Kainsbakke and Kiral Bro sites are situated in the same area as Ginnerup (Wikimedia Commons: <https://creativecommons.org/licenses/by-sa/3.0/>).

scope in the present study, it may also provide a basis for our understanding of the final extinction of the last originally wild populations of *E. ferus* in Europe as domestic horses were spread throughout Europe ~4.2 ka cal B.P. (Librado et al., 2021, 2024).

2. Materials

The samples derive from two archaeological sites within the North European Plains at the border between the Atlantic and the sub-continental Northern European temperate climate zones. The sites were primarily occupied during the 4th and early 3rd millennium BCE and the material culture primarily belongs to various Neolithic cultural groups. The selection of sites is based on the presence of high numbers of horse bones and teeth in their inventories. They are, however, not unique in the region suggesting the presence of a substantial number of horse populations in Northern Continental Europe during the Subboreal period (Nobis, 1955; Benecke, 2002; Sommer et al., 2011).¹

2.1. Ginnerup

Ginnerup is located on the Djursland peninsula in eastern Jutland, Denmark (Fig. 1). At the time of occupation, it was a coastal site on a promontory bordering the ~1 km wide Kolindsund sound located to its south. The surrounding, undulating landscape to the north, east and west is made up of sandy moraine and meltwater plateaus between 15

¹ We also sampled ($N = 10$) *E. ferus* bones for isotope analysis from the site Hundedorf/Hunte 1 at the northern end of lake Dümmer (Kossian, 2007; Brozio and Heumüller, 2022). The bones did not yield enough collagen for the analysis to be successful, and the site was removed from the study. Also, no teeth were available for tooth wear analysis.

and 60 m above sea level. The horse bones and teeth dealt with here are from structures A1 (a ditch with numerous phases of recutting, dated between ~5.45 and 4.9 ka cal B.P by ^{14}C and interpreted as ritual in nature) and A4 (a depression filled with undisturbed archaeological layers, dated between 5.1 and 4.9 ka cal BP by ^{14}C and partly ritual in nature). Both structures show stratigraphic sequences spanning the Neolithic Funnel Beaker (TRB) and Pitted Ware (PWC) cultures (Rasmussen, 2020; Klassen et al., 2023). Samples used in this study were excavated in 2020 and 2021 and derive from the uppermost layers in the structures with finds from the latest activities of the TRB (MN A II/III) and the earliest PWC, dated between 5 and 4.9 ka cal B.P.

While the faunal remains are heavily fragmented due to human bone processing and various taphonomic factors, bone preservation is excellent. Besides various bird, fish, and mollusc species and a few human bones, 23 mammal genera have been identified so far. These include four domestic species (*Canis familiaris*, *Bos taurus*, *Ovis aries*, and *Sus scrofa domesticus*), and 18 wild species including *E. ferus* (Klassen et al., 2023 and unpublished data). Although late Atlantic/early Subboreal remains of *E. ferus* from southern Scandinavia are well-attested (Davidsen, 1978; Rowley-Conwy, 1984; Richter, 1991; Aaris-Sørensen, 2009; Enghoff, 2011; Makarewicz and Pleuger, 2020), the amount (n: 389 (season 2020–2022)) of horse bones and teeth found at Ginnerup is high compared to contemporaneous Scandinavian sites (Klassen et al., 2023). Five and 13 teeth from Ginnerup respectively have been sampled for meso- and microwear (Table S3). The study further includes published data on isotopes (Klassen et al., 2023; Makarewicz, 2023) (Table S1).

2.2. Hüde I

The site of Hüde I is situated at the southern rim of lake Dümmer near the inlet of the Hunte river (Schütrumpf, 1988). The lake forms part of the predominantly shallow and sandy Diepholzer Moor Depression (Diepholzer Moorniederung) in Lower Saxony, Germany at the southern perimeter of the North European Plain (Fig. 1). The site was part of an extended network of sites around lake Dümmer (Heumüller et al., 2022). From ~6.5 cal B.P. artefacts, trackways and pollen proxies suggest the beginning of settlement activity possibly connected with Rössen influences (Bauerhochse and Leuschner, 2022; Heumüller et al., 2022). Based on typological analogies to well-dated site sequences in the Low Countries, the Hüde I settlement and bone depositions can be assigned to the Neolithic Swifterband Culture and the TRB, ~6.15/5.95–4.75 ka cal B.P. (Raemaekers, 1999; ten Anscher, 2012; ten Anscher and Raemaekers, 2023). Furthermore, frequent contacts with Neolithic groups further south and outside the northern lowlands are suggested by imports of stone adzes and pottery from the Bischheim group.

The identified faunal remains include at least 20 predominantly wild mammal species and count >10,000 identified specimens including substantial numbers (n: 660) of *E. ferus* bones and teeth. There are no obvious differences in the relative frequency of the different mammal species between the assemblage assigned to the Swifterbant and the TRB respectively, and most of the remains belong to the TRB horizon (Hübner et al., 1988). The majority of the assemblage from Hüde I is thus more or less contemporaneous with the assemblage from Ginnerup. The site has been interpreted as a seasonal hunting site (Kossian, 2007). 11 bones (calcanei), eight from *E. ferus* and three from aurochs (*Bos primigenius*) have been sampled for isotope analysis (Table S1), whereas 13 and 19 teeth have been sampled for meso- and micro wear analysis respectively (Table S3).

3. Methods

The study includes tooth meso- and microwear analyses and carbon (C), nitrogen (N), and sulphur (S) isotope analyses of bone collagen.

3.1. Tooth mesowear

Mesowear is an analytical tool to record dietary wear on herbivore teeth based on the physical properties of ungulate foods as reflected in the relative amounts of attritive (tooth-on-tooth) and abrasive (food-on-tooth) wear on the dental enamel during mastication (Fortelius and Solounias, 2000). The method is based on direct, macroscopic observations of the wear profile of the cheek tooth occlusal surface (Fig. 2 A + B). Generally, attritive wear is associated with a browse-based 'soft' diet, causing the opposing teeth to wear themselves, creating wear facets and sharpened cusp apices, whereas abrasive wear, typical of grazers, obliterates the facets and creates rounded or blunted cusp apices. Mesowear is accumulative and corresponds to a longer temporal scale (months-years) than microwear (see section 3.2) thus reflecting the average food choice of the animal (Fortelius and Solounias, 2000; Ackermans et al., 2018). As such, it can be used as a proxy for dietary and environmental reconstruction and facilitate studies of spatial or temporal dietary/environmental differences (Fortelius and Solounias, 2000; Ackermans et al., 2018).

We follow the extended mesowear method (Kaiser and Solounias,

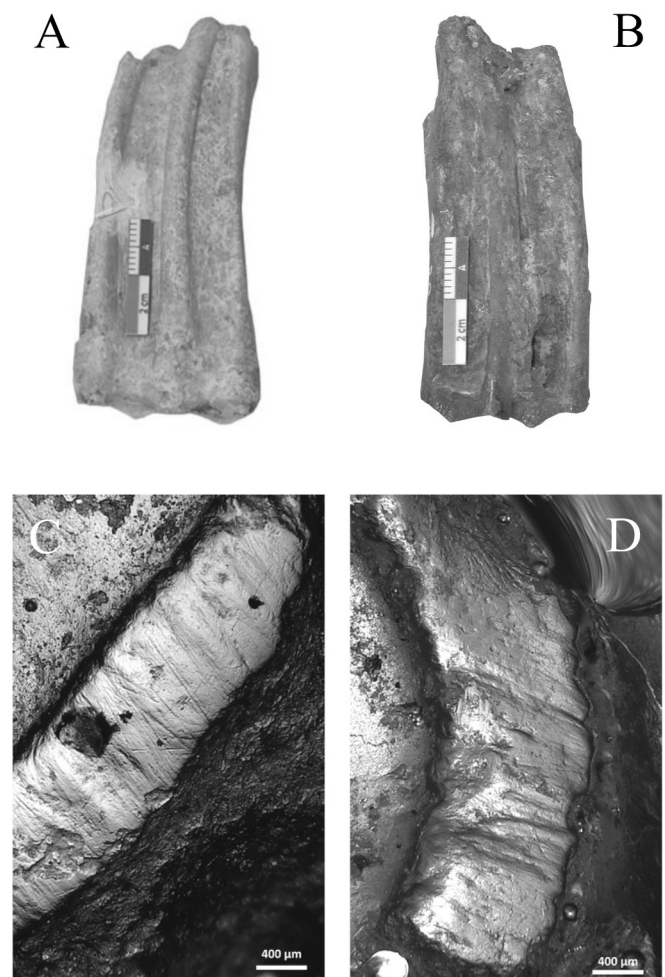


Fig. 2. Examples of mesowear (A + B) and microwear (C + D) on *Equus ferus* upper cheek teeth from Ginnerup (A + C) and Hüde I (B + D).

A) Lateral view of upper left fourth premolar (P4) from Ginnerup (sample ID: G02, tooth ID: x489) and B) upper right first molar from Hüde I (sample ID: H14, tooth ID XI 38). Scale bar = 2 cm.

C + D) Examples of microwear patterns on the metacone of two *Equus ferus* upper cheek teeth. C) upper left fourth premolar (P4) from Ginnerup (sample ID: G02, tooth ID: x489). D) second upper left molar (M2) from Hüde I (sample ID: H20, tooth ID: XIX 26). Scale bar = 400 µm.

2003). Teeth from young and old individuals have been omitted from the analysis (Fortelius and Solounias, 2000; Rivals et al., 2007b). Identification of isolated teeth is based on Kaiser and Solounias (2003). Applied to the sharpest of the two buccal cusps in upper P4-M3, mesowear is determined by two variables: cusp shape/sharpness (CS) and cusp height/occlusal relief (OR). CS is recorded as 'sharp', 'rounded', or 'blunt' and OR as 'high' or 'low'. The OR and CS recordings are presented as percentages of the entire sample from each site i.e., '%high' and '%low', and '%sharp', '%rounded', and '%blunt' respectively (Fortelius and Solounias, 2000). Additionally, the recordings are transformed into univariate numeric mesowear scores (MWS) following Kaiser (2011). Accordingly, a combination of high relief and sharp cusps is assigned a score of '0', a combination of high relief and round cusp a score of '1', a combination of low relief and sharp cusp is assigned a score of '2', a combination of low relief and round cusp a score of '3', and a combination of low relief and blunt cusp is assigned a score of '4' (Kaiser, 2011). Finally, the individual scores are averaged for each site as an expression of the mean overall mesowear signal for the group/population in question.

In our study we have avoided the univariate "mesowear ruler" method developed by Mühbachler et al. (2011) although widely used in studies involving paleodiet reconstructions in *Equus* (e.g., Rivals et al., 2015b, 2017; Uzunidis, 2021; Uzunidis and Rivals, 2023). A sizable number of *E. ferus* in the two assemblages under study have a combination of sharp cusp and low relief (Table 1). This wear stage was not included in the mesowear ruler method (Mühbachler et al., 2011).

3.2. Tooth microwear

Dental microwear refers to microscopic traces on the occlusal surface of herbivore teeth that develop during mastication (Walker et al., 1978). The wear is primarily caused by the presence of hard silica structures (phytoliths) in plants and, therefore, reflects dietary choices of the animal (Walker et al., 1978; Rivals et al., 2015a). However, external particles such as dust and grits can also produce pit and scratches (Merceron et al., 2016; Gallego-Valle et al., 2020; Schulz-Kornas et al., 2020). In contrast to mesowear, microwear reflects the diet of the last days to months of an individual's life (Teaford and Oyen, 1989; Hoffman et al., 2015; Merceron et al., 2016; Winkler et al., 2020). Differences and variability in type and density of the micro-traces are used to determine the dominant dietary type of which three major categories are employed: grazing (a diet focusing on graminoid plants), browse (a diet focusing on ligneous plants, both woody and herbaceous dicots), and mixed feeding (a diet that does not select between the two previous categories).

Here, the microwear analysis follows the protocol established by Solounias and Semprebon (2002) and Semprebon et al. (2004). The occlusal surface of each tooth was cleaned using acetone and then 99% ethanol. Then the surface was moulded with high-resolution silicone (vinylpolysiloxane) and casts were made using clear epoxy resin. The

Table 1

Equus ferus dental mesowear data from Húde I and Ginnerup. Abbreviations: n = number of specimens; m = mean; sd = standard deviation; OR = occlusal relief; CS = cusp shape; %high = percentage of specimens with high cusps; % low = percentage of specimens with low cusps; %sharp = percentage of specimens with sharp cusps; %round = percentage of specimens with rounded cusps; %blunt = percentage of specimens with blunt cusps; MWS = mesowear score (following Kaiser, 2011).

| Site | n | OR | | CS | | | MWS |
|----------|----|--------|-------|---------|---------|---------|------|
| | | % high | % low | % sharp | % round | % blunt | |
| Húde I | m | 38.46 | 61.54 | 46.15 | 53.85 | 0 | 1.77 |
| | sd | | | | | | 1.24 |
| Ginnerup | m | 0 | 100 | 20.0 | 20.0 | 60.0 | 3.4 |
| | sd | | | | | | 0.89 |

transparent casts were analysed with a stereomicroscope at magnification of x35. Observations were restricted to a standard surface of 0.16 mm² using an ocular reticule (Fig. 2C+D). We discarded second premolars that do not record the same signal as the other teeth (Kaiser and Solounias, 2003; Xafis et al., 2017). Specimens with badly preserved enamel or taphonomic defects were excluded from the analysis (King et al., 1999). Moreover, we focussed on the portion of the enamel on the paracone or metacone fossettes and avoided the edges of the occlusal surface as they are more prone to alteration by taphonomic processes in horses (Uzunidis et al., 2021).

We observed various micro-traces on the occlusal surfaces following the classification of Solounias and Semprebon (2002) and Semprebon et al. (2004) dividing the traces into pits (small and large), scratches (fine, coarse and hypercoarse), and gouges. Pits are microwear scars that are circular or sub-circular in outline and thus have approximately similar widths and lengths, while scratches are elongated microfeatures that have straight and parallel sides. Small pits are small and shallow scars that appear bright while large pits are deeper and wider and less refractive. Gouges are very deep and large pits that do not reflect the light and appear dark. Fine scratches are narrow and very superficial on the enamel surface while coarse scratches are wider and more marked. They both refract well the light and appear bright under the stereomicroscope. Hypercoarse scratches are wider, deeper and dark. Each tooth was also assigned a univariate scratch width score (SWS) as a qualitative score of the observed scratch texture based on Solounias and Semprebon (2002) and Semprebon et al. (2004) and modified by Rival et al. (2007a and 2010). Teeth with predominantly fine scratches scored '0', teeth with mixed fine and coarse scratches scored '1', and teeth with predominantly coarse scratches were assigned with a score of '2'.

We also estimated the duration of the mortality event by measuring the variability in the number of scratches (using CV – coefficient of variation and SD – Standard deviation) in each population as established by Rivals et al. (2015a). The results are plotted on a heat map (Fig. 5). The heat map is divided into three areas which correspond to three types of accumulation events: [A] one or several successive events over a season, or shorter; [B] one or several successive events longer than a season (i.e. two or more contiguous seasons); and [C] separate events that occurred over different non-contiguous seasons. Black lines separate each area, and the colour scale corresponds to the different error probabilities.

3.3. Isotope analyses

A total of 11 bones from Húde I were sampled for bone collagen carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulphur ($\delta^{34}\text{S}$) isotope analysis. All sampled bones were calcanei: Eight from horses and three from aurochs. Before sampling, the surfaces of the bones were removed with a clean scalpel. The samples were drilled. All calcanei analysed in the study, except one, are from animals older than 3y based on the fusion of the tuber calcanei (Habermehl, 1975; Barone, 1976), limiting the possible effects of suckling (Fogel et al., 1989). The aurochs samples from Húde I were added to be able to investigate inter- and intrasite differences as comparative isotope analyses including *Bos* sp. are available from Ginnerup (Klassen et al., 2023; Makarewicz, 2023).

Samples were prepared at the Archaeology Isotope Laboratory at the Department of Archaeology, Simon Fraser University, Canada, following the methods outlined in Richards and Hedges (1999) with the addition of an ultrafiltration step (Brown et al., 1988). Samples were first demineralized in 0.5 M HCl at 5 °C, then hydrolysed at 70 °C for 24 h, and then filtered using a 5-8 μm Ezee-filter and ultrafiltered using a 30 kDa filter. Afterwards, the >30 kDa fraction was lyophilized (freeze-dried) for 24 h. The resultant fraction was analysed for C, N and S isotopes using a Thermo-Fisher EA coupled to a Thermo-Fisher isotope ratio mass spectrometer. Samples were measured relative to both international and secondary (lab) standards. Errors (1 σ) on the measurements are $\delta^{13}\text{C} = 0.1\text{‰}$, $\delta^{15}\text{N} = 0.2\text{‰}$, $\delta^{34}\text{S} = 0.5\text{‰}$. For comparison, previously published

isotope data from Ginnerup have been included in our analysis. These include samples from seven horses and 18 ruminants (Klassen et al., 2023; Makarewicz, 2023) (Table S1).

3.4. Statistical analyses

Mesowear: The mesowear data are interpreted through hierarchical cluster analyses of the mesowear variables ‘%high’, ‘%sharp’, and ‘%blunt’ using the software programme Past 3 (Hammer et al., 2001). Although hierarchical cluster analyses are explorative in nature only, they may offer meaningful ways of visualizing trends in mesowear data and identifying which extant species of known dietary status that cluster closest to the fossil specimens in question and thus indicate their dietary class (Fortelius and Solounias, 2000; Schulz and Kaiser, 2007; Drennan, 2009; Kaiser, 2011; Green and Croft, 2018). MWS have been tested for equal means between the two populations using unequal variances *t*-tests (Welch’s *t*-test).

Microwear: R version 4.1.2 (R Core Team, 2019) with Rstudio (Rstudio Team, 2019) was used to run nonparametric Wilcoxon tests to test for differences in median values between groups.

Isotopes: The isotope values have been tested for equal means using unequal variances *t*-tests (Welch’s *t*-test) between the two populations of *E. ferus* and between *E. ferus* and ruminant species at Hùde I and Ginnerup respectively. In all tests, a 0.05 probability or lower ($p < .05$) is considered significant.

4. Results

4.1. Mesowear

An initial cluster analysis based on the mesowear variables %high, % sharp, and %blunt and compared to extant ungulate species classified as typical grazer, mixed feeder, or browser suggests that the two horse populations in our study group within different clusters (Fig. 3A).

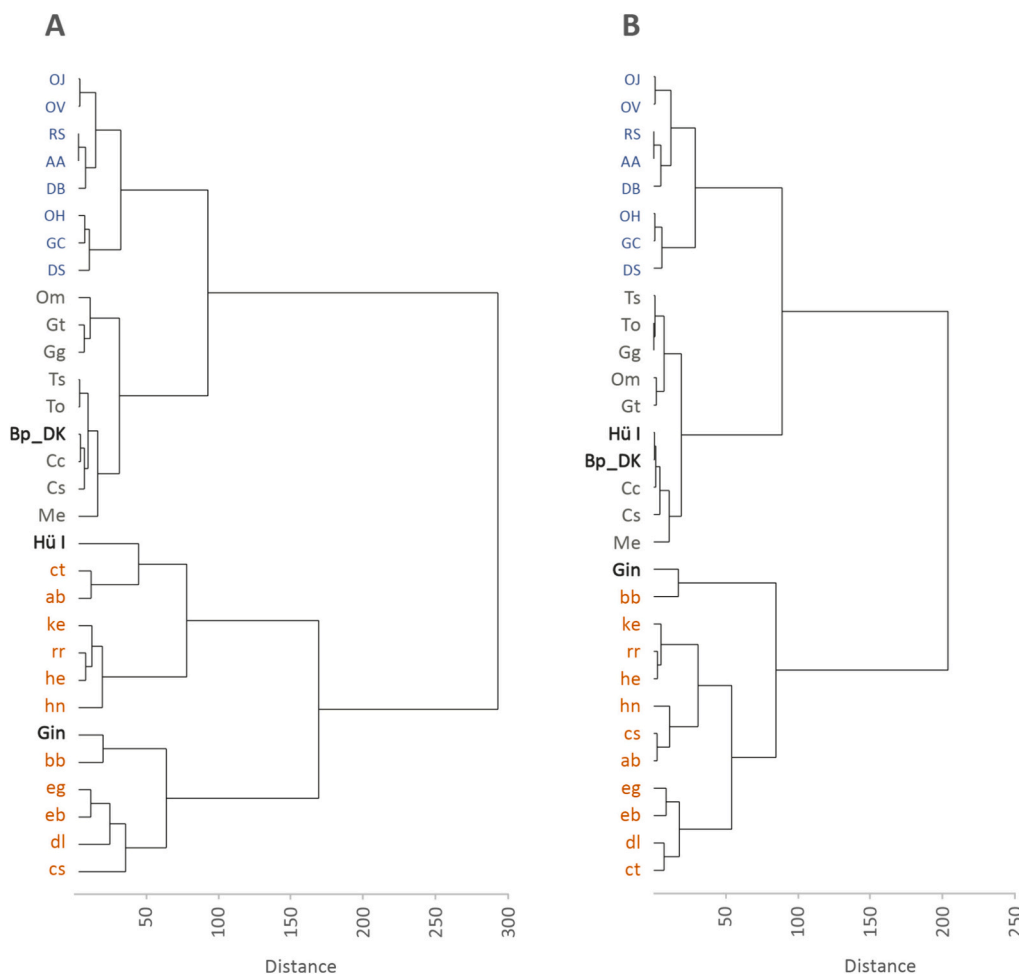


Fig. 3. Hierarchical cluster analyses of mesowear data from 27 “typical” extant species (data from Fortelius and Solounias, 2000: Table 1) and neolithic *E. ferus* from Ginnerup (Gin) ($N = 5$) and Hùde I (Hù I) ($N = 13$).

[A] Cluster analysis based on three variables: %high (OR), %sharp (CS), and %blunt (CS). [B] Cluster analysis based on two variables: %sharp (CS), and %blunt (CS). For comparison, a sample of contemporary (subboreal) aurochs (Dk Bp) have been added (data from Schulz and Kaiser, 2007: Table 2).

The analyses are computed in Past 3 (Hammer et al., 2001) using a default algorithm (Ward’s method) and Euclidean distance.

Extant species included in the clusters: moose, *Alces alces* (AA); Sumatran rhinoceros, *Dicerorhinus sumatrensis* (DS), black rhinoceros, *Diceros bicornis* (DB); giraffe, *Giraffa camelopardalis* (GC); mule deer, *Odocoileus hemionus* (OH); white-tailed deer, *Odocoileus virginianus* (OV); okapi, *Okapia johnstoni* (OJ); Javan rhinoceros, *Rhinoceros sondaicus* (RS); hartebeest, *Alcelaphus buselaphus* (ab); American plains bison, *Bison bison* (bb); white rhinoceros, *Ceratotherium simum* (cs), wildebeest, *Connochaetes taurinus* (ct); topi, *Damaliscus lunatus* (dl); Burchell’s zebra, *Equus burchelli* (eb); Grevy’s zebra, *Equus grevyi* (eg); roan antelope, *Hippotragus equinus* (he); sable antelope, *Hippotragus niger* (hn); common waterbuck, *Kobus ellipsiprymnus* (ke); bohor reedbuck *Redunca redunca* (rr); impala, *Aepyceros melampus* (Me); serow, *Carpicornis sumatraensis* (Cs); wapiti, *Cervus canadensis* (Cc); Grant’s gazelle, *Gazella granti* (Gg); Thomson’s gazelle, *Gazella thomsoni* (Gt); muskox, *Ovibos moschatus* (Om); eland, *Taurotragus oryx* (To); bushbuck, *Tragelaphus scriptus* (Ts). Lower case (orange) letters = grazers. Mixed case (grey) letters = mixed feeders. Upper case (blue) letters = browsers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Overall, four clusters can be identified: 1) a cluster of “extreme” grazers, 2) a cluster of less abrasion-dominated grazers, 3) a group of mixed feeders, and 4) “extreme” browsers. The Ginnerup horses (Gin) cluster amongst “extreme” grazers such as American plains bison *Bison bison* (bb) and Grevy’s zebra *Equus grevyi* (eg), suggesting a highly abrasive diet. The Húde I horses (Hü I) cluster together with less abrasion-dominated grazers such as wildebeest *Connochaetes taurinus* (ct) and hartebeest *Alcelaphus buselaphus* (ab). For comparison, mesowear of a sample of contemporary (Subboreal) Danish aurochs *Bos primigenius* have been added to the analysis (Dk-Bp) (Schulz and Kaiser, 2007). Unlike the two populations of *E. ferus* from Ginnerup and Húde I, they cluster amongst the mixed feeders, most closely to the wapiti *Cervus canadensis* (Cc).

38% of the OR from Húde I and none from Ginnerup are recorded as “high” (Table 1). It is worth noting that the procedure is subjective, and there is no clear-cut boundary between “high” and “low” relief. Merceron et al. (2007) have suggested a method to metrically evaluate the height of the occlusal relief. Using this method all OR in the two samples under study would classify as “low”, resulting in a confidence level lower than 95% ($p > .05$) for the univariate MWS. Omitting the OR variable from the initial exploration of the mesowear data using cluster analysis (Fig. 3B), however, seems to accentuate rather than obliterate the observed differences between the Húde I and Ginnerup populations placing the Húde I horses amongst the typical mixed feeders together with the Subboreal Danish aurochs *Bos primigenius* (Bp-DK).

The observed differences are confirmed by a two-sample Welch’s *t*-test ($t(10) = -3.097, p = .011$) of the univariate mesowear score (MWS). The test shows that the MWS in the Húde I assemblage (Mean = 1.769, SD = 1.235; Table 1) and the Ginnerup assemblage (Mean = 3.40, SD = 0.894; Table 1) are significantly different ($p < .05$).

However, assigning our samples with low relief and sharp cusp an intermediate score of both “3” and “4” following Mihlbachler et al. (2011) would still result in a confidence level well past 95% ($p < .05$) (Mean MWS: Húde I = 2.2–2.5. Ginnerup = 4.6–4.8) confirming the observed differences using the scoring system developed by Kaiser (2011).

4.2. Microwear

32 horse teeth were sampled for microwear analysis: 19 from Húde I and 13 from Ginnerup. The teeth were moderately affected by taphonomic processes and seven (36.8 %) from Húde I and three (23 %) from Ginnerup were discarded before analysis (Table S3). The result of the analysis is shown in Table 2.

The observed number of pits (NP) and scratches (NS) in the two populations of *E. ferus* are quite low (Table 2), and both populations group with extant browsers indicating a diet dominated by soft tissues from dicots the last days to months before the animals died (Fig. 4). The low number of teeth with large pits and the absence of hyper coarse scratches and gouges allow to exclude fruits, seeds and bark consumption (Semprebón et al., 2011; Rivals et al., 2015b). The SWS indicate a majority of fine to coarse texture scratches which is also consistent with a leaf browsing diet in both populations (Semprebón et al., 2011) (Table 2). The Ginnerup horse population, however, displays a

Table 2

Equus ferus dental microwear data from Húde I and Ginnerup. Abbreviations: n = number of specimens; m = mean; sd = standard deviation, cv = coefficient of variation, NP = number of pits; NS = number of scratches; %LP = percentage of specimens with large pits; %G = percentage of specimens with gouges; %XS = percentage of specimens with crossed scratches; %HC = percentage of specimens with hyper coarse scratches; SWS = scratches width score.

| Site | n | | NP | NS | %LP | %G | %XS | %HC | SWS |
|----------|----|----|------|------|-------|----|-------|-----|------|
| Húde I | 12 | m | 9.96 | 8.29 | 36.36 | 0 | 45.45 | 0 | 0.79 |
| | | sd | 2.99 | 2.4 | | | | | |
| | | cv | | 0.29 | | | | | |
| Ginnerup | 10 | m | 13.8 | 12.7 | 33.33 | 0 | 50 | 0 | 1 |
| | | sd | 3.77 | 3 | | | | | |
| | | cv | | 0.1 | | | | | |

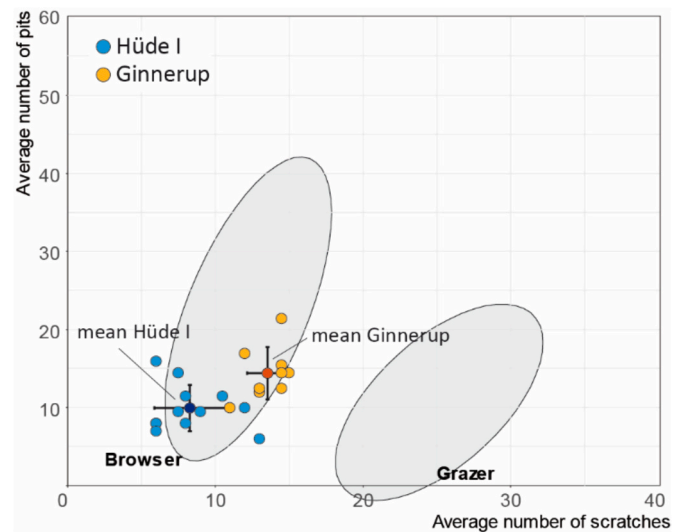


Fig. 4. Bivariate plot of the mean number of microwear pits and scratches of horses from Ginnerup ($N = 10$) (orange) and Húde I ($N = 12$) (blue). The error bars correspond to the standard deviation (± 1 SD). The ellipses correspond to the Gaussian confidence ellipse ($p = .95$) on the centroids of extant grazers and browsers published by Solounias and Semprebón (2002). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

significant higher number of pits (Wilcoxon test, $p = .0124$) and scratches (Wilcoxon test, $p = .0022$) compared to Húde I, suggesting a larger amount of abrasive food in the diet of the former.

As a proxy of short-term wear, microwear is sensitive of changes in diet of the individual over the last days to months (Semprebón et al., 2004; Sánchez-Hernández et al., 2016; Winkler et al., 2020). Consequently, the variability of the recorded wear in the entire assemblage is strongly influenced by the overall duration of the cohort mortality event (Rivals et al., 2015a; Uzunidis and Rivals, 2023). In Ginnerup, the variability of the scratch density amongst the horses is quite low, which may be attributed to one or more same-season (or shorter) mortality events (Fig. 5; Table 2). The variability in scratch density at Húde I is higher than at Ginnerup (Fig. 5; Table 2). Unfortunately, it is not possible to attribute the observed variability at Húde I to any of the outlined mortality scenarios (A-C) with any certainty (Rivals et al., 2015a; Uzunidis and Rivals, 2023).

4.3. Isotopes

The results of the isotope analysis are shown in Table S1 and summarized in Table 3. Table S1 also include previously published data from Ginnerup (Klassen et al., 2023; Makarewicz, 2023). For summary statistics see Table S2.

4.3.1. Húde I

The collagen extraction yield of the Húde I samples (mean: 9.7 ± 4.4

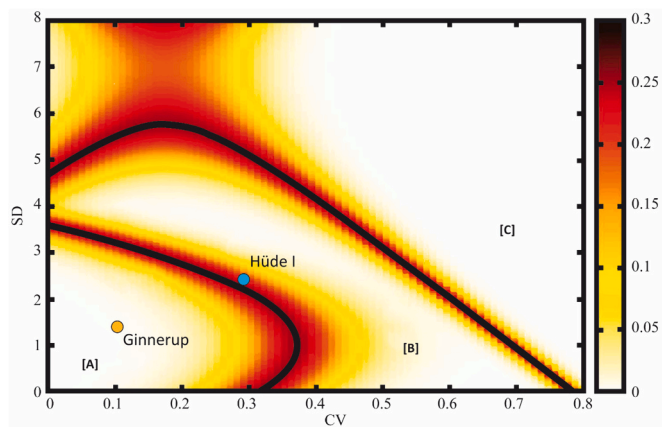


Fig. 5. Microwear data of the horses from Ginnerup (N = 10) and Húde I (N = 12). Bivariate plot: standard deviation (SD) and coefficient of variation (CV) are calculated based on the number of scratches (Table 2). Boundary lines (in black) between the three areas with the error probability (heat map/colour scale). [A] season-long or shorter events; [B] events longer than a season; and [C] separate events (at least two) that occurred over different non-contiguous seasons.

%) was generally good. One sample (SFU3701), however, falls below the accepted range for good quality collagen and has been discarded (Ambrose, 1993; van Klinken, 1999). The remaining samples range from 6.8 to 19.5% (mean: 10.5 ± 3.5 %) with nitrogen and carbon wt% between 25.8 and 41.8 %, and 9.5 and 15.3 %, respectively. Furthermore, the C/N ratios range between 3.2 and 3.4 (mean: 3.3 ± 0.1), which is also within the expected range of 2.9 to 3.6 for well-preserved collagen (DeNiro, 1985). The C/S ratio varies between 138.7 and 264.9 (mean: 197 ± 43.9) with wt% varying between 0.3 and 0.8% (mean: 0.5 ± 0.2 %) which are within the acceptable range (Nehlich and Richards, 2009).

The 11 samples from Húde I yielded $\delta^{13}\text{C}$ values between -24.0 ‰ and -21.8 ‰ (mean: -22.9 ± 0.6 ‰), $\delta^{15}\text{N}$ between 3.3 ‰ and 6.1 ‰ (mean: 4.4 ± 0.8 ‰), and $\delta^{34}\text{S}$ between 1.1 ‰ and 12.9 ‰ (mean: 6.4 ± 3.8 ‰) (Fig. 6; Table 3). In general, all $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values fall within the expected range for herbivore collagen from this region with $\delta^{13}\text{C}$ values clustering around -22 ‰ and $\delta^{15}\text{N}$ clustering around 5 or 6 ‰, although some animals show remarkably low values (see section 5.6.) (Fischer et al., 2007; Hedges et al., 2004; Richards and Hedges, 2003). The horses ($n = 8$) had $\delta^{13}\text{C}$ values between -24 ‰ and -21.8 ‰ (mean: -22.8 ± 0.7 ‰), $\delta^{15}\text{N}$ values between 3.3 ‰ and 4.4 ‰ (mean: 4.0 ± 0.5 ‰) and $\delta^{34}\text{S}$ values ranging from 1.1 ‰ and 12.9 ‰ (mean: 6.5 ± 4.0 ‰) (Table 3). The values for aurochs ($n = 3$) range between -23.3 ‰ and -23.2 ‰ (mean: -23.3 ± 0.1 ‰), 4.9 ‰ and 6.1 ‰ (mean: 5.5 ± 0.6 ‰), and 2.8 ‰ and 10.1 ‰ (mean: 6.2 ± 3.7 ‰) for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$,

Table 3

Summary table of *Equus ferus* and *Bos primigenius* isotopic data from Húde I including minimum (min), maximum (max), and mean values \pm standard deviations (SD).

| Species | n | $\delta^{13}\text{C}$ mean \pm SD (min to max) | $\delta^{15}\text{N}$ mean \pm SD (min to max) | $\delta^{34}\text{S}$ mean \pm SD (min to max) |
|------------------------|----|--|--|--|
| <i>Equus ferus</i> | 8 | -22.81 ± 0.68 (-23.97 to -21.82) | 3.98 ± 0.47 (3.33 to 4.42) | 6.45 ± 4.03 (1.05 to 12.88) |
| <i>Bos primigenius</i> | 3 | -23.28 ± 0.05 (-23.31 to -23.22) | 5.45 ± 0.53 (4.85 to 6.10) | 6.17 ± 3.71 (2.77 to 10.13) |
| Σ | 11 | -22.94 ± 0.61 (-23.97 to -21.82) | 4.38 ± 0.84 (3.33 to 6.10) | 6.38 ± 3.76 (1.05 to 12.88) |

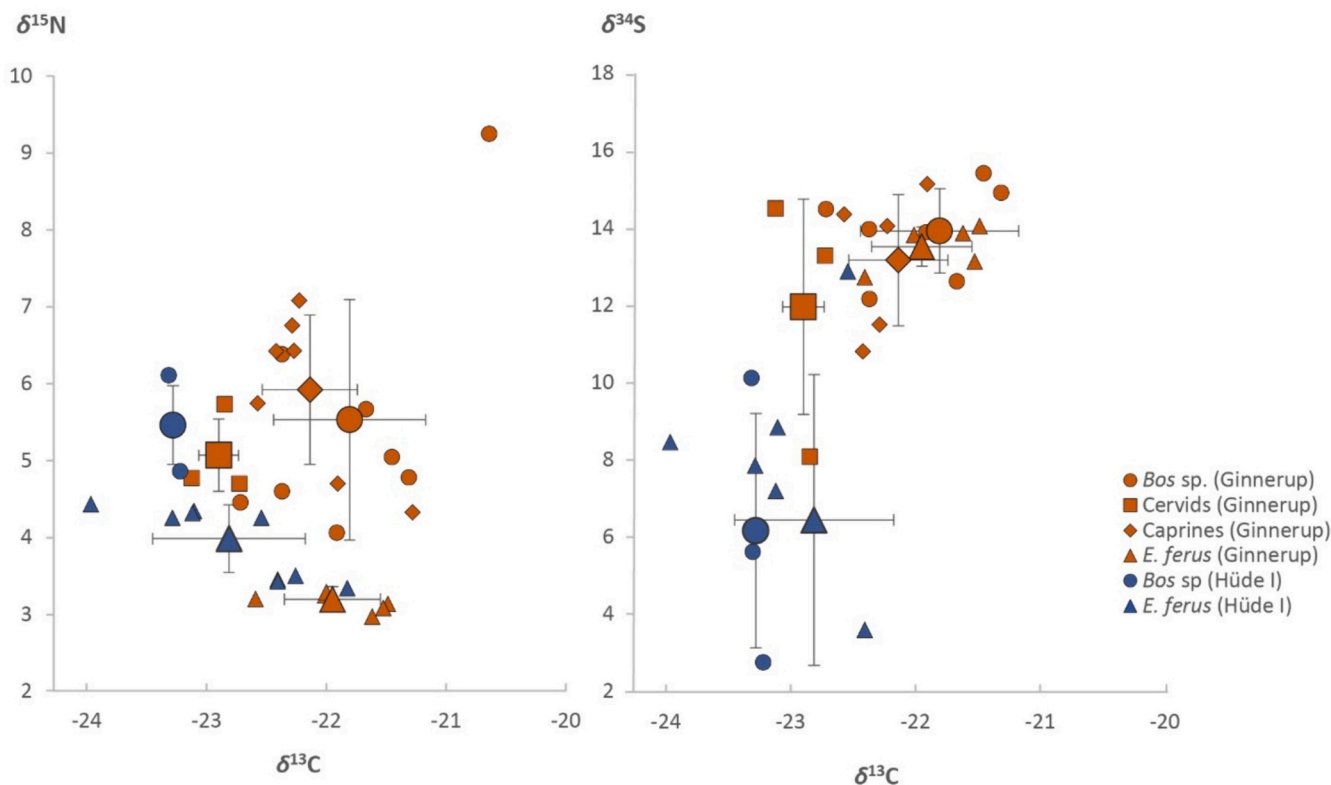


Fig. 6. Diagram of isotope values of Subboreal herbivore fauna from Húde I and Ginnerup. Left: Carbon and nitrogen (N = 36). Right: Carbon and sulphur (N = 31). Large icons = mean + standard deviations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and $\delta^{34}\text{S}$ respectively (Table 3). There are significant differences ($t(3) = -3.715$, $p = .034$) between the means in $\delta^{15}\text{N}$ between *E. ferus* and *B. primigenius* from Hude I, but not in $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ (Table S2b).

4.3.2. Ginnerup

As stated in section 3.3, previously published isotope data from Ginnerup have been included in our analysis. These include samples from seven horses and 18 ruminants (Klassen et al., 2023; Makarewicz, 2023) (Table S1). Overall, the 25 herbivore samples yielded $\delta^{13}\text{C}$ values between -23.1‰ and -20.6‰ (mean: $-22.1 \pm 0.6\text{‰}$), $\delta^{15}\text{N}$ between 3.0‰ and 9.2‰ (mean: $4.9 \pm 1.6\text{‰}$), and $\delta^{34}\text{S}$ between 15.4‰ and 8.1‰ (mean: $13.4 \pm 1.7\text{‰}$) (Fig. 6; Table S2a). The horses ($n = 7$) produced $\delta^{13}\text{C}$ values between -22.6‰ and -21.5‰ (mean: $-22.0 \pm 0.4\text{‰}$), $\delta^{15}\text{N}$ values between 3.0‰ and 3.4‰ (mean: $3.2 \pm 0.2\text{‰}$) and $\delta^{34}\text{S}$ values ranging from 12.7‰ to 14.1‰ (mean: $13.5 \pm 0.6\text{‰}$). The values for *Bos* sp. ($n = 8$) range between -22.7‰ and -20.6‰ (mean: $-21.8 \pm 0.7\text{‰}$), 9.2‰ and 4.1‰ (mean: $5.5 \pm 1.7\text{‰}$), and 15.4‰ and 12.2‰ (mean: $13.9 \pm 1.2\text{‰}$) for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ respectively, whereas the $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ for caprines ($n = 7$) range between -22.6‰ and -21.3‰ (mean: $-22.1 \pm 0.4\text{‰}$), 7.1‰ and 4.3‰ (mean: $5.9 \pm 1.0\text{‰}$), and 15.1‰ and 10.8‰ (mean: $13.2 \pm 1.9\text{‰}$). For cervids see Table S2a. There are statistical significant differences in $\delta^{15}\text{N}$ means between *E. ferus* and all ruminants species but not in $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$, except in $\delta^{13}\text{C}$ between *E. ferus* and cervids ($t(8) = 4.7$, $p = .002$), with mean carbon values c. 1‰ lower in cervids (Table S2b). Based on Welch's *t*-tests there are significant differences in means in all three isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$) between the *E. ferus* population from Hude I and Ginnerup (Table S2b).

5. Discussion

5.1. Dietary and seasonal differences in resource utility from tooth wear analysis

Although both populations of *E. ferus* cluster amongst grazers based on the mesowear analysis, there are statistically significant differences in their dietary signal according to the univariate mesowear score (MWS) (see section 4.1). The Hude I horses apparently included more browse in their diet, resulting in higher percentages of high and sharp cusps than in the Ginnerup population (Table 1). This is partly supported by the cluster analyses (Fig. 3). The cluster analyses group the Ginnerup horses amongst extreme grazers – most closely American bison (*Bison bison*), whereas the Hude I horses group amongst less abrasion-dominated grazers such as the wildebeest *Connochaetes taurinus* and the hartebeest *Alcelaphus buselaphus* based on the three variables %high, %sharp, and %blunt and together with Subboreal aurochs (*Bos primigenius*) and mixed feeders such as the wapiti (*Cervus canadensis*) based on the variables %sharp and %blunt only. This suggests that the two populations of *E. ferus* from Hude I and Ginnerup had overall diets dominated by abrasive food such as grasses, but with varying amounts of attritive diets, i.e., browse.

Unlike mesowear, the microwear analysis groups both populations of *E. ferus* amongst extant browsers, suggesting a diet dominated by forbs and/or soft tissues from woody plants the last days to months before they were killed (Fig. 4). In the Ginnerup assemblage the low variability in the number of microwear scratches hints at a series of short-duration events at a time, when the horses were browsing (Fig. 5). This interpretation is supported by the overall mesowear signal (predominantly low occlusal relief and blunt cusps) suggesting that the observed dietary shift from grazing to browsing occurred shortly before the mortality event. With the nature and overall duration of the site in mind (see section 2.1 and 5.3), and although caution is needed due to a limited number of analysed specimens ($N = 10$), this hints at recurring kill-offs at a specific time of the year. In principle, this pattern of dietary shift could also occur in animals that were in one way or another corralled and fed (e.g. a diet of forbs and leaves) by humans prior to death –

although such a scenario would be significantly more likely in cases concerning domestic or semi-feral animals.

Regarding the Hude I assemblage, the results of both the microwear and mesowear analysis are more ambiguous. As indicated by the mesowear analysis the relative number of high and sharp cusps are higher in the Hude I assemblages than at Ginnerup. As mesowear form over a considerable length of time this indicates that the period(s) of feeding on soft tissue plants was of considerable length to be able to alter the shape of the tooth cusps. As indicated by the microwear scratch variability analysis we also cannot rule out that the horses were killed at different seasons, which may add to the equivocal tooth wear signal (Fig. 5). The interpretation of the microwear is further hampered by a limited sample size ($N = 12$).

Contrasting seasonal patterns in dietary intake has also been observed in extant feral horses at the Mols laboratory, Djursland (Thomassen et al., 2023). Similar clearcut differences are, however, not always the case and may be an effect of food availability, especially the amount of available grass biomass year-round (Cromsigt et al., 2018).

5.2. Human impact on *E. ferus* habitat and diet from isotope analysis

Apart from differences in available foodstuff, competition with humans and their domesticates and the impact of the latter pair on the landscape may also play an important role in wild herbivore choice of diet and habitat as suggested by two studies of Danish *Bos primigenius* (Noe-Nygaard et al., 2005; Schulz and Kaiser, 2007). Schulz and Kaiser (2007) observed a significant shift in aurochs mesowear from late Atlantic to early Subboreal from grazing-dominated wear to a more moderate grazing regime similar to that of extant mixed feeders. Further, the study of Noe-Nygaard et al. (2005) shows a substantial difference in $\delta^{13}\text{C}$ values between late Atlantic aurochs and early domestic cattle and suggests that the observed depletion in aurochs carbon isotope (similar to what is observed in *Cervus elaphus*) may be attributed to the canopy effect, which suggests that plant ^{13}C in closed forests is depleted along a gradient from the forest floor to the canopy with the most negative values at ground level (van der Merwe and Medina, 1991). In both of the above cited Neolithic studies the results may indicate increasing competition (including hunting) between farmers and their cattle and wild herbivore fauna, of which the latter had to take refuge in and adapt to less open landscapes (Noe-Nygaard et al., 2005; Schulz and Kaiser, 2007), i.e., in line with the refuge species concept (Kerley et al., 2012).

On a local level, the above suggestions are supported by a large-scale isotopic study of mammals from the Subboreal, Neolithic Kainsbakke and Kiral Bro sites situated a few kilometres northeast of Ginnerup (Makarewicz, 2023). Based on consistent differences in $\delta^{13}\text{C}$ values between species and extensive variation in $\delta^{13}\text{C}$ values in some species, the study indicates the existence of a diverse range of habitats utilized by different herbivore species (Makarewicz, 2023). Also, the study suggests seasonal changes in habitat use by domestic cattle, indicating shifting seasonal management practices (Makarewicz, 2023).

Based on chronological continuity, geographical proximity and cultural affinity between Ginnerup, Kainsbakke and Kiral Bro, the utilized mammals (with the possible exception of less frequent animal species (e.g., *Ursus arctos*, *Lynx lynx* and *Alces alces*) are believed to represent a coherent locally available fauna, just as the cultural conception and utility of the different animal species may be presumed to be similar across the sites (Klassen et al., 2020, 2023). Combining available carbon and nitrogen isotope data from the three sites may therefore reveal some interesting trends. Here, we investigate possible differences in mean values between wild herbivores and presumed domesticates (Fig. 7; Table S2c). Interestingly, and although samples of *Sus scrofa* ssp. and *Bos* sp. might include both domestic and wild species, wild species (large-bodied cattle (*Bos* cf. *primigenius*), *E. ferus*, and cervids (*Cervus elaphus* and *Capreolus capreolus*)) have larger ranges of $\delta^{13}\text{C}$ values than small-bodied *Bos* sp., *Sus scrofa* ssp., and caprines (*Ovis aries* and *Capra*

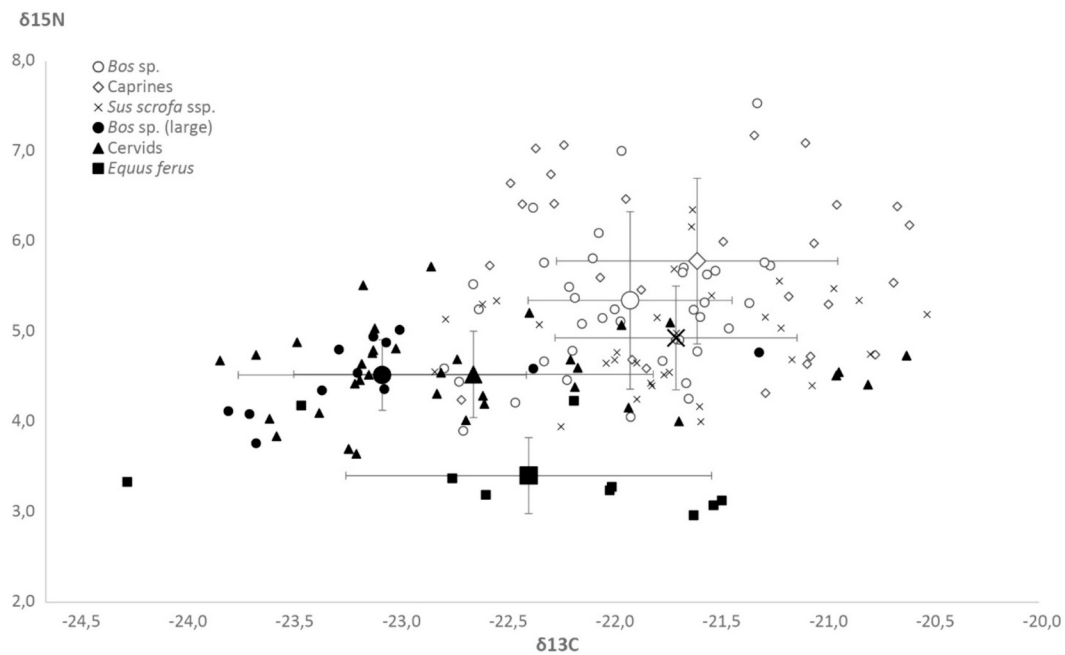


Fig. 7. Carbon and nitrogen isotope values of herbivores from Ginnerup, Kainsbakke, and Kiral Bro ($N = 160$). Data: [Klassen et al., 2023](#); [Makarewicz, 2023](#). Large icons = mean values + sd. The category 'Bos sp.' includes small-bodied cattle (including presumed domesticates (*Bos domesticus*) and cattle of indefinite size. The category 'Bos sp. (large)' includes presumed aurochs (*Bos primigenius*). The category 'Sus sp.' includes both wild (*Sus scrofa scrofa*) and domestic pigs (*Sus scrofa domesticus*). The category 'Cervids' includes both red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*).

hircus). Both large-bodied cattle, *E. ferus* and cervids also have lower minimum $\delta^{13}\text{C}$ values than any of the presumed domesticates. Combined, wild herbivore mean $\delta^{13}\text{C}$ value is almost 1‰ lower than in the presumed domesticates. Conversely, the range of $\delta^{15}\text{N}$ values are larger in the domestic stock than amongst presumed wild animals, and the maximum values are higher. The observed differences between presumed wild and domestic herbivores are confirmed by Welch's *t*-tests (Table S2d). Although speculative, we suggest that the differences are the result of different habitat uses and diets.

As suggested by other scholars, the lower $\delta^{13}\text{C}$ values ($\approx 1\text{‰}$) in Subboreal wild mammals may be a result of the canopy effect ([Noe-Nygaard et al., 2005](#); [Makarewicz, 2023](#)). The observed differences between domestic species and wild species (especially *E. ferus*) in our study are, however, quite low, just as the overall depletion does not match the observed depletion in studies of human and animals living in closed tropical forest environments ([van der Merwe and Medina, 1991](#)). As a result, we suggest that the observed depletion in wild mammals $\delta^{13}\text{C}$ in our study is best explained as a result of the hunting of animals living in a landscape with varied vegetation structure (e.g., a mixture of woodland, scrub, and grass- and heathland).

5.3. Feasting and seasonal gatherings at Ginnerup?

As suggested, the low variability in microwear-scratches in the Ginnerup horse assemblage correlates with same-season or shorter harvest events (Fig. 5). Bearing in mind that the site was in use for at least a few hundred years around 5 ka cal B.P. as shown by radiocarbon dating ([Klassen et al., 2023](#)), a straightforward interpretation of this would be that the horses were slaughtered as part of a series of successive same-season (or shorter) events at or near the site. The excavated features at Ginnerup have been interpreted as ritual (A1) or partly ritual (A4) in nature ([Klassen et al., 2023](#)). Following this line of interpretation, and although caution is needed due to the limited number of analysed specimens, the horses from Ginnerup may have been killed and slaughtered as part of a successive series of special events including seasonal hunting and feasting at the site. Several other scenarios are however possible including seasonal changes in both human and animal

behavior, e.g., animal husbandry practices, the number of people to be fed, changing seasonal focus on different food sources (hunting, fishing, gathering, agriculture etc.), and recurring seasonal movements of the horse population due to shortage of food making them more readily available at specific times of the year and therefore more easily hunted.

5.4. Hüde I

The reconstruction of the landscape and the human utility of the horse population at Hüde I is more ambiguous than at Ginnerup, as we have no direct measures of comparison and because the chronology and stratigraphy is less settled. Hüde I has been interpreted as a seasonal hunting station and the avian remains hint at a summer/autumn camp ([Kossian, 2007](#)). This is not contradicted by the mesowear analysis, which overall suggests that the Hüde I horses included a substantial amount of attritive diet i.e., browse compared to the Ginnerup horses (Fig. 3; Table 1). This is also indicated by the overall microwear signal (Fig. 4; Table 2). The variation in microwear is larger than at Ginnerup. This is possibly a result of the nature of the assemblage, which represents a much longer time period than the Ginnerup assemblage increasing the probability of both cultural and environmental changes and variability. Consequently, the results may be a result of a more varied seasonal utility of the horse population, the killing of horses from spatially separate populations, or changing climatic conditions through time resulting in vegetational changes ([Bauerochse and Leuschner, 2022](#)). Furthermore, we cannot rule out divergent utilization patterns over time amongst the different human groups that occupied the area during the 5th- 4th millennium BCE.

The low $\delta^{13}\text{C}$ values of both *E. ferus* and *B. primigenius* correlates well with the above interpretation of the tooth wear analyses. As less abrasion-dominated grazers and mixed feeders, respectively, both species may have spent a considerable amount of time feeding in forested areas in addition to grazing in more open vegetation, resulting in more depleted carbon values compared to what is seen at the Subboreal, Neolithic sites at Djursland, Denmark. The presence of woodland around Lake Dümmer is further indicated by vast numbers of bones from Eurasian beaver, *Castor fiber* in the faunal record from Hüde I ([Hübner](#)

et al., 1988). Interestingly, the low $\delta^{13}\text{C}$ values at Hde I match the measured $\delta^{13}\text{C}$ value (-23.1‰) of a beaver from Kainsbakke (Makarewicz, 2023), supporting the presence of a varied vegetational structure in both Djursland and the Dmmer area (cf. Aaby, 1985; Schtrumppf, 1988; Bauerochse and Leuschner, 2022) and acting as a reference for animals living in freshwater systems with a preference for forested areas.

5.5. Locally exploited fauna?

The isotope analyses show that there are substantial differences in $\delta^{34}\text{S}$ values between the two sites (Fig. 6). Methodological studies suggest that sulphur isotopes can be used as indicator of both diet and mobility, and thus help identifying the food source origin (Nehlich, 2015). In coastal zones, $\delta^{34}\text{S}$ values of animal tissues are generally higher than further inland due to the addition of marine sulphur via rainfall or seaspray to the sulphur from soil/bedrock. As the study from Ginnerup shows (Klassen et al., 2023), most $\delta^{34}\text{S}$ values are quite high compared to the Hde I values, in line with the coastal and inland location of Ginnerup and Hde I respectively (Fig. 6). One sample, however, is an exception to this pattern. A roe deer from Ginnerup has a significantly lower $\delta^{34}\text{S}$ value (8.1‰) than the remaining fauna and probably originated from a population further inland and was likely brought to the site from outside (Klassen et al., 2023). Although we cannot rule out the possibility that the remaining Ginnerup fauna originate in other areas with similar $\delta^{34}\text{S}$ values e.g., along the east coast of Jutland, the rather homogeneous values are consistent with a local origin and the presence of a locally available population of *E. ferus* in Djursland ~ 5 ka cal B.P. The picture given by the Hde I assemblage is more ambiguous. Although not identified as an outlier, one $\delta^{34}\text{S}$ value stands out as rather elevated (12.9‰) compared to the mean (6.4‰) and may originate from an animal hunted in or migrating from another area than the remaining sampled fauna (Fig. 6; Table S2). The values are also less homogenous than the Ginnerup assemblages. This may be a direct consequence of a much wider chronological range ($>1500\text{y}$) but may also reflect a more varied seasonal exploitation of the fauna by the human inhabitants, the utility of spatially different populations, or the geographical position of the Hde I site in a cultural hotspot with evidence of several cultural influences, as suggested in section 2.2. and 5.4.

5.6. $\delta^{15}\text{N}$ values of *E. ferus*

The $\delta^{15}\text{N}$ values of *E. ferus* from both Ginnerup and Hde I are remarkably low compared to other species. At Ginnerup the difference in mean nitrogen values between *E. ferus* and the ruminant species combined is 2.4‰ , whereas the difference at Hde I is 1.5‰ between *E. ferus* and *B. primigenius* (Klassen et al., 2023; Makarewicz, 2023; Table S2). For comparison, somewhat less substantial but still significant differences (1.2‰) are observed between *E. ferus* and ruminant species at Kainsbakke (Makarewicz, 2023).

Nitrogen isotope values in animal tissues appear to be a good indicator of climate and trophic level, including weaning, but may also be affected by a complex range of anthropogenic and natural factors such as soil manipulation and development, plant and animal physiology, feeding habits, and pasture practices (e.g., Schoeninger and DeNiro, 1984; Iacumin et al., 2000; Balasse et al., 2001; Gislum and Griffith, 2005; Makarewicz, 2014; Richards et al., 2017; van der Sluys and Reimer, 2021). As a result, interpretations are often equivocal. Trying to identify possible reasons behind the low $\delta^{15}\text{N}$ values in samples from *E. ferus* from Ginnerup and Hde I we can rule out some of the above factors including climate and trophic level including weaning. First, our samples are all dated to the early part of the Subboreal period and are confined to northwestern continental Europe with broadly similar macroclimates. Second, careful selection of samples in this and earlier studies (Makarewicz, 2023) partly rules out possible effects of weaning. We might also partly exclude animal physiology as a possible factor. Isotope analysis of domestic horses (*Equus caballus*), cattle (*Bos taurus*)

and caprines (*Ovis aries* and *Capra hircus*) from the Danish Iron Age (IA) ($\sim 2.45\text{--}1.75$ ka cal B.P.) do not show similar difference in mean $\delta^{15}\text{N}$ values as in the present study (Horses ($n = 29$): mean = 6.4 , sd = 1.1 , range = $4.5\text{--}9.5$. Cattle ($n = 48$): mean = 5.9 , sd = 1.1 , range = $3.1\text{--}9.5$) (Kveiborg and Olsen, 2023). Notably, the mean value of IA horses is 3‰ higher than Subboreal *E. ferus*. If we accept that wild and domestic horses are similar in respect to their physiology, including digestion, although the domestic horse derives from a different phylogeographic group of *E. ferus* than the western European branch (Librado et al., 2021), then this points towards dietary differences or changes in soil composition as the main factors behind the observed difference between Subboreal Neolithic *E. ferus* and IA *E. ferus caballus*. A possible reason for the observed shift in trophic level is the addition of fertilizer (including manure) to improve the soil indicating increased agricultural activity and that both horses and cattle were fed a nitrogen enriched diet during IA. This, however, does not explain the observed differences between Subboreal *E. ferus* and ruminants. Based on the above, we suggest that the observed differences are best explained as a result of dietary niche partitioning, i.e., the utility of different plant species or different plant parts by horses and ruminants. Similar conclusions have been reached in studies of Pleistocene fauna (Britton et al., 2012).

5.7. Landscape openness

Large-scale interregional palynological studies indicate that the direct anthropogenic impact on the vegetation in continental southern Scandinavia was minimal during the late Atlantic/early Subboreal period, i.e., in terms of out-right deforestation (Nielsen et al., 2012). While unambiguous large-scale anthropogenic transformation of vegetation remains to be shown, intraregional studies indicate small-scale clearings and subtle manipulation of the vegetation during the pre-agricultural Holocene in different parts of Europe, suggesting that anthropogenic impact on the landscape may have varied considerably as well as it may have included substantial impacts other than deforestation (Bishop et al., 2015; Pokorny et al., 2022; Sevink et al., 2023). The pollen record recovered from the bog Fugls Mose, c. 12 km northwest of Ginnerup has been interpreted to indicate rather dense forest and small-scale agricultural and grazing activities during the Middle Neolithic (Aaby, 1985). Large-scale studies based on REVEALS landscape reconstruction models, however, indicate that traditional pollen analysis underestimates the amount of open vegetation (Nielsen et al., 2012; Trondman et al., 2015). This approach suggests a general coverage of open vegetation by $20\text{--}30\%$ in the eastern Jutland Peninsula ~ 5 ka cal B.P. (Nielsen et al., 2012).

Accepting the evidence for substantial amount of natural open landscape in the coastal Atlantic zone including the Jutland Peninsula may help understand the survival and population expansion or spread of *E. ferus* into this area before the advent of agriculture. In addition, it may help explain the overall grazing signal in horses from Ginnerup. Although, the Nielsen et al. (2012) study does not cover the area around lake Dmmer, we suggest a degree of forest cover similar to or a bit denser than at Ginnerup based on their results (Nielsen et al., 2012).

While it is impossible to pinpoint the exact origin of animals deposited at archaeological sites, the depleted values in $\delta^{13}\text{C}$ in the Hde fauna compared to most of the Ginnerup fauna points towards different diets, which possibly reflect different landscape types. As stated, the Dmmer area was wetter and probably more densely wooded than along the coastline of Kolindsund, Djursland. This aligns with the mesowear signal which suggest a more attritive diet amongst the Hde I horses than at Ginnerup. As discussed in section 5.4., local and regional palynological and archaeobotanical analyses suggest that Hde I was situated in a low and wet landscape with high abundance of alder (*Alnus* cf. *glutinosa*), but also pine (*Pinus* cf. *sylvestris*) and birch (*Betula* sp.) and mixed oak forest trees in varying numbers through time (Schtrumppf, 1988; Bauerochse and Leuschner, 2022). Based on the different proxies used in the study, this may be interpreted as an expression of the fact

that the landscape and diet of the two horse populations in the study were substantially different. The study thus supports earlier studies indicating substantial dietary flexibility (including seasonal) in *E. ferus* during the Pleistocene and Holocene (van Asperen, 2010; Rivals, 2012; Rivals et al., 2015b; Rivals and Lister, 2016; Saarinen et al., 2016, 2021; Boulbes and van Asperen, 2019; Uzunidis, 2021; Cirilli et al., 2022), as also seen in the present (e.g., Putman et al., 1987; Thomassen et al., 2023).

6. Conclusions

The study presents the first detailed dietary study of middle Holocene *E. ferus* (~ 5 ka cal B.P.) based on tooth meso- and microwear and stable isotope analyses from two sites (Ginnerup (DK) and Húde I (DE)) within the North European Plains. The mesowear analysis groups both populations of horses amongst typical grazers. The recorded mesowear in the two assemblages are, however, statistically different suggesting significant dietary differences in the overall diet of the horses in the two assemblages. Regarding microwear, the Ginnerup horses display significant higher numbers of microwear pits and scratches compared to Húde I, suggesting a larger amount of abrasive food in the diet of the former. The short-term microwear signals differ from the overall mesowear signals, grouping both populations amongst typical browsers, suggesting a diet dominated by soft tissue plants immediately prior to their death. Despite small sample sizes, our results support previous studies suggesting that *E. ferus* were flexible feeders capable of shifting their diet according to circumstances including seasonal changes. Although we cannot pinpoint the specific season, the limited variability in the number of microwear scratches suggests the Ginnerup horses were killed during a specific season. We hypothesise that the horses were killed as part of recurring hunting parties possibly as parts of special events (e.g., feasting), although this is a proposal that needs to be scrutinized further. Nonetheless, our results affirm the potential of using dental wear as a proxy for studies of seasonality. The less abrasive diet amongst the Húde I horses compared to Ginnerup hints at a more forested landscape, albeit still with substantial open, grassy vegetation. This is partly supported by more depleted $\delta^{13}\text{C}$ values than at Ginnerup. Also, our study highlights the potential of using stable isotope analysis to suggest different uses of the landscape by wild and domestic animals, with wild animals showing somewhat depleted $\delta^{13}\text{C}$ compared to the livestock. The $\delta^{15}\text{N}$ values of *E. ferus* from both Ginnerup and Húde I are remarkably low compared to other herbivore species from the sites. As a tentative hypothesis, in need of further testing, we suggest that this is best explained as a result of dietary niche partitioning. The result of our $\delta^{34}\text{S}$ analysis, which is still rarely used in archaeology, shows significant differences in line with the geographical (coastal vs. inland) location of the two sites. This finding supports that the horses from both Húde I and Ginnerup are derived from local populations, showing potential of including sulphur in zooarchaeological studies of mobility and provenance. Further work on the Ginnerup and Húde I assemblages is needed to develop a more detailed picture of the immediate landscape and of the seasonal dietary and mobility patterns amongst horses.

CRedit authorship contribution statement

Jacob Kveiborg: Writing – review & editing, Writing – original draft, Visualization, Project administration, Investigation, Formal analysis, Conceptualization. **Antigone Uzunidis:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis. **Lutz Klassen:** Writing – review & editing, Resources. **Florian Klimscha:** Writing – review & editing, Resources. **Niels Nørkjær Johannsen:** Writing – review & editing, Resources. **Uffe Lind Rasmussen:** Writing – review & editing, Resources. **Michael P. Richards:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Jens-Christian Svenning:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Jens-Christian Svenning reports financial support was provided by VILLUM FONDEN. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available as supplementary tables

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Appendix A. Supplementary data

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