



The composition of a Neandertal social group revealed by the hominin footprints at Le Rozel (Normandy, France)

Jérémy Duveau^{a,1}, Gilles Berillon^a, Christine Verna^a, Gilles Laisné^b, and Dominique Cliquet^{b,c,d,1}

^aUMR 7194 Histoire Naturelle de l'Homme Préhistorique, CNRS, Muséum National d'Histoire Naturelle, Université Perpignan Via Domitia, 75013 Paris, France; ^bProjet Collectif de Recherche, Les Premiers Hommes en Normandie, Ministère de la Culture, 14052 Caen Cedex 4, France; ^cService Régional de l'Archéologie, Direction Régionale des Affaires Culturelles Normandie, Ministère de la Culture, 14052 Caen Cedex 4, France; and ^dUMR 6566 Centre de Recherche en Archéologie, Archéosciences, Histoire, CNRS, Université de Rennes 1, 35042 Rennes, France

Edited by Erik Trinkaus, Washington University, St. Louis, MO, and approved July 15, 2019 (received for review February 4, 2019)

Footprints represent a unique snapshot of hominin life. They provide information on the size and composition of groups that differs from osteological and archeological remains, whose contemporaneity is difficult to establish. We report here on the discovery of 257 footprints dated to 80,000 y from the Paleolithic site at Le Rozel (Normandy, France), which represent the largest known Neandertal ichnological assemblage to date. We investigate the size and composition of a track-maker group from this large set by developing a morphometric method based on experimental footprints. Our analyses indicate that the footprints were made by a small group comprising different age classes, from early childhood to adult, with a majority of children. The Le Rozel footprints thus provide direct evidence for the size and composition of a Neandertal social group.

footprints | Neandertals | Le Rozel | morphometry | group composition

Like living humans and most primates, Neandertals lived in social groups, probably composed of individuals of both sexes and various age classes (e.g., refs. 1–3). The size and composition of Neandertal groups may have played an important role in their adaptive success, as is the case for current primates (e.g., refs. 4 and 5), but they are difficult to infer from the archeological and paleoanthropological records (e.g., ref. 3). Indirect approaches of group size, using occupational or sleeping surface areas and ethnographic analogies (e.g., refs. 3, 6, and 7), suggest that Neandertal groups were small, from 10 to 30 individuals on average per site (e.g., ref. 3). Such approaches assume that the accumulations of archeological remains reflect a single occupation, which is not certain (8–10). The composition of the relevant social group can be obtained in rare cases from catastrophic mortality events, where osteological remains are assumed to be contemporaneous (e.g., refs. 11 and 12). Such profiles are exceptional for Neandertals, and their interpretation as catastrophic is not always accepted (12, 13).

Fossil footprints are preserved when rapidly buried and thus represent a snapshot of life (e.g., refs. 14–16). As such, ichnological assemblages give the opportunity to directly investigate hominin group size and composition, based on trackways (e.g., refs. 17–19), morphometric analyses, or expert trackers' readings of isolated footprints (e.g., refs. 20–23). However, despite significant discoveries in recent years (e.g., refs. 24 and 25), sites with hominin footprints are relatively scarce (26–28), with less than forty reported sites for pre-Holocene periods (*SI Appendix, Fig. S1 and Table S1*), including 4 sites that yielded only 9 footprints assigned to Neandertals (refs. 29–32 and *SI Appendix, Text S1 and Fig. S2*).

Here we report on the discovery of 257 hominin footprints at Le Rozel (Manche, France), dated to ~80,000 y (33) and associated with in situ archeological material (34, 35). Focusing on the 104 best preserved footprints from the densest stratigraphic subunit (D3b-4), we investigate the size and age-class composition of a single Neandertal group.

Archeological Site of Le Rozel

The site of Le Rozel (49°28'20.92"N, 1°50'25.58"W) (Manche, France) is part of a paleodune system formed during the Upper Pleistocene, between ~115,000 and ~70,000 y ago (33–36). It currently lies in a creek between the beach of Surtainville to the south and a Cambrian schist cliff to the northwest (*SI Appendix, Figs. S3–S5*). First discovered and excavated in the 1960s (36, 37), Le Rozel has been annually excavated since 2012 (D. Cliquet, Director), yielding hundreds of hominin footprints as well as 8 handprints, but also 6 animal tracks (Fig. 1). This ichnological assemblage belongs to a single subhorizontal stratigraphic unit (D3b) made up of fine and medium brown to black sand dated to ~80,000 y (33–36). The prints are distributed over 5 subunits, D3b-1 to D3b-5 (*SI Appendix, Figs. S6–S8*), and are mainly concentrated in the sandy muds of the 2 lower subunits (D3b-4 and D3b-5). Field and sedimentological data show that the moisture conditions were not uniform for the whole ichnological assemblage (from sandy mudflows to a dry ground). Within each of the 5 stratigraphic subunits, the hominin footprints are associated with an abundant archeological material (refs. 34 and 35 and *SI Appendix, Fig. S9*). This assemblage includes a rich Middle Paleolithic lithic industry and about 8,000 faunal remains, which attest anthropic activities (e.g., butchery operations,

Significance

The limited knowledge we have of the size and composition of Neandertal social groups is usually based on indirect approaches using archeological or osteological data. In contrast, footprints provide more direct information about group size and composition. However, they are scarce in the fossil record, particularly for Neandertals. The discovery of 257 footprints at Le Rozel (Normandy, France) opens up a new approach for studies of the composition of Neandertal groups. By applying a morphometric method to a sample of fossil footprints made during a single brief occupation event, our analysis shows that they represent a small group with a majority of children and thus provides direct evidence of the composition of a Neandertal group.

Author contributions: J.D., G.B., C.V., and D.C. designed research; J.D. took part in the excavations of the tracks, 3D digitization of the tracks, and direction of the experimental study; G.L. identified and excavated the tracks; D.C. is responsible for the whole project on Le Rozel, excavated the site, and provided the ichnological and archeological assemblages; J.D. performed research; J.D., G.B., and C.V. analyzed data; G.B. found funding; and J.D., G.B., C.V., G.L., and D.C. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Published under the PNAS license.

¹To whom correspondence may be addressed. Email: jeremy.duveau@edu.mnhn.fr or dominique.cliquet@culture.gouv.fr.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1901789116/-DCSupplemental.

First published September 9, 2019.

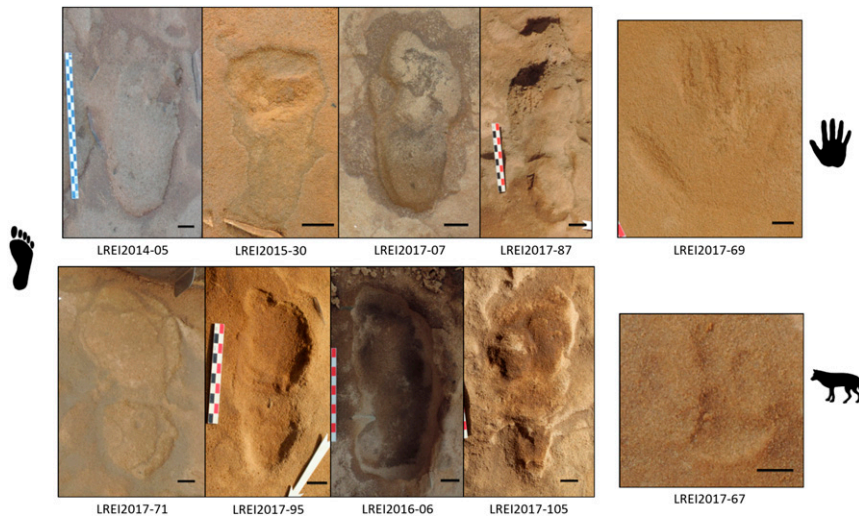


Fig. 1. Le Rozel tracks: hominin footprints, a handprint, and an animal track. (Scale bar, 2 cm.) (Photos by D.C.)

lithic industry production). These occupation levels also yielded intrasite spatial patterning with several structures such as hearths and lithic-knapping areas. Sedimentological and geochronological studies have shown that each subunit was formed and rapidly covered by aeolian sand (33–35), which allowed the footprints to be protected from surface erosion. Thanks to such aeolian dynamics, the archeological and ichnological remains found within each subunit are considered to reflect a single brief occupation event.

Results

Footprint Assemblage. Qualitative and quantitative analyses of the ichnological material discovered between 2012 and 2017 led to the identification of 257 hominin footprints (Fig. 1 and *SI Appendix*, Figs. S10–S16, Tables S2–S4, and Texts S2–S5). The footprint assemblages include 5 trackways (2 to 3 successive footprints) with foot angles ranging from 3.0° to 7.6°. The rest of the footprints are considered as isolated. About 80% of the footprints are located on the D3b-4 stratigraphic subunit, which extends over 92 m².

The footprints are variably printed or preserved, which is usual for footprints made in soft sandy ground (e.g., refs. 25, 38, and 39). Nevertheless, 88 footprints show strict criteria to identify them as longitudinally complete: a rounded heel impression proximally and, distally, clear impressions of the toes and/or 2 mediolateral rims representing the metatarsophalangeal limits and toe tips. Their lengths range from 11.4 to 28.7 cm. The smallest footprints are shallower and less mediolaterally narrow than the largest ones made in similar sediments, suggesting a flatter foot.

The geometric morphometric analysis of the 14 best preserved footprints (1 from the D3b-3 stratigraphic subunit, 12 from the D3b-4, and 1 from the D3b-5), together with Laetoli and *Homo sapiens* (experimental and archaeological from the Holocene) footprints show that the Le Rozel sample clearly differs from the Laetoli footprints along the PC1 axis. They are closer to the footprints attributed to *Homo sapiens*, but despite a partial overlapping, they represent 2 distinct morphospaces, the Le Rozel ones being wider, especially at the midfoot (Fig. 2).

Group Size and Composition. Among the 104 exploitable footprints from the D3b-4 stratigraphic subunit, 39 are longitudinally complete and 100 complete enough for width to be measured. The lengths range from 11.4 to 28.4 cm and the widths from 4.5 to 14.2 cm (Table 1 and *SI Appendix*, Tables S6 and S7 and Figs. S18 and S19).

The maximum intraindividual deviations in the lengths of experimental footprints (i.e., the largest deviation from the average for each individual) extend up to 12.8% (*SI Appendix*, Table S4). By applying this value to the length of the 39 longitudinally complete footprints from Le Rozel, a minimum of 4 metric classes can be estimated, each representing at least 1 individual (Table 1 and *SI Appendix*, Text S7 and Fig. S20). A total of 100 footprints were then divided into 4 classes based on their widths using the quartiles of their dispersion (4.5 to 12.8 cm, Table 1). For both length and width, the general pattern of distribution shows that the second and third metric classes are the most numerous (Table 1). Assuming that 1) individuals made the same average number of footprints and 2) that the metric class with the fewest footprints (metric class IV) corresponds to a single individual, one can estimate that the number of individuals would be 13 based on the footprint length (1, 6, 5, and 1 individuals per metric class) and 10 based on the width (2, 3, 4, and 1 individuals per class).

The estimated statures range from 73.8 to 184.8 cm based on footprint length and from 65.8 to 189.3 cm based on footprint width (Table 1 and *SI Appendix*, Text S8, Tables S6 and S8, and Figs. S21 and S22).

Using the age-to-stature regression curve for Neandertals, the distribution patterns of the statures estimated from footprint length and width are similar (Fig. 3). The Le Rozel footprints correspond mainly to children (64.1% for length, 47.0% for width) and adolescents (respectively 28.2 and 43.0%), and the adult age class is less represented (7.2 and 10.0%). The shortest complete footprint (11.4 cm) corresponds to an age of 2 y (Fig. 3). The longest footprints that belong to the fourth metric class (Table 1) correspond to an average stature of 175 cm (for both length and width) and were probably made by a male, according to Neandertal sexual dimorphism patterns (refs. 40 and 41 and Fig. 3). Additionally, using a variation curve defined from modern populations leads to a similar general pattern of age-class composition, with a low frequency of adults but a very high frequency of children (*SI Appendix*, Fig. S23 and Table S9).

Discussion

Taxonomic Attribution. With a few exceptions, taxonomic attributions of Pleistocene footprints are not based on associated paleoanthropological remains, but indirectly assessed from chronological criteria or, more rarely, archaeological material (ref. 16 and *SI Appendix*, Text S1). Although Le Rozel has not yielded any hominin osteological remains to date, 3 types of evidence enable a reliable taxonomic attribution of the footprints.

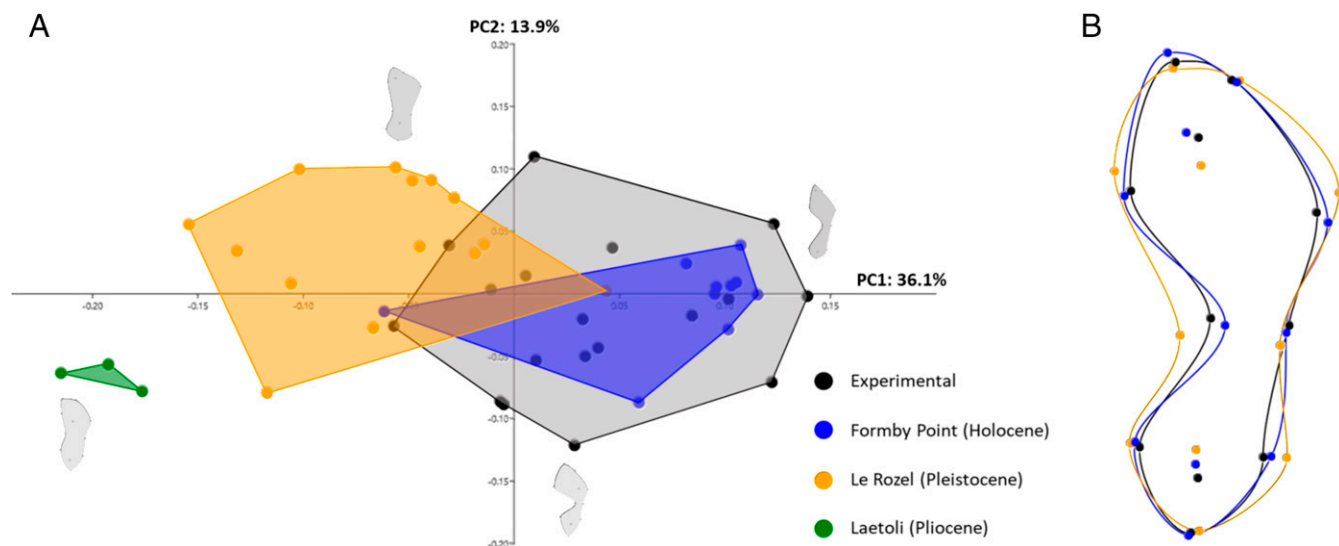


Fig. 2. Geometric morphometric analysis based on the 2D coordinates of 11 landmarks indicating the footprint outline and the locations of the deepest areas (*SI Appendix, Text S6, Fig. S17, and Table S5*). (A) Principal Component Analysis (PC1 vs. PC2). PC1 (28.9% of total variance) accounts for midfoot width, position of the maximum depth of the forefoot, and hallux abduction. High PC1 scores reflect a larger width, a more proximal maximum depth position, and a more abducted hallux. PC2 (16.5% of total variance) mainly informs about footprint width: low PC2 scores correspond to a larger width. (B) Mean shapes of the Le Rozel footprints (yellow), Holocene footprints (blue), and experimental footprints (black) made in similar deposit conditions.

First of all, the morphometric analysis (Fig. 2) reveals that the footprints from Le Rozel are wider, especially at the midfoot, than the modern human sample and suggests a less gracile morphology and a less pronounced plantar vault. Since footprint morphology partially reflects the foot anatomy of track-makers (e.g., ref. 16), this result is consistent with what is known about Neandertal foot anatomy when compared to that of modern humans (42–44). In addition, the footprints were made 80,000 y ago (33, MIS 5a-b), when Neandertals were the only hominin species known in Western Europe (e.g., refs. 45–47). Finally, the footprints are associated with Mousterian industries that show characteristics similar to those associated with Neandertal remains in other European sites (34, 35). Based on this evidence, we attribute these footprints to Neandertals.

Group Size and Composition. In the various stratigraphic subunits at Le Rozel, the large quantity of lithic material and the size of animal carcasses (34, 35) are initial evidence that the groups who occupied the site were composed of several individuals. However, more precise information on the social structure of these groups cannot be inferred from the preserved archaeological material alone. Our metric analyses of the D3b-4 footprint assemblage shows that the group was made up of at least 4 individuals, with a more realistic estimate of 10 to 13 individuals. This is consistent with estimates obtained at other Neandertal sites based on spatial data that indicate average numbers of 10 to 30 individuals (e.g., ref. 3), as well as with the known range of group sizes among recent hunter-gatherers (e.g., refs. 1 and 48).

Table 1. Dimensions and estimated statures for the footprints from the D3b-4 stratigraphic subunit

Dimensions and associated statures	Total	Average metric class (MNI = 4)			
		I	II	III	IV
Length (cm)					
Interval	11.4 to 28.4	11.4 to 14.8	15.4 to 18.8	19.2 to 23.4	24.7 to 28.4
Mean	19.0	13.2	17.0	21.5	26.9
Number of footprints	39	4	18	14	3
Relative frequency (%)		10.3	46.2	35.9	7.7
Estimated stature (cm)					
Interval	73.8 to 184.8	73.8 to 96.0	100.2 to 122.3	124.9 to 151.9	160.7 to 184.8
Mean	123.5	86.2	110.4	140.0	174.8
Width (cm)					
Interval	4.5 to 12.8	4.5 to 6.6	6.6 to 8.6	8.6 to 10.7	10.7 to 12.8
Mean	8.5	5.5	7.6	9.5	11.8
Number of footprints	100	16	31	43	10
Relative frequency (%)		16.0	31.0	43.0	10.0
Estimated stature (cm)					
Interval	65.8 to 189.3	65.8 to 93.2	97.6 to 127.2	128.6 to 156.7	164.1 to 189.3
Mean	125.6	81.4	112.6	140.1	174.5

The metric classes for footprint length define the Minimum Number of Individuals as 4. The metric classes for width measurements are determined from the quartiles of their dispersion (4.5 to 12.8 cm).

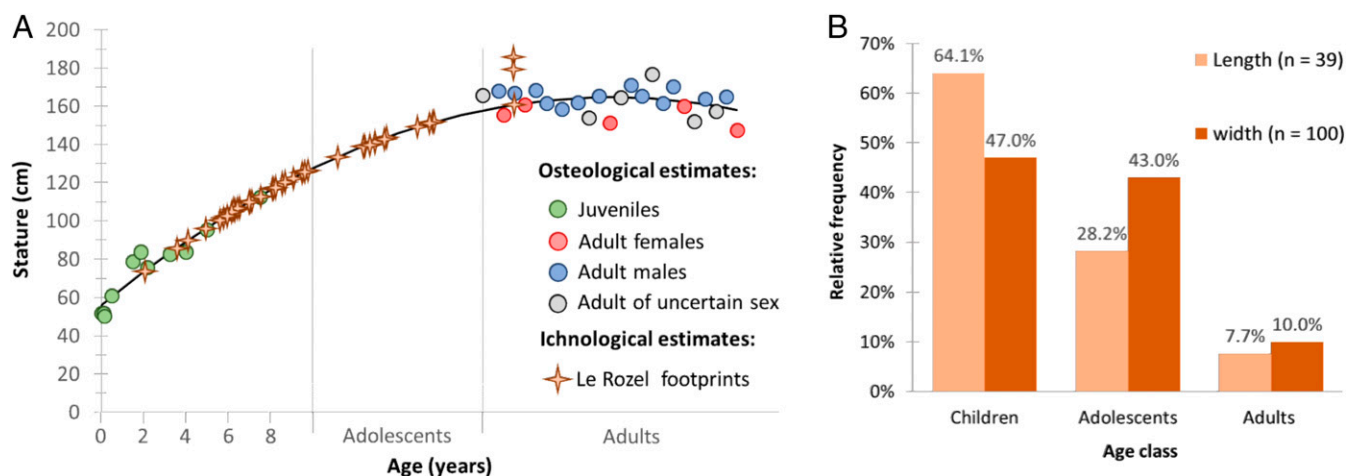


Fig. 3. Distribution by age class. (A) Positions of the 39 longitudinally complete footprints from the D3b-4 subunit placed on an age-to-stature regression curve from estimates based on Neandertal osteological remains (SI Appendix, Table S10). The curve was made using 2 relationships: the first for Neandertal children (in green) and the second, representing a constant mean stature, for adult Neandertals (in gray, red, and blue). (B) Relative frequencies per age class from both types of estimated statures (from footprint length and width).

The relative age composition of the D3b-4 group was assessed on the basis of stature estimates. After selecting footprints made on a flat ground with no evidence of sliding in order to ensure measurement consistency, we investigated 2 potential biases: the variation in foot length-to-stature ratio and the substrate impact on the footprint morphology. Because the foot length-to-stature ratio can differ significantly during development (e.g., refs. 49 and 50) or between populations (e.g., refs. 51 and 52), our estimates use a large comparative osteometric database encompassing individuals from different age groups and populations, including habitually unshod people. Additionally, any stature estimation of hominins based on comparative modern data may be questioned. There may be differences between the foot length-to-stature ratio of modern humans and that of Neandertals. Although about 20 well-preserved Neandertal skeletons are currently known, and foot remains are quite numerous, none is complete enough to know this ratio. In order to validate our stature estimations, we thus analyzed the ratio between the second metatarsal length, which is correlated to the foot length, and the femoral length, the latter being commonly used in order to estimate the statures of hominins (e.g., refs. 53 and 54). This ratio has been calculated for 7 Neandertal individuals (17%, SI Appendix, Table S11) and appears to be equal to that of modern individuals (17%, using the supplementary information from ref. 55). We also considered the substrate impact on the footprint morphology by using experimental data produced on similar sediments. These data gave a footprint length-to-foot length ratio (103.6%) close to those obtained in previous experimental studies on similar sandy sediments (56). All these data support our stature estimates.

As a result, the range of statures at Le Rozel is wide, from 66 to 189 cm, and more than half of them are less than 130 cm. The largest estimates (161 to 189 cm), which correspond to the fourth metric class (Table 1), partially overlap the adult Neandertal range estimated from osteological remains (147 to 177 cm, SI Appendix, Table S10); 7 estimates fall above this range (178.9 to 189.2 cm). Considering our conservative hypothesis using the 12.8% maximum intraindividual deviation, all of the footprints of the fourth metric class could have been made by a single individual with an estimated stature of 175 cm. However, we cannot exclude that very tall Neandertal individuals lived at Le Rozel, and our results may suggest taller Neandertal individuals than previously known.

Based on the hypothesis that each individual made on average the same number of footprints, the D3b-4 group was composed of 90% of children and adolescents. Several parameters that may impact this result need to be considered. First, in our model (Fig. 3), the stature gap between adults and adolescents is small, and footprints placed near the limit between these 2 classes could be misclassified. Nevertheless, most of the footprints fall far from this limit, and their classification is thus reliable. Based on osteological remains, the lowest limit of the adult Neandertal stature range is 147.5 cm (SI Appendix, Table S10). If we use this value as the limit between adults and adolescents in our analysis, the frequency of adult footprints does not exceed 21%. It is therefore unlikely that our model significantly underestimates the number of adults. Second, for some biometric reasons, children may have left more footprints than adults in the studied area. Given that the Le Rozel site is an occupation site and not a “passage” one, we cannot precisely quantify the influence of this parameter on our assemblage (due to an absence of data regarding walking speed, periods of standstills, frequency of movement phases in relation to rest phases, etc.). In situ observations however showed that the shallowest footprints, which mostly correspond to the smallest individuals, are the ones which are the least well preserved. Therefore, small-sized footprints are certainly underrepresented in our assemblage, which limits any important overestimation of children. All of these lines of evidence thus support that the D3b-4 group was mainly composed of children and adolescents.

The Paleolithic site at Le Rozel is the only one, besides the El Sidrón site (Spain), to provide reliable information on the composition of a Neandertal social group. The 2 sites have yielded different patterns. Le Rozel reflects a majority of children and, to a lesser extent, adolescents. The osteological remains from El Sidrón belong to 7 adults, 3 adolescents, 2 juveniles, and 1 infant. This corresponds to a larger proportion of adults (e.g., ref. 57), as is the case for present-day hunter-gatherer groups (e.g., refs. 48 and 58). The sites of Krapina and Sima de los Huesos also show a larger number of adults (e.g., refs. 12 and 13). However, it is difficult to know if the remains at these 2 sites represent contemporary individuals, since there is no consensus as to the catastrophic nature of their mortality profiles (e.g., ref. 12). If both the Le Rozel and El Sidrón assemblages represent all of the members of the groups, age structure differences would then testify to the diversity in the compositions of Neandertal social groups.

Conclusion

To conclude, the hominin tracks discovered at Le Rozel represent the largest ichnological assemblage attributed to archaic hominins and, in particular, to Neandertals, by yielding more than 95% of all of the footprints attributed to this taxon (29–32). They also represent the only Neandertal handprints with the hand stencils discovered in Maltravieso (59). It is in addition one of the rare examples (24) of prints associated with numerous archeological artifacts (34, 35). Thanks to this particularly large statistical sample, the size and composition of one of the Neandertal groups who made these footprints ~80,000 y ago were directly investigated. The results indicate the presence of a small group, probably 10 to 13 individuals, constituted in its majority of adolescents and children. They also reveal the presence of young children, the smallest footprint corresponding to an age of 2 y. Whereas the archeological data bring information about the material culture and activities of the group, such an exceptional footprint assemblage reveals a single life moment of a prehistoric group.

Methods

Footprint Identification. The identification of footprints was based on qualitative criteria. They had to reflect the dimensions, anatomy, and function of the human foot: a rounded heel, a longitudinal arch, short toes, an adducted hallux, and maximum depth areas located beneath the heel and forefoot (e.g., refs. 16, 60, and 61). Furthermore, the identification of the Le Rozel tracks was quantitatively reinforced by applying a morphometric test developed by Morse et al. (ref. 61 and *SI Appendix, Text S5 and Figs. S14–S16*).

Footprint Recording. Each identified footprint was photographed, described, and measured in situ. From 2013 to 2016, casts were made of 55 footprints. In 2017, 62 original footprints were directly extracted after they had been chemically hardened. All of the casts and extracted footprints were curated on the premises of the Direction Régionale des Affaires Culturelles (DRAC, Caen, France). They can be consulted after obtaining Dominique Cliquet's agreement. Point clouds of 180 tracks, including 169 hominin footprints, were compiled. One hundred and thirty-three footprints were digitized by using a Noomeo Optimum surface scan and 70 footprints by photogrammetry using Agisoft Photoscan (v.1.4.0) and a Canon EOS 1300D camera. The use of these different acquisition techniques required prior statistical comparisons between them, which did not detect any differences (*SI Appendix, Text S9 and Figs. S24–S26*). The 3D models of the footprints will be available in a freely accessible database within the coming years.

Comparative Material. The Le Rozel footprints were compared to 192 experimental footprints, made by 21 nonpathological individuals, from 1 to 36 y of age. They moved unshod in 2 ways, a comfortable walk and a slow run, in a similar sediment (*SI Appendix, Text S3 and Fig. S13*). We also used Laetoli and Holocene archeological footprints from freely accessible 3D databases (*SI Appendix, Text S4*). Experimental footprints were recorded on the site in agreement with the terms of the field work authorization (prefectoral decree #28-2017-339 [05/17/2017, Normandy, France], operation number: 163972). Volunteer participants and their legally responsible guardians in case of minor participants gave written and informed consent.

Geometric Morphometrics. Eleven landmarks that provide information on the footprint outline and the locations of the deepest areas were positioned in Geomagic Studio 2013 (*SI Appendix, Text S6 and Fig. S17*). Their 2D coordinates were subject to a Generalized Procrustes Analysis (62) in PAleontological STatistics (PAST v.3.0; ref. 63). The mean 2D coordinates of the footprints made by the same individual were calculated and subsequently considered in order to avoid biases caused by statistical replication. The coordinates were then subjected to a Principal Component Analysis (PCA) in PAST.

Group Size and Composition.

Measurements. Length and width were measured in the same way for the fossil and experimental footprints. Only footprints made on a flat ground with no evidence of sliding were considered. The length was measured along the longitudinal axis, and the width corresponds to the maximal breadth of the forefoot impression along the mediolateral axis.

MNI estimate. In order to estimate a Minimum Number of Individuals (MNI) from isolated footprint dimensions, we used the largest value (12.8%) of the maximum intraindividual deviations (*md*) in experimental footprint lengths from the average of each individual (*SI Appendix, Text S7*). We considered that fossil footprint lengths (*L*) falling within the interval [$L \times (1 - md)$; $L \times (1 + md)$] from each other corresponded to prints made by the same individual.

From footprint size to stature. Stature was estimated from footprint length by using 1) the foot length-to-stature ratio of different populations from published data and 2) the footprint length-to-foot length ratio that we experimentally determined (*SI Appendix, Text S8, Table S8, and Figs. S21 and S22*). A relationship between footprint length (*L*) and stature (*S*) is thus obtained by considering variations in body proportions within different populations and the impact of the substrate from Le Rozel on the footprint morphometry: $S = 6.51 \times L$. When the footprint length was not available, we estimated it from the width based on the fossil width-to-length ratio (0.44, $r = 0.83$; *SI Appendix, Fig. S19*).

From estimated stature to age class. Our stature estimates were placed on an age-to-stature regression curve established from published Neandertal osteological data (*SI Appendix, Table S10*). This curve is based on 2 relationships, 1 at either end: the variation in relation to age observed for children and the average stature for adults (162.1 cm). As it is difficult to estimate a precise age for adolescents (10 to 18 y old) from osteological material, no individual was used for this age class. This part of the curve was extrapolated from the 2 others, resulting in a logarithmic curve between stature and age. Additionally, our stature estimates were also placed on an age-to-foot length curve established from different modern populations (*SI Appendix, Fig. S23*).

ACKNOWLEDGMENTS. We are grateful for the helpful comments from the two reviewers and the editor. We particularly acknowledge the owners of the Le Rozel site, Mrs. Lecomte, Mrs. Deregeaucourt, Mrs. Guillotte, and Mrs. Maurouard. We wish to commend all the volunteers who participated in the excavations and experiments at Le Rozel, making the discovery and analysis of the archeological and ichnological material possible. We are grateful to M. Friess and F. Detroit (Musée de l'Homme, Paris, France) for their help during the photogrammetric digitization. We also thank Professor M. Bennett, who made the footprint 3D models available for study. We are grateful to I. Bossanyi for editing the English. The field work is supported by the French Ministry of Culture and the French department of La Manche. Experiments were funded by the CNRS-Institut Écologie et Environnement International Research Network IRN-GDRI0870 and metric analyses conducted within the frame of the ANR-18-CE27-0010-01 HoBiS. J.D. is currently granted funding for a doctoral degree (Muséum national d'Histoire naturelle, Paris, France).

1. R. Layton, S. O'Hara, Human social evolution: A comparison of hunter-gatherer and chimpanzee social organization. *Proc. Br. Acad.* **158**, 83–113 (2010).
2. C. Lalueza-Fox et al., Genetic evidence for patrilineal mating behavior among Neandertal groups. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 250–253 (2011).
3. B. Hayden, Neandertal social structure? *Oxf. J. Archaeol.* **31**, 1–26 (2012).
4. J. B. Silk, The adaptive value of sociality in mammalian groups. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **362**, 539–559 (2007).
5. B. Majolo, A. de Bortoli Vizioli, G. Schino, Costs and benefits of group living in primates: Group size effects on behaviour and demography. *Anim. Behav.* **76**, 1235–1247 (2008).
6. A. Burke, Neandertal settlement patterns in Crimea: A landscape approach. *J. Anthropol. Archaeol.* **25**, 510–523 (2006).
7. J. Vallverdú et al., Sleeping activity area within the site structure of archaic human groups: Evidence from Abric Romaní level N combustion activity areas. *Curr. Anthropol.* **51**, 137–145 (2010).
8. F. Bordes, J.-P. Rigaud, D. de Sonneville-Bordes, Des butts, problèmes et limites de l'archéologie paléolithique. *Quaternaria* **16**, 15–34 (1972).
9. C. Farizy, Spatial patterning of Middle Paleolithic sites. *J. Anthropol. Archaeol.* **13**, 153–160 (1994).
10. P. B. Pettitt, High resolution Neanderthals? Interpreting Middle Palaeolithic intrasite spatial data. *World Archaeol.* **29**, 208–224 (1997).
11. T. A. Chamberlain, *Demography in Archaeology* (Cambridge University Press, Cambridge, UK, 2006).
12. M. H. Wolpoff, R. Caspari, Does Krapina reflect early Neandertal paleodemography? *Period. Biol.* **108**, 425–432 (2006).
13. J.-P. Bocquet-Appel, Age distributions of hominid samples at Atapuerca (SH) and Krapina could indicate accumulation by catastrophe. *J. Archaeol. Sci.* **26**, 327–338 (1999).
14. G. Mastrolorenzo, P. Petrone, L. Pappalardo, M. F. Sheridan, The Avellino 3780-yr-B.P. catastrophe as a worst-case scenario for a future eruption at Vesuvius. *Proc. Natl. Acad. Sci. U.S.A.* **103**, 4366–4370 (2006).
15. H. U. Schmincke, J. Rausch, S. Kutterolf, A. Freundt, Walking through volcanic mud: The 2,100 year-old Acahualinca footprints (Nicaragua) II: The Acahualinca people, environmental conditions and motivation. *Int. J. Earth Sci.* **99**, 279–292 (2010).
16. M. R. Bennett, S. A. Morse, *Human Footprints: Fossilised Locomotion?* (Springer, Heidelberg, 2014).
17. M. D. Leakey, R. L. Hay, Pliocene footprints in the Laetoli beds at Laetoli, northern Tanzania. *Nature* **278**, 317–323 (1979).
18. F. T. Masao et al., New footprints from Laetoli (Tanzania) provide evidence for marked body size variation in early hominins. *eLife* **5**, e19568 (2016).

19. N. T. Roach *et al.*, Pleistocene footprints show intensive use of lake margin habitats by *Homo erectus* groups. *Sci. Rep.* **6**, 26374 (2016).

20. N. Ashton *et al.*, Hominin footprints from early Pleistocene deposits at Happisburgh, UK. *PLoS One* **9**, e88329 (2014).

21. D. Webb *et al.*, Ancient human footprints in Ciur-Izbut Cave, Romania. *Am. J. Phys. Anthropol.* **155**, 128–135 (2014).

22. P. Citton, M. Romano, I. Salvador, M. Avanzini, Reviewing the upper Pleistocene human footprints from the 'Sala dei Misteri' in the Grotta della Bàsura (Toirano, northern Italy) cave: An integrated morphometric and morpho-classificatory approach. *Quat. Sci. Rev.* **169**, 50–64 (2017).

23. A. Pastoors *et al.*, Experience based reading of Pleistocene human footprints in Pech-Merle. *Quat. Int.* **430**, 155–162 (2017).

24. F. Altamura *et al.*, Archaeology and ichnology at gombore II-2, Melka Kunture, Ethiopia: Everyday life of a mixed-age hominin group 700,000 years ago. *Sci. Rep.* **8**, 2815 (2018).

25. D. Bustos *et al.*, Footprints preserve terminal Pleistocene hunt? Human-sloth interactions in North America. *Sci. Adv.* **4**, eaar7621 (2018).

26. J. Y. Kim, K. S. Kim, M. G. Lockley, N. Matthews, Hominid ichnotaxonomy: An exploration of a neglected discipline. *Ichnos: An Int. J. Plant Anim. Traces* **15**, 126–139 (2008).

27. M. Lockley, G. Roberts, J. Y. Kim, In the footprints of our ancestors: An overview of the hominid track record. *Ichnos: An Int. J. Plant Anim. Traces* **15**, 106–125 (2008).

28. M. Lockley, J. Meldrum, J. Y. Kim, "Major events in hominin evolution" in *The Trace-Fossil Record of Major Evolutionary Events Volume 2: Mesozoic and Cenozoic*, M.G. Mángano, L.A. Buatois, Eds. (Springer, Dordrecht, 2016), pp. 411–448.

29. A. Tuffreau, Les habitats du Paléolithique inférieur et moyen dans le Nord de la France (Nord, Pas-de-Calais, Somme). *Revue Archéologique de Picardie* **1**, 91–104 (1988).

30. S. Manolis, C. L. Aiello, R. Henessy, N. Kyparissi-Apostolika, "The Middle Palaeolithic footprints from Theopetra Cave (Thessaly, Greece)" in *Theopetra Cave. Twelve Years of Excavation and Research 1987–1998*, N. Kyparissi-Apostolika, Ed. (Greek Ministry of Culture and Institute for Aegean Prehistory, Athens, 2000), pp. 87–93.

31. B. P. Onac *et al.*, U–Th ages constraining the Neanderthal footprint at Vârtope Cave, Romania. *Quat. Sci. Rev.* **24**, 1151–1157 (2005).

32. F. Muñoz *et al.*, Following the last Neanderthals: Mammal tracks in late Pleistocene coastal dunes of Gibraltar (S Iberian Peninsula). *Quat. Sci. Rev.* **217**, 297–309 (2019).

33. N. Mercier, L. Martin, S. Kreutzer, V. Moineau, D. Cliquet, Dating the palaeolithic footprints of 'Le Rozel' (Normandy, France). *Quat. Geochronol.* **49**, 271–277 (2019).

34. D. Cliquet *et al.*, "Le site paléolithique moyen du « Pou » au Rozel (Manche): Des aires de travaux spécialisés et des habitats vieux d'environ 80 000 ans" in *Journées archéologiques de Normandie*, J.-P. Ollivier, Ed. (Presses Universitaires de Rouen et du Havre, Mont-Saint-Aignan, 2018), pp. 13–35.

35. D. Cliquet *et al.*, *Le Rozel (Manche), Le Pou, Section B no 486 et 572* (Rapport de fouilles, SRA Normandie, 2018).

36. B. van Vliet-Lanoë *et al.*, L'abri sous-roche du Rozel (France, Manche): Un habitat de la phase récente du Paléolithique moyen dans son contexte géomorphologique. *Quaternaire* **17**, 207–258 (2006).

37. F. Scuvée, J. Verague, *Paléolithique supérieur en Normandie occidentale: L'Abri-sous-Roches de la Pointe du Rozel (Manche)* (LITTUS CEHP, Cherbourg, 1984).

38. J. R. Allen, Subfossil mammalian tracks (Flandrian) in the Severn Estuary, SW Britain: Mechanics of formation, preservation and distribution. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **352**, 481–518 (1997).

39. S. A. Morse *et al.*, Holocene footprints in Namibia: The influence of substrate on footprint variability. *Am. J. Phys. Anthropol.* **151**, 265–279 (2013).

40. C. B. Ruff, E. Trinkaus, T. W. Holliday, Body mass and encephalization in Pleistocene Homo. *Nature* **387**, 173–176 (1997).

41. J.-M. Carreiro *et al.*, Stature estimation from complete long bones in the Middle Pleistocene humans from the Sima de los Huesos, Sierra de Atapuerca (Spain). *J. Hum. Evol.* **62**, 242–255 (2012).

42. E. Trinkaus, *The Shanidar Neanderthals* (Academic Press, New York, 1983).

43. E. Trinkaus *et al.*, Robusticity versus shape: The functional interpretation of Neanderthal appendicular morphology. *Anthropol. Sci.* **99**, 257–278 (1991).

44. G. Berillon, *Le pied des hominoides miocènes et des hominidés fossiles: Architecture, locomotion, évolution* (CNRS, Paris, 2000).

45. S. Benazzi *et al.*, Early dispersal of modern humans in Europe and implications for Neanderthal behaviour. *Nature* **479**, 525–528 (2011).

46. P. R. Nigst *et al.*, Early modern human settlement of Europe north of the Alps occurred 43,500 years ago in a cold steppe-type environment. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 14394–14399 (2014).

47. J.-J. Hublin, The modern human colonization of western Eurasia: When and where? *Quat. Sci. Rev.* **118**, 194–210 (2015).

48. R. L. Kelly, *The Lifeways of Hunter-Gatherers: The Foraging Spectrum* (Cambridge University Press, New York, 2013).

49. C. B. Davenport, The growth of the human foot. *Am. J. Phys. Anthropol.* **17**, 167–211 (1932).

50. M. Anderson, M. Blais, W. T. Green, Growth of the normal foot during childhood and adolescence; length of the foot and interrelations of foot, stature, and lower extremity as seen in serial records of children between 1–18 years of age. *Am. J. Phys. Anthropol.* **14**, 287–308 (1956).

51. P. Topinard, *L'Anthropologie* (C. Reinwald, Paris, 1876).

52. A. Hrdlička, The Pueblos. With comparative data on the bulk of the tribes of the southwest and northern Mexico. *Am. J. Phys. Anthropol.* **20**, 235–460 (1935).

53. M. Trotter, G. C. Gleser, Estimation of stature from long bones of American Whites and Negroes. *Am. J. Phys. Anthropol.* **10**, 463–514 (1952).

54. H. M. McHenry, Femoral lengths and stature in Plio-Pleistocene hominids. *Am. J. Phys. Anthropol.* **85**, 149–158 (1991).

55. J. L. Arsuaga *et al.*, Postcranial morphology of the middle Pleistocene humans from Sima de los Huesos, Spain. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 11524–11529 (2015).

56. H. L. Dingwall, K. G. Hatala, R. E. Wunderlich, B. G. Richmond, Hominin stature, body mass, and walking speed estimates based on 1.5 million-year-old fossil footprints at Ileret, Kenya. *J. Hum. Evol.* **64**, 556–568 (2013).

57. A. Rosas *et al.*, Identification of Neanderthal individuals in fragmentary fossil assemblages by means of tooth associations: The case of El Sidrón (Asturias, Spain). *C. R. Palevol* **12**, 279–291 (2013).

58. K. Hill, A. M. Hurtado, *Ache Life History: The Ecology and Demography of a Foraging People* (Routledge, New York, 2017).

59. D. L. Hoffmann *et al.*, U-Th dating of carbonate crusts reveals Neanderthal origin of Iberian cave art. *Science* **359**, 912–915 (2018).

60. R.H. Tuttle, Footprint clues in hominid evolution and forensics: Lessons and limitations. *Ichnos: An Int. J. Plant Anim. Traces* **15**, 158–165 (2008).

61. S. A. Morse, M. R. Bennett, S. Gonzalez, D. Huddart, Techniques for verifying human footprints: Reappraisal of pre-Clovis footprints in Central Mexico. *Quat. Sci. Rev.* **29**, 2571–2578 (2010).

62. J. C. Gower, Generalized procrustes analysis. *Psychometrika* **40**, 33–51 (1975).

63. Ø. Hammer, D. A. T. Harper, P. D. Ryan, PAST-palaeontological statistics, ver. 1.89. *Palaeontol. Electron.* **4**, 1–9 (2001).