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The Le Rozel footprints: snapshots of Neandertal groups in the Late Pleistocene. A combined morphometric and experimental approach

Les empreintes de pieds du Rozel : instantanés de groupes néandertaliens au Pléistocène supérieur. Approche combinée morphométrique et expérimentale

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Abstract – Hominin footprints represent brief moments of life and provide access to the locomotor and biological features of the individuals who left them. Because of the particular time scale that they represent and the information they provide, they make it possible to approach the size and composition of hominin groups in a different way from the methods used with the more common archaeological artefacts and osteological assemblages. Since 2012, several hundred Neandertal footprints have been discovered at Le Rozel (Normandy, France), within 5 stratigraphic sub-units dated to about 80,000 years ago. Analyses of the ichnological assemblage discovered at Le Rozel between 2012 and 2017 have identified 257 footprints, 132 of which have been digitized in 3D. This represents the largest ichnological assemblage attributed to Neandertals to date. Morphometric analyses of the 3D models of the footprints, combined with an experimental study under substrate conditions similar to those at Le Rozel, have quantified the size and composition of the groups that left them. The footprints from the most ichnologically dense stratigraphic sub-unit were left by a small group and represent 90% of children and adolescents. These results not only enhance our understanding of the Palaeolithic occupations at Le Rozel but also provide new methods and data for assessing the size and composition of Neandertal groups.

Keywords – footprints, Le Rozel, Neandertals, morphometrics, group composition

Résumé – Les empreintes de pieds des hominines représentent de brefs moments de vie et donnent accès aux caractéristiques locomotrices et biologiques des individus qui les ont laissés. Par l'échelle de temps particulière qu'elles représentent et les informations qu'elles fournissent, elles permettent d'approcher la taille et la composition des groupes d'hominines d'une manière différente des méthodes utilisées

sur les artefacts archéologiques ou les assemblages ostéologiques plus communs. Depuis 2012, plusieurs centaines d'empreintes ont été découvertes au Rozel (Normandie, France) au sein de 5 sous-unités stratigraphiques datées d'environ 80 000 ans. L'analyse de l'assemblage ichnologique découvert entre 2012 et 2017 au Rozel a permis l'identification de 257 empreintes de pieds, dont 132 ont été modélisées en 3D, ce qui représente à ce jour le plus gros assemblage ichnologique attribué aux Néandertaliens. L'analyse morphométrique des modèles 3D des empreintes de pieds, conjuguée à une étude expérimentale menée dans les conditions de substrat similaires au Rozel, a permis de quantifier la taille et la composition des groupes qui les ont laissés. Les empreintes issues de la sous-unité stratigraphique la plus dense ichnologiquement ont été laissées par un groupe de petite taille et représentent à 90 % d'entre elles des enfants et des adolescents. Ces résultats améliorent non seulement notre compréhension des occupations paléolithiques au Rozel mais fournissent également de nouvelles méthodes et données pour évaluer la taille et la composition des groupes néandertaliens.

Mots clés – empreintes de pieds, Le Rozel, Néandertaliens, morphométrie, composition des groupes

Introduction

In mammals, and particularly in primates, the size and composition of social groups play a key role in their adaptive success (e.g. Silk, 2007; Majolo et al., 2008) thanks to their impact on factors such as access to resources, competition with predators or rival groups, and reproductive success. Group size and composition therefore probably had an important role in hominin evolution. However, such data are particularly scarce for fossil species, especially for Neandertals, who are probably the best-known hominin fossil taxon. Moreover, their estimation based on skeletal remains or

surface accumulations of archaeological artefacts (Hayden, 2012) remains challenging since it is difficult to determine the exact time-span covered by each accumulation and whether they reflect the whole of a single group, part of it only or several groups (Walker et al., 1988; Farizy, 1994).

Hominin footprints are a particular type of vestige that provides information on hominin groups. Footprints are the result of substrate deformation due to foot contact and require a soft substrate to be formed, which makes them particularly fragile, especially when they were left in open air sites where they are subject to numerous taphonomic agents (wind erosion, precipitation, trampling) that can quickly damage and even destroy them (Bennett and Morse, 2014). They can only be preserved if rapidly covered by sediment. A footprint assemblage from a single surface therefore represents a brief moment of life, comparable to a snapshot (e.g. Hatala et al., 2020), which is a time scale that cannot be approached from skeletal remains or archaeological artefacts. At this particular time scale, footprints not only directly reflect locomotor behaviour patterns and their anatomical and functional correlates (foot morphology including soft tissue, gait features) but also the size and composition (age, stature) of the groups who made the tracks (e.g. Bennett and Morse, 2014). The study of footprints thus represents a new approach, distinct from those used with osteological assemblages or archaeological artefacts, to characterize, at least partially, the composition of hominin social groups. However, the study of footprints is a challenging task. Indeed, even if the morphology of footprints reflects the biological and biomechanical characteristics of the individuals, it is also affected by the nature of the substrate (lithology, granulometry, humidity) in which they were made, as well as by taphonomic agents (Bennett and Morse, 2014). Furthermore, despite several significant discoveries in the last decade (e.g. Altamura et al., 2018; Stewart et al., 2020; Mayoral et al., 2021), footprints are a rare vestige compared to the more common archaeological artefacts or skeletal remains. This is particularly the case for Neandertals as until recently, only 9 footprints discovered in 4 sites have been attributed to this taxon (Duveau et al., 2021).

In this context, 595 footprints potentially attributable to Neandertals have been discovered since 2012 at Le Rozel (Normandy, France), in association with rich archaeological material within layers dated to about 80,000 years ago (Cliquet et al., 2018; Mercier et al., 2019). The particularly large number of footprints and their geological and archaeological context offer an opportunity to learn more about the characteristics of Neandertal social groups. This note focuses on the study of the footprints discovered at Le Rozel between 2012 and 2017, in order to better characterize the size and composition of the groups who left them from morphometric analyses combined with an experimental study. Based on the information obtained, we discuss whether the track-making groups of Le Rozel are representative of all the social groups who occupied the site. To conclude, we discuss the contribution of these footprints to knowledge on Neandertals and the Palaeolithic occupations at Le Rozel.

Material

The archaeological site of Le Rozel and its ichnological assemblage

The Le Rozel site (figure 1) is located in a coastal environment in a palaeodune formation that began to form 115,000 years ago (Van Vliet-Lanoë et al., 2006). Discovered in the 1960s by Y. Roupin, it has been the object of annual excavations directed by D. Cliquet since 2012, following observations of gradual damage to the site by wind erosion at its summit and tidal erosion at its base. These excavations have yielded rich archaeological material, including faunal remains, lithic industries (Levallois flakes, lamellar productions) and hearths (Cliquet et al., 2018). This abundant material is distributed within 6 stratigraphic sub-units (D3b-1 to D3b-6). OSL quartz grain dating of samples from the Le Rozel sedimentary sequence collected above, within and below the 6 sub-units, have dated the formation of these sub-units to MIS 5, between 86,000 and 75,000 years ago (Mercier et al., 2019). Stratigraphic, geochronological and archaeological analyses have shown that each sub-unit probably represents a single phase of occupation (Cliquet et al., 2018). The periods between occupation phases are currently unknown. However, the duration of these phases

Figure 1. The site of Le Rozel a- Location; b- View of the site / Le site du Rozel. a- Localisation ; b- Vue du site

can be assessed from the age at slaughter of prey (especially deer and horses), and shows that occupations were seasonal, each taking place between autumn and spring (Sévêque, 2017; Cliquet et al., 2018).

Between 2012 and 2017, 595 tracks identified as hominin footprints were discovered in 5 of the 6 stratigraphic sub-units that yielded the archaeological material. They are unevenly distributed within these sub-units: about 80% of the tracks are from the D3b-4 sub-unit and about 10% from the D3b-5 sub-unit, the remaining 10% being evenly distributed in the 3 other sub-units. The 595 tracks are in different fine-grained sandy surfaces composed of dune sand for the footprints left in sub-units D3b-1 to D3b-3 or sandy mud for the majority of the footprints in sub-units D3b-4 to D3b-5.

The different occupation phases and the footprints that were made during them may be attributed to Neandertals based on both the dating of these occupations, during a period when Neandertals were the only known taxon in Europe, and the discovery of Mousterian industries that are characteristic of this taxon.

Footprint selection

A selection was made among the 595 potential footprints in order to retain only footprints with enough anatomical detail to be identified with certainty as human footprints and to ensure the reproducibility of the morphometric analyses. The selection also avoids footprints with

few anatomical details and whose morphology could have been affected by taphonomic agents, which would have biased the palaeobiological interpretations made from the morphometric analyses. The footprint selection was based on the anatomical characteristics of the human foot: the footprints had to reflect a rounded heel, a foot arch and relatively short toes including an adducted hallux (Morse et al., 2010; Bennett and Morse, 2014).

Among the 595 footprints, 257 were selected (figure 2) including 132 footprints digitized in 3D by surface scanner (Noomeo Optinum) or by photogrammetry using Metashape software (v.1.4.0). The selected footprints follow a similarly heterogeneous distribution pattern within the stratigraphic sub-units as the whole set of 595 footprints: the vast majority (79%) are from stratigraphic sub-unit D3b-4, the rest being distributed among sub-units D3b-5 (11%), D3b-3 (5%), D3b-1 (4%) and D3b-2 (1%). Within these five sub-units, the selected footprints, with one exception, were made on sub-horizontal ground. Laterality was determined for 86% of the footprints (44% of right footprints, 42% of left footprints). The footprints are spatially orientated in different directions, and most frequently towards the north. The feet were printed variably, which is common for prints made in a soft substrate, as is the case in a dune context (e.g. Morse et al., 2013). 10 footprints show only the heel and 3 only the forefoot. A total of 88 footprints are longitudinally complete: each of these footprints show the heel impression proximally and clear impressions of the toes distally.

Figure 2. Selected footprints from Le Rozel (black scale bar: 2 cm) (photos: D. Cliquet) / *Empreintes sélectionnées du Rozel (mire noire : 2 cm) (clichés : D. Cliquet)*

Among these longitudinally complete footprints, not all the toes were systematically printed. The hallux impression, and to a lesser extent that of the second toe, are the deepest and most common toe impressions, which is consistent with the distribution of plantar pressures during human walking (e.g. Elftman and Manter, 1935). The remaining 156 footprints can be described as sub-complete: they show a relatively complete outline of the foot but do not show enough detail, such as toe impressions that can be clearly differentiated from the rest of the footprint. One of the main characteristics of the footprint assemblage at Le Rozel is the difficulty of identifying trackways (a succession of footprints made by the same individual): only 5 trackways including 2 to 3 footprints were identified. The great majority of the footprints are therefore considered as isolated since it is impossible to associate them with other footprints made by the same individual.

The 338 unselected footprints were rejected because of morphological inconsistencies (figure 3): these prints did not reflect enough anatomical detail or had an aberrant shape. However, the non-selection of these tracks does not mean that they are not Neandertal footprints: taphonomic agents may have damaged them, making their identification impossible. However, there is currently no reproducible and indisputable method allowing them to be unambiguously certified as footprints, especially since some climatic agents,

such as wind erosion or runoff, can produce tracks whose morphology is close to these unselected tracks (e.g. Panarello et al., 2018). Moreover, these tracks do not show the homologous anatomical points needed for morphometric analyses and their reproducibility.

Experimental footprints

The footprints from Le Rozel were compared to footprints made during an experimental study conducted in 2017 (prefectural order #28-2017-339, operation number: 163972) with the aim of quantifying the impact of the substrate at Le Rozel on footprint morphometry. Experimental areas of dune sand and sandy mud were built from sediments extracted from the fossil footprint layers in order to have depositional conditions as close as possible to those of the Le Rozel site. 22 volunteers (1 child aged 1 year, 4 adolescents from 10 to 13 years old and 17 adults from 19 to 36 years old) were asked to participate in this experimental study. After obtaining written consent from the participants, or from their legal guardians for minors, their body characteristics (stature, mass, foot dimensions) were measured and their age was recorded. They were then asked to make footprints by moving barefoot at different speeds (walking, slow running, fast running). A total of 221 experimental footprints were recorded.

Figure 3. Tracks not selected among the footprints because of morphological inconsistencies (black scale bar: 2 cm) (photos: D. Cliquet) / *Traces n'ayant pas été sélectionnées parmi les empreintes de pieds à cause d'incohérences morphologiques (mire noire : 2 cm) (clichés : D. Cliquet)*

Methods

Methodological approach

The size and composition (stature and age) of the track-making groups of Le Rozel were determined by applying experimental data to the morphometric characteristics measured from the 3D models of the selected footprints (figure 4). For this purpose, the selected footprints were grouped according to the stratigraphic sub-unit where they were found, each sub-unit representing a phase of occupation by a single group.

Morphometric characterization

Although different morphometric variables (dimensions, outline, depths) were used during the morphometric characterization of the footprints (Duveau et al., 2019), this note will focus on 3 dimensions: the total length L_{tot} (measured along the longitudinal axis of the footprint between the base of the heel and the end of the second toe impression), the tarsometatarsal length L_{tmt} (measured along the longitudinal axis between the base of the heel and the rim separating the second toe impression from the rest of the footprint) and the width w (corresponding to the maximum width of the forefoot along the medio-lateral axis that is perpendicular to the longitudinal axis).

Assessing the size of the track-making groups

As the footprints from Le Rozel are mostly considered isolated, it is more difficult to estimate a number of individuals than if they could be associated as trackways. However, a Minimum Number of Individuals (MNI) can be determined for each occupation phase thanks to the experimentally defined intra-individual morphometric dispersion. This approach is based on the fact that the same individual

makes footprints of different dimensions but with limited variation. When the limit of this intra-individual variation is known and applied to the dimensions of the isolated footprints from Le Rozel, it is possible to determine an MNI. First, it was determined from the experimental footprints that the total length was the morphometric variable with the lowest intra-individual variation, and therefore the one giving the best MNI estimate. Then, MNI were determined based on the maximum intra-individual deviation from the mean of the total length (12.8%). Thus, if the range [$L_{tot} \times (1-0.128)$; $L_{tot} \times (1+0.128)$] of a footprint does not overlap the analogous range of another, then they were made by different individuals. Therefore, this method estimates an MNI for each occupation phase by grouping footprints by length classes, each metric class representing one of the individuals of the MNI.

Assessing the composition of the track-making groups

Stature estimates, based on the strong correlation between stature and total footprint length quantified experimentally, were performed in two steps (Duveau et al., 2019). First, an average foot length to stature ratio (14.8%) was determined from the experimental sample and bibliographic data (38 population samples; 37,328 individuals) including individuals of different geographical origins and behaviour (e.g. unshod and shod populations). This ratio was then applied to the experimental ratio between the footprint total length and the foot length (103.7%) in order to obtain a linear relationship between the total length of the footprints (L_{tot}) and the stature (S): $S = 6.54 L_{tot}$. A stature was also estimated for the footprints whose state of preservation did not allow measurement of the total length, by using the strong correlations of this length with the tarsometatarsal length ($L_{tmt} / L_{tot} = 0.82$; $r^2 = 0.89$) or, when it could not be measured, with the footprint width ($w / L_{tot} = 0.43$; $r^2 = 0.66$).

Figure 4. Methodological approach used to determine the size and composition of the track-making groups from the footprint morphometrics / *Approche méthodologique utilisée pour déterminer la taille et la composition des groupes ayant laissé les empreintes à partir de la morphométrie des empreintes*

The stature estimates were then used to determine an age class for each footprint. To do this, the estimated statures were positioned on a curve representing the variation between stature and age defined from published estimates of Neandertal osteological remains (figure 5; Duveau et al., 2019). This curve takes into account the variation of stature with age in children and assumes a constant stature in adults, equivalent to the average stature of all adults in the database (162.5 cm; Duveau et al. 2019). Given the small number of Neandertal adolescents and the difficulty of estimating a precise age for them, no individuals were used for this age class. The corresponding part of the curve was extrapolated to obtain a logarithmic variation. The results obtained with the model defined from Neandertal bone remains could, however, be questioned because of the small relative number of individuals and the lack of adolescents. For this reason, a control was carried out by estimating the age classes using a model defined from different modern populations (about 20,000 individuals; Duveau et al. 2019).

Figure 5. Curve representing the variation between stature and age of the Neandertals (Duveau et al., 2019) used to estimate an age class from each estimated stature for each footprint / *Courbe représentant la variation de la stature en fonction de l'âge chez les Néandertaliens (Duveau et al., 2019) utilisée pour estimer une classe d'âge pour chaque estimation de stature des empreintes*

Interpretations and hypotheses

To interpret the results obtained for the size and composition of the groups of track-makers, it is important to bear in mind that the number of footprints may vary according to the individual, particularly in relation to differences in stature. Biometrically, a person of small size makes more footprints than a taller individual to travel the same distance. However, although this logic is applicable to passageways where the footprints may reflect an uninterrupted progression, it is difficult to verify in occupation contexts such as that of Le Rozel because, in this type of context, phases of rest alternate with phases of activity (e.g. searching for resources, processing carcasses, lithic production) that may vary in intensity according to the age of the individuals,

thus affecting the number of footprints made. In the absence of ethnographic data, it is therefore impossible to determine, in the context of the Palaeolithic occupations at Le Rozel, whether there is a difference in the number of footprints made according to the stature of the individuals.

Therefore, two different hypotheses were used. The first hypothesis (hypothesis 1), used in the initial study on the footprints from Le Rozel (Duveau et al., 2019), considers that all individuals made the same average number of footprints, regardless of their age class and stature. The second hypothesis (hypothesis 2) considers that a smaller individual makes more footprints than a taller individual to travel the same distance. According to this hypothesis, the number of footprints made is inversely proportional to the stature of the individual. To apply this hypothesis, the footprint frequency was weighted according to the stature estimates. The weighted frequency was determined by dividing the estimated stature of each footprint by the largest estimated stature in the footprint sample. This second hypothesis can be understood thanks to a simple example: an individual three times shorter than another individual makes three times more footprints than the latter.

Results

Morphometric characterization

Among the 132 footprints digitized as 3D models that were morphometrically characterized, 105 come from the D3b-4 stratigraphic sub-unit, 18 from D3b-5, 5 from D3b-3, 2 from D3b-1 and 2 from D3b-2. Due to the different states of preservation of the footprints, not all morphometric variables could be measured on each one.

The ranges for the total length (11.4-28.4 cm, figure 6a), tarsometatarsal length (10.0-21.8 cm, figure 6b) and width (4.5-12.8 cm, figure 6c) of the footprints from the D3b-4 sub-unit overlap with those from the other sub-units (table 1). It is therefore not possible to metrically differentiate the footprints from the D3b-1, D3b-2, D3b-3 or D3b-5 sub-units from the D3b-4 footprints.

Assessing the size and composition of the track-making groups

Particular attention was given to the group that made the footprints in the D3b-4 sub-unit, since the 105 footprints measured from this sub-unit are much more numerous than in the other sub-units and therefore give more robust information on the size and composition of the track-making group.

By applying the knowledge of intra-individual dispersion gained experimentally to the total lengths of the 39 complete footprints from the D3b-4 sub-unit, it was possible to divide them into 4 morphometric classes, each representing at least one individual. The distribution of footprints in these 4 classes is heterogeneous. The majority of the footprints are included in the second and third metric classes, which can

Figure 6. Dimensions of the selected footprints from Le Rozel grouped according to the stratigraphic sub-units where they were found / *Dimensions des empreintes du pied sélectionnées du Rozel réparties en fonction des sous-unités stratigraphiques où elles ont été découvertes.*

Stratigraphic subunit	Dimensions of the footprints (cm)												Estimated statures (cm)			
	Total length				Tarsometatarsal length				Width							
	n	Min.	Mean	Max.	n	Min.	Mean	Max.	n	Min.	Mean	Max.	n	Min.	Mean	Max.
D3b-1	2	12.3	15.4	18.4	2	10.1	12.7	15.2	2	5.1	6.8	8.4	2	80.4	100.4	120.3
D3b-2	1		21.4		0				2	6.7	8.1	9.4	2	99.6	119.9	140.1
D3b-3	4	17.5	22.0	24.9	2	14.7	16.4	18.2	4	7.8	8.7	9.6	5	111.5	137.5	162.8
D3b-4	39	11.4	19.0	28.4	21	10.0	15.1	21.8	100	4.5	8.5	12.8	105	66.9	125.7	190.3
D3b-5	8	15.0	19.7	26.8	7	10.0	16.2	23.5	18	5.9	7.9	10.9	18	79.8	121.3	175.2
Total	54	11.4	19.2	28.4	32	10.0	15.3	23.5	126	4.5	8.4	12.8	132	66.9	125.1	190.3

Table 1. Dimensions and estimated statures for the footprints distributed in the 5 stratigraphic sub-units / *Dimensions et statures estimées des empreintes de pieds réparties en fonction des 5 sous-unités stratigraphiques*

be explained by a greater number of individuals with footprints whose dimensions correspond to these two classes. From this heterogeneous distribution, a more likely estimate of the number of individuals can be made. Thus, considering that the morphometric class with the fewest footprints corresponds to a single individual, the number of individuals would vary between 13 and 14 depending on the hypothesis used (hypothesis 1 or hypothesis 2). A similar estimate can be made from the 100 footprint widths by dividing them into 4 groups on the basis of the quartiles of their range (4.5–12.8 cm). In this case, if the morphometric class with the fewest footprints corresponds to a single individual, the number of individuals would be 10 regardless of the hypothesis considered.

The 105 measured footprints from the D3b-4 sub-unit correspond to statures between 66.9 and 190.3 cm (table 1; figure 7a). These different statures correspond to different age classes: child, adolescent, and adult. The smallest footprint corresponds to a 1 year-old child. The 8 largest footprints can be attributed to males based on their estimated statures (165.7–190.3 cm) and on the sexual dimorphism of Neandertals (figure 7a; Carretero et al., 2012). The 4 largest footprints represent taller statures (179.9–190.3 cm) than the maximum stature known for Neandertals from estimates based on skeletal material (Duveau et al., 2019; Amud 1:

177 cm). The footprints are overwhelmingly associated with children (51.4%) or adolescents (40.0%) and much less with adults (8.6%). Therefore, if all individuals had left the same average number of footprints regardless of stature (Hypothesis 1), the group that made the footprints in the D3b-4 sub-unit would have been composed of a large majority of children and adolescents (figure 7b). The age distribution would be similar if the number of footprints made is inversely proportional to the stature of the individual (hypothesis 2). Considering this second hypothesis, the proportion of adolescents (45.2%) increases slightly relatively to children (42.9%) compared to the first. In both cases, the proportion of adults is small (figure 7b).

Concerning the other sub-units (table 2), the 2 measured footprints from the D3b-1 sub-unit correspond to 2 children whose estimated ages are respectively 2 and 6 years. The 2 footprints from the D3b-2 sub-unit correspond to 2 individuals: a child (estimated age of 2 years) and an adolescent. The 5 footprints from the D3b-3 sub-unit correspond to at least 2 individuals: a child with an estimated age of 7 years and an adolescent or an adult. Finally, the 18 measured footprints from the D3b-5 sub-unit were left by at least 3 individuals: a child (probably between 4 and 7 years old), an adolescent and an adult, probably a male, based on his estimated stature (175 cm).

Figure 7. Age classes attributed to the 105 measured footprints from the D3b-4 stratigraphic sub-unit. a-Positions of the footprints placed on an age-to-stature curve; b- Relative frequencies of the footprints per age class according to the two hypotheses / Attribution des classes d'âges pour les 105 empreintes de pieds mesurées de la sous-unité stratigraphique D3b-4. a-Position des empreintes sur la courbe représentant la variation de la stature en fonction de l'âge ; b-Fréquence des empreintes par classe d'âge suivant les deux hypothèses

Stratigraphic subunit	Statistical parameter	Number of footprints by age class		
		Child (0-10 years)	Adolescent (10-18 years)	Adult (> 18 years)
D3b-1	Frequency	2	0	0
	Relative Frequency	100.0%	0.0%	0.0%
D3b-2	Frequency	1	1	0
	Relative Frequency	50.0%	50.0%	0.0%
D3b-3	Frequency	2	2	1
	Relative Frequency	40.0%	40.0%	20.0%
D3b-4	Frequency	54	42	9
	Relative Frequency	51.4%	40.0%	8.6%
D3b-5	Frequency	12	5	1
	Relative Frequency	66.7%	27.8%	5.6%
Total	Frequency	71	50	11
	Relative Frequency	53.8%	37.9%	8.3%

Table 2. Frequencies and relative frequencies of the footprints by estimated age classes for each of the 5 stratigraphic sub-units / *Effectifs et fréquences des empreintes de pieds par classes d'âge estimées pour chacune des 5 sous-unités stratigraphiques*

Discussion

The ichnological assemblage from Le Rozel

The analyses performed in this study are based on the selection of 257 footprints discovered at Le Rozel between 2012 and 2017, which represents the largest ichnological assemblage attributed to a hominin taxon other than *Homo sapiens*. More particularly, the footprints from Le Rozel considerably enrich the Neandertal ichnological record, which was relatively poor. With the exception of the 87 footprints recently discovered at the Spanish site of Matalascañas (Mayoral et al., 2021), only 9 footprints had previously been attributed to this taxon. These footprints were distributed in 4 different sites: 1 footprint at the French site of Biache-Saint-Vaast (Tuffreau, 1988), 4 in the Greek cave of Theopetra (Manolis et al., 2000; Kyparissi-Apostolika and Manolis, 2021), 3 in the Romanian cave of Vârtope (Onac et al., 2005; 2021) and 1 near Gibraltar (Muñiz et al., 2019).

Assessment of the size and composition of the track-making groups

In addition to the importance for the Neandertal ichnological record, the analyses conducted on the 132 selected footprints digitized in 3D provided essential information on the size and the composition of the track-making groups, particularly for the group that occupied the D3b-4 sub-unit.

Firstly, the knowledge of the intra-individual morphometric dispersion of footprints gained from our experimental approach is a unique tool for determining the size of a track-making group from isolated footprints when no trackways are identified. The footprints from the D3b-4 sub-unit reflect a minimum of 4 individuals, with a more realistic prediction of 10-14 individuals. The group that left these footprints was therefore small. This estimate is consistent

with those based on the occupational surface areas, of 10 to 30 individuals per Neandertal site (Hayden, 2012), as well as with the size of modern hunter-gatherer groups composed of a few dozen individuals (Kelly, 2013).

Experimental relationships also allow estimations of stature from footprint morphometrics. The use of modern anthropometric data to estimate the stature of a fossil taxon can be questioned since body proportions may have varied during hominin evolution. However, these modern data can be applied to the footprints from Le Rozel since the foot length to stature ratio of Neandertals differs little, if at all, from the *Homo sapiens* ratio (Duveau et al., 2019). Some of the footprints from Le Rozel reflect larger statures (179.9-190.3 cm) than previously estimated from Neandertal skeletal material. However, it must be kept in mind that an individual makes footprints of different dimensions. Therefore, a stature estimated from an isolated footprint may be greater than the actual stature of the individual who made it. Since the experimental data show that the maximum intra-individual deviation from the mean of the total length is 12.8%, it follows that the four largest footprints, reflecting statures (179.9-190.3 cm) greater than those found in the bibliography, could all have been made by a single individual measuring at least 169 cm.

The D3b-4 footprints reflect a track-making group composed of individuals belonging to the different age classes, with a majority of children and adolescents and a minority of adults. This composition helps to characterize, at least partially, the Neandertal social group who occupied the D3b-4 sub-unit at Le Rozel. The composition of Neandertal social groups have otherwise only been approached from skeletal assemblages reflecting a catastrophic mortality profile, where the osteological remains are assumed to be contemporaneous. Such profiles are rare among Neandertals and are not always consensual (e.g. Wolpoff and Caspari, 2006). Only the Spanish site of El Sidrón has provided

reliable information on the composition of a Neandertal social group supported by genetic evidence (Lalueza-Fox et al., 2011). While children and adolescents form the majority of the D3b-4 track-making group in Le Rozel, 7 of the 13 individuals identified at El Sidrón are adults, only 3 are adolescents and 3 are children (e.g. Rosas et al., 2013). This larger proportion of adults can also be observed in current hunter-gatherer populations (e.g. Kelly, 2013).

Is the D3b-4 track-making group representative of the social group?

Such differences in age-class profiles raise the question of whether the D3b-4 sub-unit footprints represent the entire social group that occupied the site of Le Rozel or a portion of it.

The representativeness of the D3b-4 track-making group as a proxy for the wider social group who occupied this sub-unit can first be questioned because of taphonomic agents such as wind action, which is particularly erosive at Le Rozel, trampling or rainfall. These agents may have destroyed or damaged some footprints shortly after their formation, leading to biases in the representation of groups that occupied the site. Observations during the experimental study conducted in 2017 showed that the smallest footprints (corresponding to the youngest individuals), which were shallower than the others, were those that were damaged the fastest (some anatomical details such as the toe impressions are likely to disappear with the effect of wind action only a few minutes after the formation of the footprints). Therefore, taphonomic changes could have biased the representation of the groups, leading to under-representation of the footprints of children.

The representativeness of the group can also be debated because of the very nature of the footprints. The D3b-4 footprints are distributed across different surfaces and each surface represents brief moments of life, comparable to snapshots, because the sedimentary layer must have covered the particularly fragile footprints very quickly to preserve them from taphonomic changes. As snapshots, the footprints could represent a truncated image of the social group, part of which may have been absent during the formation of the footprints. The first possible explanation of the unusual age profile at Le Rozel could be linked to a different spatial distribution of children and adults during the occupation of the D3b-4 sub-unit, for example in connection with specific activities carried out in dedicated areas (carcass processing, lithic industry...) within the site. The apparent majority of children could thus be explained by the presence of adults in other parts of the site where they were carrying out activities in which children were not necessarily participating. However, the large area excavated for the D3b-4 sub-unit (almost 100 m²), including activity zones, limits such a bias. A second explanation, which can be added to the first, would be that some adults did not leave footprints because they were absent from the site at the time of their formation. This hypothesis raises questions about the period during

which the footprints were made in relation to the total duration of the seasonal occupation of the D3b-4 sub-unit. The period separating the most recent surface from the oldest within this sub-unit is currently unknown. The D3b-4 footprints could thus represent snapshots that are representative of the entire seasonal occupation or only a portion of it. If the footprints represent a short period of time during the occupation, the majority of children could be explained by the absence of older individuals, who may have left the site in search of resources.

It is therefore currently impossible to know whether the D3b-4 track-making group is representative or not of the whole social group. If the track-making group is not representative of the whole social group, this would explain the differences in the age distribution patterns between the Le Rozel footprints on the one hand, the Neandertal site of El Sidrón on the other hand, and modern hunter-gatherer populations. The D3b-4 social group could indeed have been composed of more adults than the footprints suggest. The footprints at Le Rozel would thus support a limit to be taken into account in footprint studies. As detailed previously, the representation of a social group can be biased not only by taphonomic agents but also by the particular time scale that footprints represent. While it is difficult to quantify the period of accumulation of archaeological artefacts or skeletal assemblages, the footprints accumulated on each surface represent very brief periods of time that can be compared to snapshots. However, by representing such snapshots, footprints may offer a truncated picture of a social group, even for sites where hundreds of footprints have been found, such as at Le Rozel, since part of the group could have been elsewhere during the brief period in which the footprints, even in large numbers, were made. Caution is therefore needed when making inferences from footprints about the size and composition of social groups. In this respect, ichnological assemblages do not provide a better estimate of the size and composition of social groups than archaeological artefacts or skeletal assemblages but represent remains of a different type corresponding to a different time scale, with its own drawbacks. However, this particular time scale represented by footprints also has advantages and provides important information. Although they cannot inform with certainty on a whole social group, footprints provide biological information about some individuals of this group, data which remains essential to understand the nature of an occupation site, especially when no human skeletal remains have been discovered, as is the case at Le Rozel. Moreover, by representing brief moments of life, footprints give direct access to variables other than group size and composition. In particular, they reflect the behaviour of individuals by illustrating, for example, potential hunting strategies (e.g. Bustos et al., 2018). They also capture locomotor characteristics and their anatomical correlates, as attested by the footprints from Laetoli (Leakey and Hay, 1979) and Ileret (Bennett et al., 2009), but also Le Rozel. Studies have shown that the individuals who left the footprints at Le Rozel had a more robust foot with a

less pronounced arch than modern populations, which is consistent with our knowledge of Neandertal anatomy (Duveau et al., 2019).

On the other hand, if the track-making group is representative of the whole social group, then the high proportion of children and the low proportion of adults would raise questions about the adaptive success of this group (e.g. competition with other Neandertal groups composed of a larger proportion of adults, survival against predators) and the distribution of activities, since the archaeological material associated with the footprints at Le Rozel point to different activities (carcass processing, lithic production). One issue would be whether young Neandertal children could have contributed to complex tasks, such as lithic industry production, or potentially dangerous tasks such as hunting. The answer to this question could bring totally new information to our knowledge of Neandertal culture, particularly as regards learning in the youngest individuals.

Conclusion

To summarise, the footprints at Le Rozel represent the largest ichnological sample attributed to Neandertals known to date. Their analysis, combining morphometric and experimental studies, have provided information on the size and composition of the groups that made them, which is essential for a better understanding of the Palaeolithic occupations at Le Rozel 80,000 years ago. However, as with archaeological artefacts or osteological assemblages, but for different reasons, the study of footprints from Le Rozel is limited by the constraints of palaeontology: it is impossible to know whether a fossil sample is representative of a population or a social group.

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