IN PURSUIT OF OUR ANCESTORS' HAND LATERALITY

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Abstract

The aim of this paper is to apply a previously published method (Bargalló and Mosquera, 2014) to the archaeological record, allowing us to identify the hand laterality of our ancestors and determine when and how this feature, which is exhibited most strongly in humans, appeared in our evolutionary history. The method focuses on identifying handedness by looking at the technical features of the flakes produced by a single knapper, and discovering how many flakes are required to ascertain their hand preference.

This method can potentially be applied to the majority of archaeological sites, since flakes are the most abundant stone tools, and stone tools are the most widespread and widely-preserved remains from prehistory. For our study, we selected two Spanish sites: Gran Dolina-TD10.1 (Atapuerca) and Abric Romaní (Barcelona), which were occupied by pre-Neanderthal and Neanderthal populations, respectively.

Our analyses indicate that a minimum number of ~~8~~ eight flakes produced by the same knapper is required to ascertain their hand preference. Even though this figure is relatively low, it is quite difficult to obtain from many archaeological sites. In addition, there is no single technical feature that provides information about handedness, instead there is a combination of eight technical features, localised on the striking platforms and ventral surfaces. The raw material is not relevant where good quality rocks are used, in this case quartzite and flint, since most of them retain the technical features required for the analysis. Expertise is not an issue either, since the technical features analysed here only correlate with handedness (Bargalló and Mosquera, 2014). Our results allow us to tentatively identify one right-handed knapper among the pre-Neanderthals of level TD10.1 at Gran Dolina (Atapuerca), while four of the five Neanderthals analysed from Abric Romaní were right-handed. The hand preference of the fifth knapper from that location (AR5) remains unclear.

Keywords: Hand laterality, flakes, lithic technology, Atapuerca, Abric Romaní

Introduction

Laterality is the preference that living beings display for one half of the body over the other. This organisation settles in the structure of the brain, the organ that designates the role played by each extremity when performing a task.

Hand laterality is well known in our species, *Homo sapiens.* Various studies point to about 97% of the current population being lateralised, among which between 85% and 90% of individuals are right-handed, and between 10% and 15% are left-handed, depending on whether the communities are preindustrial, illiterate, and so on (Annett, 2002; Uomini, 2009). Hand laterality in apes has also been studied (Hopkins, 1996; McGrew and Marchant, 1997, 2001; Hopkins and Cantalupo, 2005), but it is less marked than human handedness and depends on several environmental and social conditions (Mosquera et al., 2007; Llorente et al., 2009, 2011). According to Llorente and colleagues: "…there must have been continuity in the evolution of handedness, at least between apes (chimpanzees) and the hominin family" (2011:569. Translated by us). However, the subject is not as straightforward as simply being right- or left-handed, since some studies have highlighted the fact that chimpanzees become more and more lateralised as the task to be done becomes increasingly complex. This condition also leads to an increase ~~of~~ in their technological behaviour, which has been interpreted as a landmark in the evolution of our hominin clade (Mosquera et al., 2012).

In fact, some researchers support that the most widespread tasks undertaken by humans are those where both hands play different roles: e.g., cutting, where one hand holds the matter to be cut, and the other uses the knife to do the actual cutting. In addition, cutting is not usually needed in the world of apes (Schick and Toth, 2009), which may have marked a strong difference between their ancestors and hominins. These type of tasks are also known as bimanual complementary tasks (McGrew and Marchant, 1999), bimanual complex tasks (Hopkins et al., 2004), and complementary role differentiation tasks (Uomini, 2009), which are indeed the most complex, as well as the most lateralising tasks, as demonstrated by Uomini (2009) in her experimental study with humans. Interpretation has led to the view that there is a feedback mechanism in the origin of handedness, where the recurring use of one hand gives it more skills compared with the other, in turn favouring the preferential use of the "skilled" hand. Both skill and practice reinforce handedness, a trait that may have favoured brain lateralisation (Teixeira and Okazaki, 2007). From a phylogenetic point of view, hand laterality may have been on the increase since the earliest hominins, as far back as *Australopithecus*

(Mosquera et al., 2012). In this sense, cut-marks found at Dikika (Ethiopia) from 3.3 my ago (McPherron et al., 2010) do not inform us about hand laterality, but they are by-products of bimanual complementary tasks (i.e., cutting, defleshing), which reinforce our hypothesis.

The issue then, is to ascertain when handedness evolved in our hominin clade. Previous approaches to the question of hand laterality in our ancestors mostly focused on the hominin remains recorded from certain sites. Such is the case ~~of~~ in the dental-wear studies ~~of~~ with the so-called use of the third hand ("stuff and cut") in some of the pre-Neanderthal individuals deposited at the Sima de los Huesos site (Atapuerca, Spain) (Bermúdez et al., 1988, 2003; Lozano et al., 2009). Other studies have centred on the endocrania (Poza-Rey, 2015), humerus and other limb bones (Carretero, et al., 1997; Lazenby, 2002; Shaw, 2011). All these studies point to a similar handedness in Neanderthals as is found in modern humans (Frayer et al., 2010; Fiore et al., 2015). For its part, the pre-Neanderthal population of Sima de los Huesos (until recently, *Homo heidelbergensis*) from 450,000 years ago, is under debate: some researchers find evidence~~s~~ enough to interpret a similar pattern as in modern humans (Frayer et al., 2012), and others find no~~t~~ well-defined brain lateralization (Poza-Rey et al., 2015).

In fact, the relation between brain asymmetry and hand laterality is not definitively solved (see Poza-Rey et al., 2015 for debate), and even just at the paleoanthropological level we may obtain divergent results. As mentioned, several studies pointed out that hand laterality (right-handedness) of Sima de los Huesos hominins may be identified in five ~~5~~ individuals by means of labial striations of the frontal dentition (Bermúdez et al., 1988; 2003; Lozano et al., 2009). However, in their recent publication on skulls from

Sima de los Huesos (Atapuerca, Spain), Poza-Rey and colleagues (2015) have compared these data with the brain endocasts asymmetries found in four of the skulls to which some of that dentition belongs: crania/endocrania 16, 10, 9 and 6. Individual 16 and 6 did not show a right-handed manual preference in their endocasts asymmetries, but individual 16 shows dental striations to the left, while individual 6 shows dental striations to the right. Individuals 10 and 9 demonstarated right-handed manual preferences in their endocasts asymmetries, both associated with dental striations to the right. The authors suggest that the discrepancy obtained in individual 6 may be the result of ambidextrous handedness, but also a product of learning by imitation.

Anyway, hominin remains are scarce in the archaeological record, and they do not always include the body parts that give us information on this matter. Tests have been carried out on the direction and trajectory of the cut-marks accidentally left on bone surfaces by the stone tools used by hominins when processing prey for consumption (Bromage and Boyde, 1984; Bromage et al., 1991;). However, the results of this method have been also contested (Pickering et al., 2008).

For this study we have used the only remains that appear commonly at the majority of Pleistocene archaeological sites: stone tools. Because they are the most abundant remains at this type of sites, they can be an excellent source of information.

One approach that uses stone tools is use-wear analyses, the study of the use-wear developed along the edges of stone tools during use. Use-wear studies have revealed that one of the pre-Neanderthals that used tools to cut the meat off a carcass at the Middle Pleistocene Acheulean site of Galería (Atapuerca, Spain) was right-handed

(Ollé, 2003). This type of study can be successful in identifying the hand preference of the user, but the approach requires that the tools themselves were both sufficiently used and well preserved.

Determining hand laterality through the technical study of flakes has been approached from two different perspectives: the knapping method used to produce the flakes (Toth, 1985), and the analyses of a single technical feature (Rugg and Mullane, 2001; Domínguez-Ballesteros and Arrizabalaga, 2015). Both of these approaches have been discussed and their results questioned because of the methods used (see Patterson and Sollberger, 1986, and Pobiner, 1999 for Toth, 1985, and Bargalló and Mosquera, 2014 for Rugg and Mullane, 2001).

In this paper, we apply the method we previously published, on how to identify handedness through the technical features of the flakes obtained by a knapper (Bargalló and Mosquera, 2014), with the aim of finding out how many flakes produced by a single Pleistocene knapper are needed to ascertain his/her hand preference. As mentioned previously, the benefit of this method is that it can potentially be applied to the majority of archaeological sites.

To do this, we selected two Spanish sites: Gran Dolina-TD10.1 (Atapuerca) and Abric Romaní (Barcelona), which were occupied by pre-Neanderthal and Neanderthal populations, respectively. In both species, the handedness of some individuals has been identified, so this study serves to both confirm the previous results and to test the reliability of this method when applied to older sites and hominin species, until the first hominin species that was completely lateralised is found, as well as any evolution in that process. Furthermore, given that the TD10-1 archaeological record was made by pre-Neanderthal populations peri-contemporary to that of SH, our results may provide more evidence on the current debate.

Method

In Bargalló and Mosquera (2014) we presented a new method for inferring handedness from lithic evidence. The study was conducted by means of an experimental programme in stone knapping, after which the resulting lithic flakes were analysed. These flakes were produced by 15 inexpert knappers (eight right-handed and seven left-handed), because we were not able to find a statistically significant number of left-handed expert knappers. We considered inexpert knappers to include individuals who had never struck two pebbles together, as well as individuals who were quite familiar with prehistoric tools and had had some degree of practice. Importantly, the Mann-Whitney U test proved that all of them produced flakes with the same technical features concerning handedness, meaning that, within this sample group, expertise was not a factor that affected the presence or absence of these technical features analysed to determine hand laterality. On the contrary, expertise clearly affects the quality of the flakes in technological terms (i.e., longer, sharper edges, regular morphologies, etc.). The results of the experiment indicate that no single variable can be used to determine the laterality of the knapper, but instead this requires a combination of several variables. Furthermore, not all flakes display the entire set of significant features. The conclusion of this study is, therefore, that it is not possible to determine the hand preference of a knapper through a single variable present on their flakes, but it may be possible to determine his or her laterality by examining a combination of technical variables on a number of their pieces.

Experimental sample

The experimental sample corresponds to that published by Bargalló and Mosquera (2014). This experimental sample included 1,774 pieces knapped by seven left-handed and eight right-handed individuals. Of these, 1,159 were flakes and broken flakes, and 615 were fragments of flake and angular knapping fragments. The latter were not analysed, since they did not retain the necessary technological features. Of the 1,159 flakes and broken flakes, 629 (54.23%) were produced by right-handers and 530 (45.76%) by left-handers. The knapper who produced the fewest flakes made 49 pieces, and the knapper who generated the most flakes made 140 (Table 1). All the flakes were created from the same type of flint as used by *H. neandertalensis* at the Abric Romaní site (Barcelona, Spain) (Gómez de Soler, 2007; Carbonell, 2012; Soto et al., 2014).

Table 1

Handedness analysis

According to Bargalló and Mosquera (2014), only eight technical features from the complete catalogue of characteristics are informative to ascertain the hand laterality of the knapper. However, given that many pieces do not show the eight technical features indicative of hand preference, and also that the technical characteristics of a single piece may be the result of chance, a number of flakes knapped by the same individual must be analysed (Figure 1).

Figure 1

The following are the eight technical features and their variables (*n*=21) that provide information about handedness:

a) Ventral surface:

1. Location of the ridge on the bulb, recorded by Rugg and Mullane (2001) as "skew". This small ridge starts at the impact point and runs along the cone of percussion, the proximal part of the whole bulb. It may be located to the right or left.
2. Location of the éraillure scars on the cone. These are small squamae that sometimes accidentally appear in the bulb. If present, they may be centred, or located to the right or left.
3. Location of the hackles. Small hackles may appear near the edges of the ventral surface. They may be distal, right or left located.
4. Location of the ripples. Long curved wrinkles that appear along the ventral surface and follow the detaching axis of the flake. They may be located distally, or to the right or left.
5. Orientation of the extracting axis of the flake. This may be right or left-oriented

b) Striking platform:

1. Location of the impact point on the striking platform. This may be right or left located.
2. Inclination of the striking platform. It may be to the right, left, or sinuous

3. Morphology of the striking platform. This may be platform (plan), linear (lineal), or punctiform (pointed).

Figure 2

The correspondence analyses performed at Bargalló and Mosquera (2014) (Figure 2) showed that these features clearly allow the right-handed and left-handed knappers from the experiment to be distinguished. The first two factors explain 55.56% of the variability (factor 1:36.57%, factor 2:18.99%). In Figure 2 all the left-handed knappers are placed above factor 2, and the right-handed knappers are placed below factor 2. Therefore, left-handed knappers tend to produce ripples (39.39%), hackles (31.79%), the ridge of the cone of percussion (42.41%), the éraillure scars (15.67%), and the impact points (88.34% of the total relative inertia) on the left side of the flake. Interestingly they also tend to detach flakes with the striking platform sloped towards the right side of the piece (33.81% of the total relative inertia). In contrast, right-handed knappers tend to form ripples (36%), hackles (29.49%), the ridge of the cone of percussion (49.59%), the éraillure scars (25.78%), and the impact points (49.58% of the total relative inertia) on the right side of the flake. As opposed to left-handers, right-handed knappers tend to detach flakes with the striking platform sloped towards the leftside of the piece (45.89% of the total relative inertia).

This work is based on the fact that the patterns of the experimental knappers help us identify the handedness of prehistoric knappers, as the archaeological samples are expected to follow the same patterns as the experimental ones (Figure 2).

Refit analysis

In order to apply this method to the archaeological record, we need to find flakes detached by the same knapper. This can only be achieved by means of searching refits from knapping sequences of cores, which is a rather complicated process in many archaeological deposits. Although refits do not fully guarantee that only one knapper exploited one core, it is the best approach under the circumstances. Therefore, the first step is to search for as many refits as possible in archaeological samples.

In this study, we only analysed archaeological pieces longer than 10 mm. Depending on the type of raw material, the archaeological assemblage needs to be classified into Raw Material Units (RMU; Roebroeks, 1988; Schäfer, 1990; Odell, 2004; Vaquero, 2008) and Minimum Analytical Nodules (MAN) (Bleed, 2004; Hall, 2004; Larson, 2004; Odell, 2004; Copper and Qiu, 2006). RMU are the blanks from which one, two or several cores may be exploited by different knappers. For example, these may be big blanks of flint that are fragmented in order to allow the knappers to take a piece and start the process of stone tool production. Archaeologically, we are unlikely to obtain the entire refit of the blank, since they were often large fragments selected, transported, knapped, abandoned, reused, and so on. Only workshops provide the chance of refitting a whole RMU. For their part, the MAN are each of the cores knapped. For example, a cobble knapped into a discoid is one MAN, as is each of the flint-knapped fragments from the abovementioned blank. Archaeologically, MAN are easier to complete by refitting than RMU, although the occupational traits of the sites, their post-depositional conditions, as well as the area excavated usually make this task difficult. Although theoretically the distinction between RMU and MAN is clear, archaeologically it is not always easy to determine whether a particular variety of raw material belongs to a RMU or a MAN. Therefore, throughout this work we will use the general term RMU. Both RMU and MAN allow us to identify the single cobbles/blanks from which the flakes were detached, and indeed, the single knapping events. Associating flakes into RMU and MAN is based on the macroscopic features of the artefacts (e.g., grain-size and colour of the cortical and non-cortical surface, internal inclusions such as microfossils, fractures, and veins) (Schäfer, 1990; Roebroeks, 1998; Odell, 2004; Vaquero, 2008).

Once the pieces have been grouped into RMU and/or MAN, the refitting process begins. There are ~~3~~ three types of refits: flakes detached in production/knapping sequences (refits sensu stricto), breakages (conjoins), and modifications (small pieces detached when retouching a flake) (Cziesla, 1990). In this study, only flakes coming from production sequences (refits) have been used, and only those that refit together.

Data analysis

In this study, we applied a multivariate statistical analysis (Correspondence analysis) using the program PAST (Paleontological Statistics Software) to identify the hand laterality of prehistoric knappers by comparing them with the experimental sample (Hammer, Harper and Ryan, 2001, 2008). More conventional, classification methodologies were also considered and evaluated using the experimental data. Specifically, we fitted our data with a Binary Logistic Regression and applied a simple

Machine Learning algorithm (i.e., k- nearest neighbours). In both cases, the performance of the resulting classifiers could not significantly outperform the null model (i.e., random laterality attribution).

Archaeological Material

Gran Dolina TD10.1 (Atapuerca, Spain)

Gran Dolina is one of the ~~cavities~~ caves located at Sierra de Atapuerca, in the north of the Iberian Peninsula, near the city of Burgos. It is filled with 18 m of sediments divided into 11 lithostratigraphic units named TD1 to TD10, from bottom to top, and with a chronology ranging from the Early to Middle Pleistocene (Berger et al., 2008; Falguères et al., 2013; Arnold et al., 2014; Arnold and Demuro, 2015). In this work, we looked at the lithic remains of subunit TD10.1, which has a mean date of 244 - 337±29 ka (Falguères et al., 1999, 2013; Berger et al., 2008; Rodríguez et al., 2011), but may be closer to 350 ka (Moreno et al., in press).

Up to now, TD10.1 has been the richest subunit of not only Gran Dolina, but all the Sierra de Atapuerca sites, both in terms of lithic and faunal remains. The subunit has yielded roughly 21,000 lithic artefacts and 48,000 faunal remains, most of them near the north and east sectors of the excavation (Ollé et al., 2013). The lithic remains probably represent the local-scale evolution from Mode 2 to Mode 3 technology at Sierra de Atapuerca. While the lithic remains from upper TD10.1 show features typical of the

Mode 2 to Mode 3 transition, the main archaeological assemblage of this subunit comprises centripetal cores, with diverse and standardised reduction sequences aimed at obtaining small and medium-sized flakes, and a number of Levallois cores combined with typical Mode 2 elements, such as large cutting tools (Rodríguez-Álvarez, 1997; Carbonell et al, 2001; Rodríguez-Álvarez, 2004; Ollé et al., 2013).

Up to now, 42 RMU of quartz (*n*=215), and 148 RMU of quartzite (*n*=869) have been identified from subunit TD10.1. From among these, it has been possible to identify 15 quartz connections (seven refits and eight conjoins), and 72 quartzite connections (38 refits and 34 conjoins) (López-Ortega et al, 2015). Of these, 80 flakes and broken flakes of quartzite, belonging to 34 refit groups, are useful for our purposes (Figure 3). Two to five refitting flakes form most of these groups. This means that we have as many as ~~5~~ five flakes produced by a single knapper.

Figure 3

Abric Romaní (Barcelona, Spain)

The Abric Romaní rock shelter is located in the NE of the Iberian Peninsula, approximately 50 km west of Barcelona. The site is located in the town of Capellades, in the tufa formations that rise on the right bank of the Anoia River. The stratigraphy is composed of 20 m of well-stratified travertine sediments dated by U-Series as being between 40 and 70 ka (Vaquero et al., 2013).

The archaeological units tested for this study are levels J and M, aged between 45 and 54 ka, which also show well-defined discrete accumulations (Vaquero and Pastó, 2001). Technologically, the lithic assemblage of both levels J and M correspond to Mode 3, here characterised by discoid and expeditious knapping methods.

Level J has yielded 7,000 lithic artefacts, and 8,460 faunal remains. There are two main archaeostratigraphic units: sublevels Ja and Jb, which have been distinguished only in the central area of the occupation. The U-series dates are *c*. 49 ka BP for the overlying tufa (49.3 ± 1.6 and 49.2 ± 2.9 ka BP) and around 50 ka BP (50.0 ± 1.6 and 50.8 ± 0.8 ka BP) for the underlying tufa (Bischoff et al., 1988). In addition, a charcoal sample has been dated as 47.1 ± 2.1 ^{14}C ka BP (NZA-2316) (Vaquero et al., 2012). According to the refits and the macroscopic characteristics of the raw materials, more than 500 RMU have been identified, each corresponding to a singular technical event. Moreover, 262 refitting groups, totalling 719 artefacts, have been found. In addition, level J has also yielded 50 hearths that seem to have spatially structured the site.

The tufa layer immediately above level M is dated at around 51.8 ± 1.4 ka BP (Bischoff et al., 1988; Vallverdú et al., 2012). The number of recorded archaeological remains is 18,946, of which 7,614 are faunal remains, 6,084 are lithic remains, 114 are wood imprints, 260 charcoal fragments and 37 hearths. In level M it has been possible to identify 76 RMU (under study). Moreover, 216 refitting groups, totalling 827 artefacts, have been found.

We have selected the refit groups with the most connecting flakes from a single core (MAN): one refit group from level Ja and seven refit groups from level M. All of them are flint. The smallest refit comprises ~~5~~ five flakes (AR3), while the largest is made up of 36 flakes (AR8) (Figure 4).

Figure 4

Results

The total sample set analysed comprised 1,355 flakes and broken flakes. Of these, 80 are from Gran Dolina (level TD10.1), 116 from Abric Romaní (level Ja and M) and 1,159 are from the experimental programme. Of the 1,355 pieces, 971 were complete flakes and 384 were broken flakes.

Tables 2 and 3 show the frequency at which the technical features of hand preference appear in the experimental sample together with Abric Romaní refit groups (Table 2), and Gran Dolina refit groups (Table 3). Interestingly, there are differences between the archaeological and experimental samples: 63% of the variables included in the technical features were not identified in any of the 80 flakes from level TD10.1 of Gran Dolina, and 27% of these variables were not identified in any of the 116 flakes from Abric Romaní. In contrast, just 3.26% of the variables could not be identified in any of the 1,159 experimental flakes. Furthermore, two variables of the technical features were not identified in any of the 196 archaeological flakes analysed: the distal location of hackles, and the sinuous inclination of the striking platform. Both these variables tended to appear in low frequencies in the experimental sample. Therefore, and taking into account the figures, it is likely that the presence/absence of some of the variables is directly linked to the number of flakes analysed: the more flakes detached by a single knapper, the more the possibilities of them containing all the variables included in each technical feature. The frequencies of each technical feature will be used in the correspondence analysis to identify the hand laterality of prehistoric knappers.

Table 2

Table 3

In order to ascertain the minimum number of flakes required to identify at 100% confidence the hand laterality of the knapper, we first performed a correspondence analysis, including all the archaeological and experimental samples. Figure 5 shows all the samples, and the way the archaeological groups of refits are located around the experimental ones. Compared to Figure 2 (only experimental samples) we can see that both left- and right-handed experimental knappers situate closer, concentrate, hence losing their spatial variability. This is probably because there are too few flakes in some of the archaeological refits, some of them having just two or three refit flakes.

Figure 5

Because of this distortion in the distribution pattern of the experimental groups, a second correspondence analysis was undertaken, this time excluding all archaeological refit groups with less than five flakes. By doing this we lose most of the Gran Dolina refit groups, since just one (GD29) comprises five flakes. Figure 6 shows the distribution of all the remaining samples, which is more similar to the experimental-only pattern (Figure 2). Although the relative position of the right- and left-handed samples is correct (right-handers above the X axis, left-handers below), the experimental samples maintain the distorted pattern, particularly the position of the sample R-Nu (a right-handed participant), which is below the X axis, in a similar position to some of the left-handed participants. In other words, individual R-Nu locates outside the sector of her true hand preference. This means that although better, this sampling is not selective enough to give a perfect fit to the experimental, real pattern. In summary, analysing five flakes may lead to a false positive result.

Figure 6

However, given that few flakes make up most of the archaeological samples (Figure 3 and 4) we decided to perform a series of new simulations involving downscaled experimental samples, instead of removing archaeological groups from the analysis. As Table 1 shows, the number of flakes per group from the experimental sample ranged between 47 and 140 flakes. Consequently, we downscaled each experimental group of refits to fewer flakes per knapper. This simulation was made by taking the median of each variable, preserving the weight of each technical feature from the original distribution pattern. We reduced the experimental sample to five flakes (Figure 7a), six flakes (Figure 7b), seven flakes (Figure 7c), and eight flakes per knapper (Figure 7d), the last group showing the same pattern between the downscaled experimental subsamples and the original experimental sample group. Therefore, eight is the minimum number of flakes required to identify the hand laterality of a knapper above a confidence level of 93.75%.

These simulations allowed us to obtain the confidence rate for each downscaling of the experimental sample. As Figure 7a shows, the distribution pattern of the downscaled experimental subsample is quite similar to the pattern of the original experimental sample (Figure 2). An analysis of ~~5~~ five flakes entails only a 73.33% probability of correctly targeting the hand laterality of the knapper, since groups of five flakes fail to achieve their correct position in the plot: individuals L_Et, L_4, L_3, R_4 and R_3 are positioned outside the sector of their true hand preference, when analysing just ~~5~~ five flakes. Actually, these individuals are showing false positives. Besides, the margin of success is greater for the right-handed population (75%), than for the left-handed population (71.42%).

By analysing ~~6~~ six flakes (Figure 7b) we still have some individuals that are positioned outside the sector of their true hand preference. These individuals are R-Mn, L_1, L-2, L-3, L-4. Interestingly, by analysing six flakes (Figure 7b) the probability of correctly identifying the hand preference of the sample reduces to 66.66%, even though with this number the probability of correctly assigning right-handers is higher (87.5%, with left-handers being only 42.85%). Nevertheless, by analysing seven flakes the improvement in the results is notable, since the probability of targeting the hand preference of the knapper rises to 93.33% (Figure 7c). In this case, only one group of flakes (L_3) belonging to a left-handed knapper is wrongly positioned as a right-handed individual. Therefore, the margin of error, the probability of a false positive has decreased to 6.66%. Finally, analysing eight flakes per knapper guarantees the correct distribution of the experimental population with regard to their hand preference (Figure 7d), above a confidence level of 93.75%.

Figure 7

With this information, we looked once again at the archaeological sample group using refits formed by eight or more flakes. Only five groups of refits fulfil this condition, all from the Abric Romaní site: one from level Ja (sample AR1), and 4 four from level M (samples AR5; AR6; AR7; AR8). Figure 8 shows the distribution of these samples, where all the archaeological groups fit the right-handed pattern of knappers, similar to that of the experimental participant R_A_B. However, experimental right-handed knapper R_Nu appears in the area of left-handed knappers, showing a false positive. This false positive means that there is still a small margin of error (6.66%). This fact particularly affects the archaeological group of refits AR5, nearest the X axis, which varies its position depending on whether the experimental knapper R_Nu is included in (Figure 8), or excluded from (Figure 9) the analysis. In the first case, AR5 appears as a right-handed knapper; in the second case, she is left-handed.

Figure 8

Figure 9

In summary, right-handed Neanderthals knapped four of the five groups of flakes detached at Abric Romaní with about 94% level of certainty, while one remains difficult to assign to a group. In Gran Dolina-TD10-1, only one group of flakes (GR29) contains enough information to be 73.33% certain that they were produced by a right-handed knapper.

Discussion

The aim of this paper is to apply a method to the archaeological record that allows us to identify the hand laterality of our ancestors, and discern when and how this feature, which is most prominent in humans, appeared in our evolutionary history. The importance of this issue lies in the organisation of the brain, where our motor, sensory and cognitive functions are structured accord with this laterality.

Previous approaches to the hand laterality of our ancestors have mainly involved the hominin remains found at certain sites. However, these remains are scarce and do not always include the body parts that provide information on this question. Other approaches using stone tools, such as use-wear analysis, have been successful, but require the tools to have been both used sufficiently and be well preserved. Other proxies drawn from the study of single technological features of flakes (i.e., Toth, 1985; Rugg and Mullane, 2001; Domínguez-Ballesteros and Arrizabalaga, 2015) have been questioned from the beginning by authors such as Patterson and Sollberger (1986), Pobiner (1999), and Bargalló and Mosquera (2014). These papers discuss the reliability of finding out the hand preference of one individual by using only one technical feature.

The study presented here applies a previously published method (Bargalló and Mosquera, 2014), which deals with handedness in human evolution by analysing a combination of certain technical features of the most widely-produced stone tools in the Pleistocene world: flakes. We used a multivariate statistical analysis (Correspondence analysis), since alternative classification methodologies (i.e., Binary Logistic Regression and applied a simple Machine Learning algorithm) could not significantly outperform the null model (i.e., random laterality attribution).

The selected method requires flakes produced by the same knapper, meaning that these flakes must be identified from the archaeological assemblage. It is quite difficult to isolate an individual knapping event in an archaeological assemblage, given that most archaeological levels are actually palimpsests. Preliminary archaeostratigraphic approaches to isolating the remains of each living floor, and a subsequent search for refits, are required to identify singular events (Lucas, 2005; Bailey, 2007; Bargalló et al., 2015; Machado et al., 2015). Because these singular knapping events may involve more than one core (Vaquero, 2008), it is necessary to identify a unique core and the flakes that refit one another. However, ethnographic records show that different knappers (Stout, 2002; Bril et al., 2005) may have worked on the same core. Nevertheless, the archaeological lithic samples we used in this study have the following characteristics: 1) all the archaeological groups of refits are formed by relatively few pieces, never exceeding forty flakes, and 2) the technical features of the flakes are completely homogeneous within each group of refits, suggesting that they were all produced by the same person.

The matter of how much raw material may condition the analysis has been solved by selecting archaeological refit groups of quartzite for Atapuerca and flint from Abric Romaní. Both rock types were frequently used in prehistory, as well as at each of these sites, and they are good quality materials, retaining the maximum number of technical features produced by the knapping process, unlike quartz, where the large crystal structures makes it difficult to preserve many striking platforms (de Lombera-Hermida, 2009).

In addition, this paper also highlights other potential uses of refit studies. Until now, they have been used to analyse the spatial distribution of remains within occupations; to understand the way the tools were produced; to identify how hominins organised the tasks performed inside the settlements; and to identify the movements of the individuals within these activity areas (Cahen et al., 1979; Hofman, 1981; Bodu et al., 1990; Ashton, 2004; Turq et al., 2013). Now, refits can also be used to facilitate the identification of individuals and provide an understanding of their technological cognition.

In this sense, studying the handedness of the fossil hominins is not mere "storytelling", providing anecdotal information, but the information may help us understand the development of the complex brain organisation during human evolution, and to discover how individuals engaged within their communities. In the words of Foulds: "…this is a reference to an individual agent within a wider society founded on the social relationships that they both create and maintain, irrespective of how they conceived of themselves" (Foulds, 2014: 13).

Conclusions

The minimum number of flakes necessary to successfully identify hand laterality at about 94% of confidence is eight. They must be produced by the same knapper, and the only way to ensure this from the archaeological record is to find eight flakes that refit one other because they were produced from a single core-knapping event. In addition, there is no single technical feature that provides information about hand preference, but instead there is a combination of eight technical features, located on the striking platforms and the ventral surfaces. Raw material is not relevant in the case of the most-widely used rocks in Europe, flint and quartzite, since the majority retain the technical features required for analysis. The exception to this is quartz, where many flakes from the striking platform are lost during the percussion. Expertise is not an issue either, since the technical features analysed here correlate only with handedness, and not the technical quality of the tools (Bargalló and Mosquera, 2014).

Our results indicate that just one pre-Neanderthal knapper from TD10.1 at Gran Dolina (Atapuerca) may be suitable for analysis, since only one refit group containing ~~5~~ five quartzite flakes was found. It has been ascertained with a 73.3% confidence rate that this individual was right-handed. The Abric Romaní Neanderthal knappers provide us with better results. Levels Ja and M yielded five refit groups made up of more than eight flakes, allowing us to clearly distinguish the presence of four right-handers, with the hand preference of one remaining unclear.

Even though eight flakes is a relatively low figure, this number is still quite difficult to obtain at many archaeological sites. This is the case of Gran Dolina-TD10.1, which up to now has yielded 29 groups of quartzite refits from knapping sequences, none of which exceeds ~~5~~ five flakes. Nevertheless, these figures may increase in the near future, and more success may be seen when applying the method to the Neogene chert assemblage, which is much more numerous, but also much more difficult to refit, due to the poor preservation of this rock type.

The possibility of identifying the handedness of our ancestors, in this case from 300 ka and 50 ka ago at Gran Dolina-TD10.1 and Abric Romaní, respectively, signifies a big step forward in the field of human evolution, no matter the age of the samples. Further study should eventually allow us to fix the time when handedness arose and, by extension, know at what point brain laterality developed in humans at both the individual and population levels, as well as which hominin species were partially or totally lateralised. It is possible that our earliest ancestors started to display handedness, but perhaps more sporadically, as seen in living chimpanzee populations. We will also be able to understand the progression of this cognitive feature through our phylogeny, and whether it was a progressive change or one that appeared suddenly. In addition, we will be able to study the role that social and cultural environments may have played in the evolution of this characteristic. Our method ensures this goal through studying the knapping activities of our ancestors, one of the best-recorded tasks with well-preserved remains.

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Figure legends

Figure 1: Technical features analysed. Top: technical features present on the flakes. Bottom: possible locations of the ridge of the bulb, the éraillure scars, hackles, ripples, inclination of the extraction axis, inclination of the striking platform and the type of striking platform.

Figure 2: Correspondence analysis of the experimental sample: left-handed knappers (L-x) are located above factor 2, while right-handed knappers (R-x) are located below this. All the samples are represented by triangles.

Figure 3: Left: Complete and broken flakes belonging to 34 groups of refits found ~~from~~ in level TD10.1 at the Gran Dolina site (Sierra de Atapuerca, Spain). Right: Archaeological refit groups GD8 and GD2 (photographs from López-Ortega, 2015).

Figure 4: Top: Complete and broken flakes belonging to eight groups of refits selected from levels Ja and M from the Abric Romaní Neanderthal site (Barcelona, Spain). Bottom: Archaeological refit groups AR1 (photograph from Vaquero et al., 2012) and AR8 (photograph by F. Romagnoli).

Figure 5: Correspondence analysis of the entire set of experimental and archaeological samples. Triangles: experimental refit groups. + : refit groups from TD10.1, Gran Dolina (*GD*). Circles: refit groups from levels Ja and M, Abric Romaní (*AR*). (Axis 1= 19.7% eigenvalue; Axis 2= 16.86% eigenvalue). The two axes represent 36.56% of the total.

Figure 6: Correspondence analysis of the experimental and archaeological samples, selecting just the archaeological refit groups with five or more flakes. Triangles: experimental refit groups. +: the only refit group from TD10.1 (*GD29*) with five flakes. Circles: the eight refit groups from Abric Romaní (*AR*) with five or more flakes (Axis 1= 28.36% eigenvalue; Axis 2= 18.63% eigenvalue). The two axes represent 46.99% of

the total. Shadowed individual (R_Nu) is positioned outside the sector of her real hand preference.

Figure 7. Correspondence analysis of the experimental sample downscaled to “n” flakes per knapper. Triangles: right-handed knappers, both for the original experimental sample (R_”x”) and the subsample downscaled to “n” flakes (R_”n”). +: left-handed knappers, both for the original experimental sample (L_”x”) and the subsample downscaled to “n” flakes (L_”n”). **7a.** Downscaling the experimental subsample to five flakes (Axis 1= 28.49% eigenvalue; Axis 2= 18.53% eigenvalue). The two axes represent 47.02% of the total. **7b.** Downscaling the experimental subsample to six flakes (Axis 1= 28.56% eigenvalue; Axis 2= 17.11% eigenvalue). The two axes represent 45.66% of the total. **7c.** Downscaling the experimental subsample to seven flakes (Axis 1= 28.49% eigenvalue; Axis 2= 15.83% eigenvalue). The two axes represent 45.66% of the total. **7d.** Downscaling the experimental subsample to eight flakes (Axis 1= 26.65% eigenvalue; Axis 2= 17.76% eigenvalue). The two axes represent 44.41% of the total. Shadowed samples are outside their real handedness position.

Figure 8: Correspondence analysis. Triangles: experimental subsample downscaled to eight flakes. Circles: the only five archaeological refit groups with eight or more flakes, all from the Abric Romaní site. Experimental knapper R_Nu (shadowed) is outside her real hand preference position (Axis 1= 30.93% eigenvalue; Axis 2= 17.03% eigenvalue). The two axes represent 47.96% of the total.

Figure 9: Correspondence analysis. Triangles: experimental subsample downscaled to eight flakes, without the knapper R_Nu. Circles: the five archaeological refit groups with eight or more flakes from Abric Romaní. (Axis 1= 29.64% eigenvalue; Axis 2= 18.11% eigenvalue). The two axes represent 47.75% of the total.

Table legend

Table 1: Number of flakes and broken flakes knapped by each participant during the experimental programme.

Table 2: Frequency of the technical features involved in handedness. The table includes the experimental and archaeological samples from Abric Romaní refit groups (AR). R_"x" and L_"x": refit groups of right- and left-handed experimental knappers, respectively.

Table 3: Frequency of the technical features involved in handedness. The table includes the experimental and archaeological samples from Gran Dolina-TD10.1 level (GD).

IN PURSUIT OF OUR ANCESTORS' HAND LATERALITY

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Abstract

The aim of this paper is to apply a previously published method (Bargalló and Mosquera, 2014) to the archaeological record, allowing us to identify the hand laterality of our ancestors and determine when and how this feature, which is exhibited most strongly in humans, appeared in our evolutionary history. The method focuses on identifying handedness by looking at the technical features of the flakes produced by a single knapper, and discovering how many flakes are required to ascertain their hand preference.

This method can potentially be applied to the majority of archaeological sites, since flakes are the most abundant stone tools, and stone tools are the most widespread and widely-preserved remains from prehistory. For our study, we selected two Spanish sites: Gran Dolina-TD10.1 (Atapuerca) and Abric Romaní (Barcelona), which were occupied by pre-Neanderthal and Neanderthal populations, respectively.

Our analyses indicate that a minimum number of ~~8~~ eight flakes produced by the same knapper is required to ascertain their hand preference. Even though this figure is relatively low, it is quite difficult to obtain from many archaeological sites. In addition, there is no single technical feature that provides information about handedness, instead

there is a combination of ~~8~~ eight technical features, localised on the striking platforms and ventral surfaces. The raw material is not relevant where good quality rocks are used, in this case quartzite and flint, since most of them retain the technical features required for the analysis. Expertise is not an issue either, since the technical features analysed here only correlate with handedness (Bargalló and Mosquera, 2014). Our results allow us to tentatively identify one right-handed knapper among the pre-Neanderthals of level TD10.1 at Gran Dolina (Atapuerca), while four of the five Neanderthals analysed from Abric Romaní were right-handed. The hand preference of the fifth knapper from that location (AR5) remains unclear.

Keywords: Hand laterality, flakes, lithic technology, Atapuerca, Abric Romaní

Introduction

Laterality is the preference that living beings display for one half of the body over the other. This organisation settles in the structure of the brain, the organ that designates the role played by each extremity when performing a task.

Hand laterality is well known in our species, *Homo sapiens* ~~*sapiens*~~. ~~*sapiens*~~ Various studies point to about 97% of the current population being lateralised, among which between 85% and 90% of individuals are right-handed, and between 10% and 15% are left-handed, depending on whether the communities are preindustrial, illiterate, and so on (Annett, 2002; Uomini, 2009). Hand laterality in apes has also been studied (Hopkins, 1996; McGrew and Marchant, 1997, 2001; Hopkins and Cantalupo, 2005),

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but it is less marked than human handedness and depends on several environmental and social conditions (Mosquera et al., 2007; Llorente et al., 2009, 2011). According to Llorente and colleagues: "…there must have been continuity in the evolution of handedness, at least between apes (chimpanzees) and the hominin family" (2011:569. Translated by us). However, the subject is not as straightforward as simply being right- or left-handed, since some studies have highlighted the fact that chimpanzees become more and more lateralised as the task to be done becomes increasingly complex. This condition also leads to an increase of in their technological behaviour, which has been interpreted as a landmark in the evolution of our hominin clade (Mosquera et al., 2012).

In fact, some researchers support that the most widespread tasks undertaken by humans are those where both hands play different roles: e.g., cutting, where one hand holds the matter to be cut, and the other uses the knife to do the actual cutting. In addition, cutting is not usually needed in the world of apes (Schick and Toth, 2009), which may have marked a strong difference between their ancestors and hominins. These type of tasks are also known as bimanual complementary tasks (McGrew and Marchant, 1999), bimanual complex tasks (Hopkins et al., 2004), and complementary role differentiation tasks (Uomini, 2009), which are indeed the most complex, as well as the most lateralising tasks, as demonstrated by Uomini (2009) in her experimental study with humans (Uomini, 2009). This point of view interpretation has led to the view that there is a feedback mechanism in the origin of handedness, where the recurring use of one hand gives it more skills compared with the other, in turn favouring the preferential use of the "skilled" hand. Both skill and practice reinforce handedness, a trait that may have favoured brain lateralisation (Teixeira and Okazaki, 2007). From a phylogenetic point of view, hand laterality may have been on the increase since the earliest hominins, as far

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back as *Australopithecus* (Mosquera et al., 2012). In this sense, cut-marks found at Dikika (Ethiopia) from 3.3 my ago (McPherron et al., 2010) do not inform us about hand laterality, but they are by-products of bimanual complementary tasks (i.e., cutting, defleshing), which reinforce our hypothesis.

The issue then, is to ascertain when handedness evolved in our hominin clade. Previous approaches to the question of hand laterality in our ancestors mostly focused on the hominin remains recorded from certain sites. Such is the case of in the dental-wear studies of with the so-called use of the third hand ("stuff and cut") in some of the pre-Neanderthal individuals deposited at the Sima de los Huesos site (Atapuerca, Spain) (Bermúdez et al., 1988, 2003; Lozano et al., 2009). Other studies have centred on the endocrania (Poza-Rey, 2015), humerus and other limb bones (;Carretero, et al., 1997; Lazenby, 2002; Shaw, 2011). All these studies point to a similar handedness in Neanderthals as is found in modern humans (Frayer et al., 2010; Fiore et al., 2015). For its part, the pre-Neanderthal population of Sima de los Huesos (until recently, *Homo heidelbergensis*) from 450,000 years ago, is under debate: some researchers find evidences enough to interpret a similar pattern as in modern humans (Frayer et al., 2012), and others find not well-defined brain lateralization (Poza-Rey et al., 2015).

In fact, the relation between brain asymmetry and hand laterality is not definite definitively solved (see Poza-Rey et al., 2015 for debate), and even just at the paleoanthropological level we may obtain divergent results. As mentioned, several studies pointed out that hand laterality (right-handedness) of Sima de los Huesos hominins may be identified in five 5 individuals by means of labial striations of the frontal dentition (Bermúdez et al., 1988; 2003; Lozano et al., 2009). However, in their recent publication on skulls from Sima de los Huesos (Atapuerca, Spain), Poza-Rey and colleagues (2015) have ~~crossed~~ compared these data with the brain endocasts asymmetries found ~~at~~ in ~~4~~ four of the skulls to which some of that dentition belongs ~~to~~: ~~C~~crania/endocrania 16, 10, 9 and 6. Individual 16 and 6 ~~showed at not~~ did not show a right-handed manual preference in their endocasts asymmetries, but individual 16 shows dental striations to the left, while individual 6 shows ~~the~~ dental striations to the right. Individuals 10 and 9 ~~resulted in~~ demonstarated right-handed manual preferences in their endocasts ~~asymmetires~~ asymmetries, both associated with ~~to~~ dental striations to the right. The authors suggest that the discrepancy obtained in individual 6 may be the result ~~fruit~~ of ambidextrous handedness, but also a product of learning by imitation (~~Poza-Rey et al., 2015: 11~~).

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Anyway, hominin remains are scarce in the archaeological record, and they do not always include the body parts that give us information on this matter. Tests have been carried out on the direction and trajectory of the cut-marks accidentally left on bone surfaces by the stone tools used by hominins when processing prey for consumption (Bromage and Boyde, 1984; Bromage et al., 1991;). However, the results of this method have been also contested (Pickering et al., 2008).

~~Furthermore, f~~ For this study we have used the only remains that appear commonly at the majority of Pleistocene archaeological sites: stone tools. Because they are the most abundant remains at this ~~these~~ type of sites, they can be an excellent source of information.

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One approach that uses stone tools is use-wear analyses, the study of the use-wear developed along the edges of stone tools during use. Use-wear studies have revealed that one of the pre-Neanderthals that used tools to cut the meat off a carcass at the Middle Pleistocene Acheulean site of Galería (Atapuerca, Spain) was right-handed (Ollé, 2003). This type of study can be successful in identifying the hand preference of the user, but the approach requires that the tools themselves were both sufficiently used and well preserved.

Determining hand laterality through the technical study of flakes has been approached from two different perspectives: the knapping method used to produce the flakes (Toth, 1985), and the analyses of ~~one~~ a single technical feature (Rugg and Mullane, 2001; Domínguez-Ballesteros and Arrizabalaga, 2015). Both of these approaches have been discussed and their results questioned because of the methods used (see Patterson and Sollberger, 1986, and Pobiner, 1999 for Toth, 1985, and Bargalló and Mosquera, 2014 for Rugg and Mullane, 2001).

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In this paper, we apply the method we previously published, on how to identify handedness through the technical features of the flakes obtained by a knapper (Bargalló and Mosquera, 2014), ~~to the archaeological record~~, with the aim of finding out how many flakes produced by a single Pleistocene knapper are needed ~~for the analysis~~ to ascertain his/her hand preference. As mentioned previously, the benefit of this method is that it can potentially be applied to the majority of archaeological sites.

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To do this, we selected two Spanish sites: Gran Dolina-TD10.1 (Atapuerca) and Abric Romaní (Barcelona), which were occupied by pre-Neanderthal and Neanderthal populations, respectively. In both species, the handedness of some individuals has been identified, so this study serves to both confirm the previous results and to test the reliability of this method when applied to older sites and hominin species, until the first hominin species that was completely lateralised is found, as well as any evolution in that process. Furthermore, given that the TD10-1 archaeological record was made by pre-Neanderthal populations peri-contemporary to that of SH, our results may ~~come to~~ provide more evidence~~s~~ ~~to~~ on the current debate.

Method

In Bargalló and Mosquera (2014) we presented a new method for inferring handedness from lithic evidence. The study was conducted by means of an experimental programme in stone knapping, after which the resulting lithic flakes were analysed. These flakes were produced by 15 inexpert knappers (~~8~~ eight right-handed ~~and~~ ~~7~~ seven left-handed), because we were not able to find a statistically significant number of left-handed expert knappers. We considered inexpert knappers to include individuals who had never struck two pebbles together, as well as individuals who were quite familiar with prehistoric tools and had had some degree of practice. Importantly, the Mann-Whitney U test proved that all of them produced flakes with the same technical features concerning handedness, meaning that, within this sample group, expertise was not a factor that affected the presence or absence of these technical features analysed to determine hand laterality. On the contrary, expertise clearly affects the quality of the flakes in technological terms (i.e., longer, sharper edges, regular morphologies, etc.). The results of the experiment indicate that no single variable can be used to determine the laterality

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Comment [A6]: Here is expert because we indicated that we were not find the left-handed expert knappers.

of the knapper, but instead this requires a combination of several variables. Furthermore, not all flakes display the entire set of significant features. The conclusion of this study is, therefore, that it is not possible to determine the hand preference of a knapper through a single variable present on their flakes, but it may be possible to determine his or her laterality by examining a combination of technical variables on a number of their pieces.

Experimental sample

The experimental sample corresponds to that published ~~in~~ by Bargalló and Mosquera (2014). This experimental sample included 1,774 pieces knapped by ~~7~~ seven left-handed and ~~8~~ eight right-handed individuals. Of these, 1,159 were flakes and broken flakes, and 615 were fragments of flake and angular knapping fragments. The~~se~~ latter were not analysed, since they did not retain the necessary technological features. Of the 1,159 flakes and broken flakes, 629 (54.23%) were produced by right-handers and 530 (45.76%) by left-handers. The knapper who produced the fewest flakes made 49 pieces, and the knapper who generated the most flakes made 140 (Table 1). All the flakes were created from the same type of flint as used by *H~~omo~~. neandertalensis* at the Abric Romaní site (Barcelona, Spain) (Gómez de Soler, 2007; Carbonell, 2012; Soto et al., 2014).

Table 1

Handedness analysis

According to Bargalló and Mosquera (2014), only ~~8~~eight technical features from the complete catalogue of characteristics are informative to ascertain the hand laterality of the knapper. However, given that many pieces do not show the eight technical features indicative of hand preference, and also that the technical characteristics of a single piece may be the ~~fruit~~ result of chance, a number of flakes knapped by the same individual must be analysed (Figure 1).

Figure 1

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The following are the ~~8~~ eight technical features and their variables (*n*=21) that provide information about handedness:

a) Ventral surface:

1. Location of the ridge on the bulb, recorded by Rugg and Mullane (2001) as "skew". This small ridge starts at the impact point and runs along the cone of percussion, the proximal part of the whole bulb. It may be located to the right or left.
2. Location of the éraillure scars on the cone. These are small squamae that sometimes accidentally appear in the bulb. If present, they may be centred, or located to the right or left.
3. Location of the hackles. Small hackles may appear near the edges of the ventral surface. They may be distal, right or left located.
4. Location of the ripples. Long curved wrinkles that appear along the ventral surface and follow the detaching axis of the flake. They may be located distally, or to the right or left.
5. Orientation of the extracting axis of the flake. This may be right or left-oriented

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b) Striking platform:

1. Location of the impact point on the striking platform. This may be right or left located.
2. Inclination of the striking platform. It may be to the right, left, or sinuous
3. Morphology of the striking platform. This may be platform (plan), linear (lineal), or punctiform (pointed).

Figure 2

The correspondence analyses performed at Bargalló and Mosquera (2014) (Figure 2) showed that these features clearly allow the right-handed and left-handed knappers from the experiment to be distinguished. The first two factors explain 55.56% of the variability (factor 1:–36.57%, factor 2:–18.99%). In Figure 2 all the left-handed knappers are placed above factor 2, and the right-handed knappers are placed below factor 2. Therefore, left-handed knappers tend to produce ripples (39.39%), hackles (31.79%), the ridge of the cone of percussion (42.41%), the éraillure scars (15.67%), and the impact points (88.34% of the total relative inertia) on the left side of the flake. Interestingly they also tend to detach flakes with the striking platform sloped towards the right side of the piece (33.81% of the total relative inertia). In contrast, right-handed knappers tend to form ripples (36%), hackles (29.49%), the ridge of the cone of percussion (49.59%), the éraillure scars (25.78%), and the impact points (49.58% of the total relative inertia) on the right side of the flake. As opposed to left-handers, right-handed knappers tend to detach flakes with the striking platform sloped towards the left-side of the piece (45.89% of the total relative inertia).

This work is based on the fact that the patterns of the experimental knappers help us identify the handedness of prehistoric knappers, as the archaeological samples are expected to follow the same patterns as the experimental ones (Figure 2).

Refit analysis

In order to apply this method to the archaeological record, we need to find flakes detached by the same knapper. This can only be achieved by means of searching refits from knapping sequences of cores, which is a rather complicated process in many archaeological deposits. Although refits do not fully guarantee that only one knapper exploited one core, it is the best approach under the circumstances. Therefore, the first step is to search for as many refits as possible in archaeological samples.

In this study, we only analysed archaeological pieces longer than 10 mm. Depending on the type of raw material, the archaeological assemblage needs to be classified into Raw Material Units (RMU; Roebroeks, 1988; Schäfer, 1990; Odell, 2004; Vaquero, 2008) and Minimum Analytical Nodules (MAN) (Bleed, 2004; Hall, 2004; Larson, 2004; Odell, 2004; Copper and Qiu, 2006). RMU are the blanks from which one, two or several cores may be exploited by different knappers. For example, these may be big blanks of flint that are fragmented in order to allow the knappers to take a piece and start the process of stone tool production. Archaeologically, we are unlikely to obtain the entire refit of the blank, since they were often large fragments selected, transported, knapped, abandoned, reused, and so on. Only workshops provide the chance of refitting a whole RMU. For their part, the MAN are each of the cores knapped. For example, a

Comment [A9]: Might be better to abbreviate as RMUs and MANs and then use as needed – with or without the s throughout.

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cobble knapped into a discoid is one MAN, as is each of the flint-knapped fragments from the abovementioned blank. Archaeologically, MAN are easier to complete by refitting than RMU, although the occupational traits of the sites, their post-depositional conditions, as well as the area excavated usually make this task difficult. Although theoretically the distinction between RMU and MAN is clear, archaeologically it is not always easy to determine whether a particular variety of raw material belongs to a RMU or a MAN. Therefore, throughout this work we will use the general term RMU. Both RMU and MAN allow us to identify the single cobbles/blanks from which the flakes were detached, and indeed, the single knapping events. Associating flakes into RMU and MAN is based on the macroscopic features of the artefacts (e.g., grain-size and colour of the cortical and non-cortical surface, internal inclusions such as microfossils, fractures, and veins) (Schäfer, 1990; Roebroeks, 1998; Odell, 2004; Vaquero, 2008).

Once the pieces have been grouped into RMU and/or MAN, the refitting process begins. There are 3 three types of refits: flakes detached in production/knapping sequences (refits sensu stricto), breakages (conjoins), and modifications (small pieces detached when retouching a flake) (Cziesla, 1990). In this study, only flakes coming from production sequences (refits) have been used, and only those that refit together.

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Data analysis

In this study, Wwe applied in this study a multivariate statistical analysis (Correspondence analysis) using the program PASTast (Paleontological Statistics

Software) to identify the hand laterality of prehistoric knappers by comparing them with the experimental sample (Hammer, Harper and Ryan, 2001, 2008). ~~Alternative, m~~ More conventional, classification methodologies were also considered and evaluated using the experimental data. Specifically, we fitted our data with a Binary Logistic Regression and applied a simple Machine Learning algorithm (i.e., k- nearest neighbours). In both cases, the performance of the resulting classifiers could not significantly outperform the null model (i.e., random laterality attribution).

Archaeological Material

Gran Dolina TD10.1 (Atapuerca, Spain)

Gran Dolina is one of the ~~cavities~~ caves located at Sierra de Atapuerca, in the north of the Iberian Peninsula, near the city of Burgos. It is filled with 18 m of sediments divided into 11 lithostratigraphic units named TD1 to TD10, from bottom to top, and with a chronology ranging from the Early to Middle Pleistocene (Berger et al., 2008; Falguères et al., 2013; Arnold et al., 2014; Arnold and Demuro, 2015). In this work, we looked at the lithic remains of subunit TD10.1, which has a mean date of 244 - 337±29 ka (Falguères et al., 1999, 2013; Berger et al., 2008; Rodríguez et al., 2011), ~~possibly~~ but may be closer to 350 ka (Moreno et al., in press).

Up to now, TD10.1 has been the richest subunit of not only Gran Dolina, but all the Sierra ~~the~~ de Atapuerca sites, both in terms of lithic and faunal remains. The subunit has

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yielded roughly 21,000 lithic artefacts and 48,000 faunal remains, most of them near the north and east sectors of the excavation (Ollé et al., 2013).~~Technologically, t~~ The lithic remains probably represent the local-scale evolution from Mode 2 to Mode 3 technology at Sierra de Atapuerca. While the lithic remains from upper TD10.1 show features typical of the Mode 2 to Mode 3 transition, the main archaeological assemblage of this subunit comprises centripetal cores, with diverse and standardised reduction sequences aimed at obtaining small and medium-sized flakes, and a number of Levallois cores combined with typical Mode 2 elements, such as large cutting tools (Rodríguez-Álvarez, 1997; Carbonell et al, 2001; Rodríguez-Álvarez, 2004; Ollé et al., 2013).

Up to now, 42 RMU of quartz (*n*=215), and 148 RMU of quartzite (*n*=869) have been identified from subunit TD10.1. From among these, it has been possible to identify 15 quartz connections (~~7~~ seven refits and ~~8~~ eight conjoins), and 72 quartzite connections (38 refits and 34 conjoins) (López-Ortega et al, 2015). Of these, 80 flakes and broken flakes of quartzite, belonging to 34 refit groups, are useful for our purposes (Figure 3). Two to five refitting flakes form most of these groups. This means that we have as many as ~~5~~ five flakes produced by a single knapper.

Figure 3

Abric Romaní (Barcelona, Spain)

The Abric Romaní rock shelter is located in the NE of the Iberian Peninsula, approximately 50 km west of Barcelona. The site is located in the town of Capellades, in the tufa formations that rise on the right bank of the Anoia River. The stratigraphy is

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composed of 20 m of well-stratified travertine sediments dated by U-Series as being between 40 and 70 ka (Vaquero et al., 2013).

The archaeological units tested for this study are levels J and M, aged between 45 and 54 ka, which also show well-defined discrete accumulations (Vaquero and Pastó, 2001). Technologically, the lithic assemblage of both levels J and M correspond to Mode 3, here characterised by discoid and expeditious knapping methods.

Level J has yielded 7,000 lithic artefacts, and 8,460 faunal remains. There are two main archaeostratigraphic units: sublevels Ja and Jb, which have been distinguished only in the central area of the occupation. The U-series dates are *c*. 49 ka BP for the overlying tufa (49.3 ± 1.6 and 49.2 ± 2.9 ka BP) and around 50 ka BP (50.0 ± 1.6 and 50.8 ± 0.8 ka BP) for the underlying tufa (Bischoff et al., 1988). In addition, a charcoal sample has been dated as 47.1 ± 2.1 ^{14}C ka BP (NZA-2316) (Vaquero et al., 2012). According to the refits and the macroscopic characteristics of the raw materials, more than 500 RMU have been identified, each corresponding to a singular technical event. Moreover, 262 refitting groups, totalling 719 artefacts, have been found. In addition, level J has also yielded 50 hearths that seem to have spatially structured the site.

The tufa layer immediately above level M is dated at around 51.8 ± 1.4 ka BP (Bischoff et al., 1988; Vallverdú et al., 2012). The number of recorded archaeological remains is 18,946, of which 7,614 are faunal remains, 6,084 are lithic remains, 114 are wood imprints, 260 charcoal fragments, and 37 hearths. In level M it has been possible to identify 76 RMU (under study). Moreover, 216 refitting groups, totalling 827 artefacts, have been found.

We have selected the refit groups with the most connecting flakes from a single core (MAN): 1 one refit group from level Ja and 7 seven refit groups from level M. All of them are flint. The smallest refit comprises 5 five flakes (AR3), while the largest is made up of 36 flakes (AR8) (Figure 4).

Figure 4

Results

The total sample set analysed comprised 1,355 flakes and broken flakes. Of these, 80 are from Gran Dolina (level TD10.1), 116 from Abric Romaní (level Ja and M) and 1,159 are from the experimental programme. Of the 1,355 pieces, 971 were complete flakes and 384 were broken flakes.

Tables 2 and 3 show the frequency at which the technical features of hand preference appear in the experimental sample together with Abric Romaní refit groups (Table 2), and Gran Dolina refit groups (Table 3). Interestingly, there are differences between the archaeological and experimental samples: 63% of the variables included in the technical features were not identified in any of the 80 flakes from level TD10.1 of Gran Dolina, and 27% of these variables were not identified in any of the 116 flakes from Abric Romaní. In contrast, just 3.26% of the variables could not be identified in any of the 1,159 experimental flakes. Furthermore, two variables of the technical features were not identified in any of the 196 archaeological flakes analysed: the distal location of hackles, and the sinuous inclination of the striking platform. Both these variables tended to appear in low frequencies in the experimental sample. Therefore, and taking into account the figures, it is likely that the presence/absence of some of the variables is directly linked to the number of flakes analysed: the more flakes detached by a single knapper, the more the possibilities of them containing all the variables included in each technical feature. The frequencies of each technical feature will be used in the correspondence analysis to identify the hand laterality of prehistoric knappers.

Table 2

Table 3

In order to ascertain the minimum number of flakes required to identify at 100% confidence the hand laterality of the knapper, we first performed a correspondence analysis, including all the archaeological and experimental samples. Figure 5 shows all the samples, and the way the archaeological groups of refits are located around the experimental ones. Compared to Figure 2 (only experimental samples) we can see that both left- and right-handed experimental knappers situate closer, concentrate, hence losing their spatial variability. This is probably because there are too few flakes in some of the archaeological refits, some of them having just ~~2~~ two or ~~3~~ three refit flakes.

Figure 5

Because of this distortion in the distribution pattern of the experimental groups, a second correspondence analysis was undertaken, this time excluding all archaeological refit groups with less than ~~5~~ five flakes. By doing this we lose most of the Gran Dolina refit groups, since just one (GD29) comprises ~~5~~ five flakes. Figure 6 shows the

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distribution of all the remaining samples, which is more similar to the experimental-only pattern (Figure 2). Although the relative position of the right- and left-handed samples is correct (right-handers above the X ~~abscise~~ axis, left-handers below), the experimental samples maintain the distorted pattern, particularly the position of the sample R-Nu (a right-handed participant), which is below the X ~~abscise~~ axis, in a similar position to some of the left-handed participants. In other words, ~~the~~ individual R-Nu locates outside the sector of her true hand preference. This means that although better, this sampling is not selective enough to give a perfect fit to the experimental, real pattern. In summary, ~~byby~~ analysing ~~5~~ five~~5~~ flakes may lead to a false positive result.

Figure 6

However, given that few flakes make up most of the archaeological samples (Figure 3 and 4) we decided to perform a series of new simulations involving downscaled experimental samples, instead of removing archaeological groups from the analysis. As Table 1 shows, the number of flakes per group from the experimental sample ranged between 47 and 140 flakes. Consequently, we downscaled each experimental group of refits to fewer flakes per knapper. This simulation was made by taking the median of each variable, preserving the weight of each technical feature from the original distribution pattern. We reduced the experimental sample to ~~5~~ five flakes (Figure 7a), ~~6~~ six flakes (Figure 7b), ~~7~~ seven flakes (Figure 7c), and ~~8~~ eight flakes per knapper (Figure 7d), the last group showing the same pattern between the downscaled experimental subsamples and the original experimental sample group. Therefore, ~~8~~ eight is the minimum number of flakes required to identify the hand laterality of a knapper above a confidence level of 93.75%.

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These simulations allowed us to obtain the confidence rate for each downscaling of the experimental sample. As Figure 7a shows, the distribution pattern of the downscaled experimental subsample is quite similar to the pattern of the original experimental sample (Figure 2). An analysis of ~~5~~ five flakes entails only a 73.33% probability of correctly targeting the hand laterality of the knapper, since groups of ~~5~~ five flakes fail to achieve their correct position in the plot: individuals L_Et, L_4, L_3, R_4 and R_3 are positioned outside the sector of their true hand preference, when analysing just ~~5~~ five flakes. Actually, these individuals are showing false positives. Besides, the margin of success is greater for the right-handed population (75%), than for the left-handed population (71.42%).

By analysing ~~6~~ six flakes (Figure 7b) ~~still~~ we still have some individuals that are positioned outside the sector of their true hand preference. These individuals are R-Mn, L_1, L-2, L-3, L-4. Interestingly, by analysing ~~6~~ six flakes (Figure 7b) the probability of correctly identifying the hand preference of the sample reduces to 66.66%, even though with this number the probability of correctly assigning right-handers is higher (87.5%, with left-handers being only 42.85%). Nevertheless, by analysing ~~7~~ seven flakes the improvement in the results is notable, since the probability of targeting the hand preference of the knapper rises to 93.33% (Figure 7c). In this case, only one group of flakes (L_3) belonging to a left-handed knapper is wrongly positioned as a right-handed individual. Therefore, the margin of error, the probability of a false positive has decreased to 6.66%. Finally, analysing ~~8~~ eight flakes per knapper guarantees the correct distribution of the experimental population with regard to their hand preference (Figure 7d), above a confidence level of 93.75%.

Figure 7

With this information, we looked once again at the archaeological sample group using refits formed by ~~8~~ eight or more flakes. Only ~~5~~ five groups of refits fulfil this condition, all from the Abric Romaní site: ~~1~~ one from level Ja (sample AR1), and ~~4~~ four from level M (samples AR5; AR6; AR7; AR8). Figure 8 shows the distribution of these samples, where all the archaeological groups fit the right-handed pattern of knappers, similar to that of the experimental participant R_A_B. However, experimental right-handed knapper R_Nu appears in the area of left-handed knappers, showing a false positive. This false positive means that there is still a small margin of error (6.66%). This fact particularly affects the archaeological group of refits AR5, nearest the X ~~abscise~~ axis, which varies its position depending on whether the experimental knapper R_Nu is included in (Figure 8), or excluded from (Figure 9) the analysis. In the first case, AR5 appears as a right-handed knapper; in the second case, she ~~he/she~~ is left-handed.

Figure 8

Figure 9

In summary, right-handed Neanderthals knapped four of the five groups of flakes detached at ~~the~~ Abric Romaní with about 94% level of certainty, while one remains difficult to assign to a group. In Gran Dolina-TD10-1, only one group of flakes (GR29) contains enough information ~~enough~~ to be 73.33% certain that they were produced by a right-handed knapper.

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Discussion

The aim of this paper is to apply a method to the archaeological record that allows us to identify the hand laterality of our ancestors, and discern when and how this feature, which is most prominent in humans, appeared in our evolutionary history. The importance of this issue lies in the organisation of the brain, where our motor, sensory~~,~~ and cognitive functions are structured accord with ~~according to~~ this laterality.

Comment [A25]: Perhaps better as "in accord with…" or some such?

Comment [A26]: Ok I changed

Previous approaches to the hand laterality of our ancestors have mainly involved the hominin remains found at certain sites. However, these remains are scarce and do not always include the body parts that provide information on this question. Other approaches using stone tools, such as use-wear analysis, have been successful, but require the tools ~~both~~ to have been both used sufficiently~~,~~ and be well preserved. Other proxies drawn from the study of single technological features of flakes (i.e., Toth, 1985; Rugg and Mullane, 2001; Domínguez-Ballesteros and Arrizabalaga, 2015) have been questioned from the beginning by authors such as Patterson and Sollberger (1986), Pobiner (1999), and Bargalló and Mosquera (2014). These papers discuss the reliability of finding out the hand preference of one individual by using ~~just~~ only one ~~single~~ technical feature.

The study presented here applies a previously published method (Bargalló and Mosquera, 2014), which deals with handedness in human evolution by analysing a combination of certain technical features of the most widely-produced stone tools in the Pleistocene world: flakes. We used a multivariate statistical analysis (Correspondence analysis), since alternative classification methodologies (i.e., Binary Logistic Regression and applied a simple Machine Learning algorithm) could not significantly outperform the null model (i.e., random laterality attribution).

The selected method requires flakes produced by the same knapper, meaning that these flakes must be identified from the archaeological assemblage. It is quite difficult to isolate an individual knapping event in an archaeological assemblage, given that most archaeological levels are actually palimpsests. Preliminary archaeostratigraphic approaches to isolating the remains of each living floor, and a subsequent search for refits, are required to identify singular events (Lucas, 2005; Bailey, 2007; Bargalló et al., 2015; Machado et al., 2015). Because these singular knapping events may involve more than one core (Vaquero, 2008), it is necessary to identify a unique core and the flakes that refit one another. However, ethnographic records show that different knappers (Stout, 2002; Bril et al., 2005) may have worked on the same ~~single~~ core. Nevertheless, the archaeological lithic samples we used in this study have the following characteristics: 1) all the archaeological groups of refits are formed by relatively few pieces, never exceeding forty flakes, and 2) the technical features of the flakes are completely homogeneous within each group of refits, suggesting that they were all produced by the same person.

The matter of how much raw material may condition the analysis has been solved by selecting archaeological refit groups of quartzite for Atapuerca and flint from Abric Romaní. Both rock types were frequently used in prehistory, as well as at each of these sites, and they are good quality materials, retaining the maximum number of technical features produced by the knapping process, unlike quartz, ~~whose structure of~~ where the large crystal structures makes it difficult to preserve many striking platforms (de Lombera-Hermida, 2009).

In addition, this paper also highlights other potential uses of refit studies. Until now, they have been used to analyse the spatial distribution of remains within occupations; to understand the way the tools were produced; to ~~know~~ identify how hominins organised the tasks performed inside the settlements; and to identify the movements of the individuals within these activity areas (Cahen et al., 1979; Hofman, 1981; Bodu et al., 1990; Ashton, 2004; Turq et al., 2013). Now, refits can also be used to facilitate the identification of individuals and provide an understanding of their technological cognition.

In this sense, studying the handedness of the fossil hominins is not mere “storytelling”, providing anecdotal information, but the information may help us understand the development of the complex brain organisation during human evolution, and to discover how individuals engaged within their communities. In the words of Foulds: “…this is a reference to an individual agent within a wider society founded on the social relationships that they both create and maintain, irrespective of how they conceived of themselves” (Foulds, 2014: 13).

Conclusions

The minimum number of flakes necessary to successfully identify hand laterality at about 94% of confidence is ~~8~~ eight. They must be produced by the same knapper, and the only way to ensure this from the archaeological record is to find ~~8~~ eight flakes that refit one other because they were produced from a single core-knapping event. In addition, there is no single technical feature that provides information about hand preference, but instead there is a combination of ~~8~~ eight technical features, located on the striking platforms and the ventral surfaces. Raw material is not relevant in the case of the most-widely used rocks in Europe, flint and quartzite, since the majority retain the technical features required for analysis. The exception to this is quartz, where many flakes from the striking platform are lost during the percussion. Expertise is not an issue either, since the technical features analysed here ~~only~~ correlate only with handedness, and not the technical quality of the tools (Bargalló and Mosquera, 2014).

Our results indicate that just one pre-Neanderthal knapper from TD10.1 at Gran Dolina (Atapuerca) may be suitable for analysis, since only one refit group containing ~~5~~ five quartzite flakes was found. It has been ascertained with a 73.3% confidence rate that this individual was right-handed. The Abric Romaní Neanderthal knappers provide us with better results. Levels Ja and M yielded ~~5~~ five refit groups made up of more than ~~8~~ eight flakes, allowing us to clearly distinguish the presence of four right-handers, with the hand preference of one remaining unclear.

Even though ~~8~~ eight flakes is a relatively low figure, this number is still quite difficult to obtain at many archaeological sites. This is the case of Gran Dolina-TD10.1, which up to now has yielded 29 groups of quartzite refits from knapping sequences, none of which exceeds ~~5~~ five flakes. Nevertheless, these figures may increase in the near future, and more success may be seen when applying the method to the Neogene chert assemblage, which is much more numerous, but also much more difficult to refit, due to the poor preservation of this rock type.

The possibility of identifying the handedness of our ancestors, in this case from 300 ka and 50 ka ago at Gran Dolina-TD10.1 and Abric Romaní, respectively, signifies a big step forward in the field of human evolution, no matter the age of the samples. Further study should eventually allow us to fix the time when handedness arose and, by extension, know at what point brain laterality developed in humans at both the individual and population levels, as well as which hominin species were partially or totally lateralised. It is possible that our earliest ancestors started to display handedness, but perhaps more sporadically, as seen in living chimpanzee populations. We will also be able to understand the progression of this cognitive feature through our phylogeny, and whether it was a progressive change or one that appeared suddenly. In addition, we will be able to study the role that social and cultural environments may have played in the evolution of this characteristic. Our method ensures this goal through studying the knapping activities of our ancestors, one of the best-recorded tasks with well-preserved remains.

Acknowledgments

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CGL2012-38434-C03-03.AB has been founded from the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie Action grant agreement PREKARN nº702584. SL is supported by the Ramón y Cajal programme through the grant RYC-2012-01043. The authors are grateful to the participants in the experimental tests, and to G. Chacón, F. Romagnoli and M. Vaquero from Abric Romaní, and A. de Lombera-Hermida, and E. López-Ortega, from Gran Dolina, for working on the archaeological refits at the two sites.

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Comment [A28R27]: Ok I corrected

Comment [A29]: PLACE OF PUBLICATION AND IS IT MCDONALD? (one word)

Comment [A30R29]: Ok I corrected

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Comment [A43]: Use page numbers not doi if page numbers are present

Comment [A44R43]: OK I corrected

Rodríguez, J., Burjachs, F., Cuenca-Bescós, G., García, N., Van der Made, J., Pérez-González, A., Blain, H.A., Expósito, I., López-García, J.M., García-Anton, M., Allué, E., Cáceres, I., Huguet, R., Mosquera, M., Ollé, A., Rosell, J., Parés, J.M., Rodríguez-Álvarez, X.P., Díez, J.C., Rofes, J., Sala, R., Saladié, P., Vallverdú, J., Bennasar, L., Blasco, R., Bermúdez de Castro, J.M., Carbonell, E., 2011. One millions years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). Quaternary Science Reviews 30, 1396-1412.

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Comment [A45]: Isn't this Van der Made, J., ?

Comment [A46R45]: Yes I corrected

Comment [A47]: Reformat and cite correctly – are there editors, place of publication, page numbers etc?

Comment [A48R47]: Ok I corrected

Comment [A49]: Reformat and cite correctly – are there editors, place of publication, page numbers etc?

Comment [A50R49]: Ok I corrected

Schäfer, J., 1990. Conjoining of artefacts and consideration of raw-material: their application at the Middle Palaeolithic site of the Schweinskopf-Karmelenberg. In: Cziesla, E., Eickhoff, S., Arts, N., Winter, E. (Eds.), The Big Puzzle. International Symposium on Refitting Stone Artefacts. Holos, Bonn, pp. 83-100.

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Comment [A51]: Please make sure this is corrected and matches earlier citations – why the 1987?

Comment [A52R51]: Ok, I corrected

Turq, A., Roebroeks, W., Bourguignon, L., Faivre, J.P., 2013. The fragmented character of Middle Palaeolithic stone tool technology. Journal of Human Evolution 65, 641-655.

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Comment [A53]: Place of publication?

Comment [A54R53]: Ok, I completed

Vaquero, M., Allué, E., Bischoff, J.L., Burjachs, F., Vallverdú, J., 2013. Environmental, depositional and cultural changes in the Upper Pleistocene and Early Holocene: the Cinglera del Capelló sequence (Capellades, Spain). Quaternaire 24, 49-64.

Figure legends

Figure 1: Technical features analysed. ~~Above~~ Top: technical features present on the flakes. ~~Below~~ Bottom: possible locations of the ridge of the bulb, the ~~eraillure~~ éraillure scars, hackles, ripples, inclination of the extraction axis, inclination of the striking platform and the type of striking platform.

Figure 2: Correspondence analysis of the experimental sample: left-handed knappers (L-x) are located above factor 2, while right-handed knappers (R-x) are located below this. All the samples are represented by triangles.

Figure 3: Left: Complete and broken flakes belonging to 34 groups of refits found ~~from~~ in level TD10.1 at the Gran Dolina site (Sierra de Atapuerca, Spain). Right: Archaeological refit groups GD8 and GD2 (photographs from López-Ortega, 2015).

Figure 4: Top: Complete and broken flakes belonging to ~~8~~ eight groups of refits selected from levels Ja and M from the Abric Romaní Neanderthal site (Barcelona, Spain). Bottom: Archaeological refit groups AR1 (photograph from Vaquero et al., 2012) and AR8 (photograph by F. Romagnoli).

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Figure 5: Correspondence analysis of the entire set of experimental and archaeological samples. Triangles: experimental refit groups. +: refit groups from TD10.1, Gran Dolina (*GD*). Circles: refit groups from levels Ja and M, Abric Romaní (*AR*). (Axis 1= 19.7% eigenvalue; Axis 2= 16.86% eigenvalue). The two axes represent 36.56% of the total.

Figure 6: Correspondence analysis of the experimental and archaeological samples, selecting just the archaeological refit groups with ~~5~~ five or more flakes. Triangles: experimental refit groups. +: the only refit group from TD10.1 (*GD29*) with ~~5~~ five flakes. Circles: the ~~8~~ eight refit groups from Abric Romaní (*AR*) with ~~5~~ five or more flakes (Axis 1= 28.36% eigenvalue; Axis 2= 18.63% eigenvalue). The two axes represent 46.99% of the total. Shadowed individual (R_Nu) is positioned outside the sector of her real hand preference.

Figure 7. Correspondence analysis of the experimental sample downscaled to "n" flakes per knapper. Triangles: right-handed knappers, both for the original experimental sample (R_"x") and the subsample downscaled to "n" flakes (R_"n"). +: left-handed knappers, both for the original experimental sample (L_"x") and the subsample downscaled to "n" flakes (L_"n"). **7a.** Downscaling the experimental subsample to ~~5~~ five flakes (Axis 1= 28.49% eigenvalue; Axis 2= 18.53% eigenvalue). The two axes represent 47.02% of the total. **7b.** Downscaling the experimental subsample to ~~6~~ six flakes (Axis 1= 28.56% eigenvalue; Axis 2= 17.11% eigenvalue). The two axes represent 45.66% of the total. **7c.** Downscaling the experimental subsample to ~~7~~ seven flakes (Axis 1= 28.49% eigenvalue; Axis 2= 15.83% eigenvalue). The two axes represent 45.66% of the total. **7d.** Downscaling the experimental subsample to ~~8~~ eight

flakes (Axis 1= 26.65% eigenvalue; Axis 2= 17.76% eigenvalue). The two axes represent 44.41% of the total. Shadowed samples are outside their real handedness position.

Figure 8: Correspondence analysis. Triangles: experimental subsample downscaled to ~~8~~ eight flakes. Circles: the only five archaeological refit groups with ~~8~~ eight or more flakes, all from the Abric Romaní site. Experimental knapper R_Nu (shadowed) is outside her real hand preference position (Axis 1= 30.93% eigenvalue; Axis 2= 17.03% eigenvalue). The two axes represent 47.96% of the total.

Figure 9: Correspondence analysis. Triangles: experimental subsample downscaled to ~~8~~ eight flakes, without the knapper R_Nu. Circles: the five archaeological refit groups with ~~8~~ eight or more flakes from Abric Romaní. (Axis 1= 29.64% eigenvalue; Axis 2= 18.11% eigenvalue). The two axes represent 47.75% of the total.

Table legend

Table 1: Number of flakes and broken flakes knapped by each participant during the experimental programme.

Table 2: Frequency of the technical features involved in handedness. The table includes the experimental and archaeological samples from Abric Romaní refit groups (AR). R_"x" and L_"x": refit groups of right- and left-handed experimental knappers, respectively.

Table 3: Frequency of the technical features involved in handedness. The table includes the experimental and archaeological samples from Gran Dolina-TD10.1 level (GD).

Table

Site	EXPERIMENTAL											
Refit group	R_AB	R_Jo	R_Ju	R_Mn	R_Nu	R_Fd	R_H	R_Ma	L_Ag	L_Et	L_Fx	L_Kr
Nº pieces	60	93	84	72	91	82	91	56	140	61	62	47

Table

PB	TECHNICAL FEATURES	VARIABLES	AR1	AR2
VENTRAL SURFACE	Ridge of the Bulb	RIGHT	8	2
		LEFT	2	5
	Location éraillure	CENTRE	1	2
		RIGHT	1	0
		LEFT	3	0
	Location hackles	DISTAL	0	0
		RIGHT	1	1
		LEFT	4	2
	Location ripples	DISTAL	2	0
		RIGHT	7	0
		LEFT	5	4
	Extraction axis	RIGHT	8	0
		LEFT	7	5
STRIKING PLATFORM SURFACE	Location impact point	RIGHT	10	1
		LEFT	5	3
	Inclination striking platform	RIGHT	7	1
		LEFT	5	2
		SINUOUS	0	0
	Morphology striking platform	LINEAL	5	1
		PLAN	16	6
		POINTED	0	0

Table

PB	TECHNICAL FEATURES	VARIABLES	GD1	GD2
VENTRAL SURFACE	Ridge of the Bulb	RIGHT	1	0
		LEFT	1	3
	Location of éraillure	CENTER	0	0
		RIGHT	0	1
		LEFT	2	1
	Location of hackles	DISTAL	0	0
		RIGHT	1	1
		LEFT	1	0
	Location of ripples	DISTAL	1	0
		RIGHT	0	2
		LEFT	0	2
	Extraction axis	RIGHT	0	1
		LEFT	2	3
STRIKING PLATFORM SURFACE	Location of impact point	RIGHT	2	3
		LEFT	0	1
	Inclination striking platform	RIGHT	0	3
		LEFT	0	1
		SINUOUS	0	0
	Morphology striking platform	LINEAL	0	0
		PLAN	2	4
		POINTED	0	0

Figure
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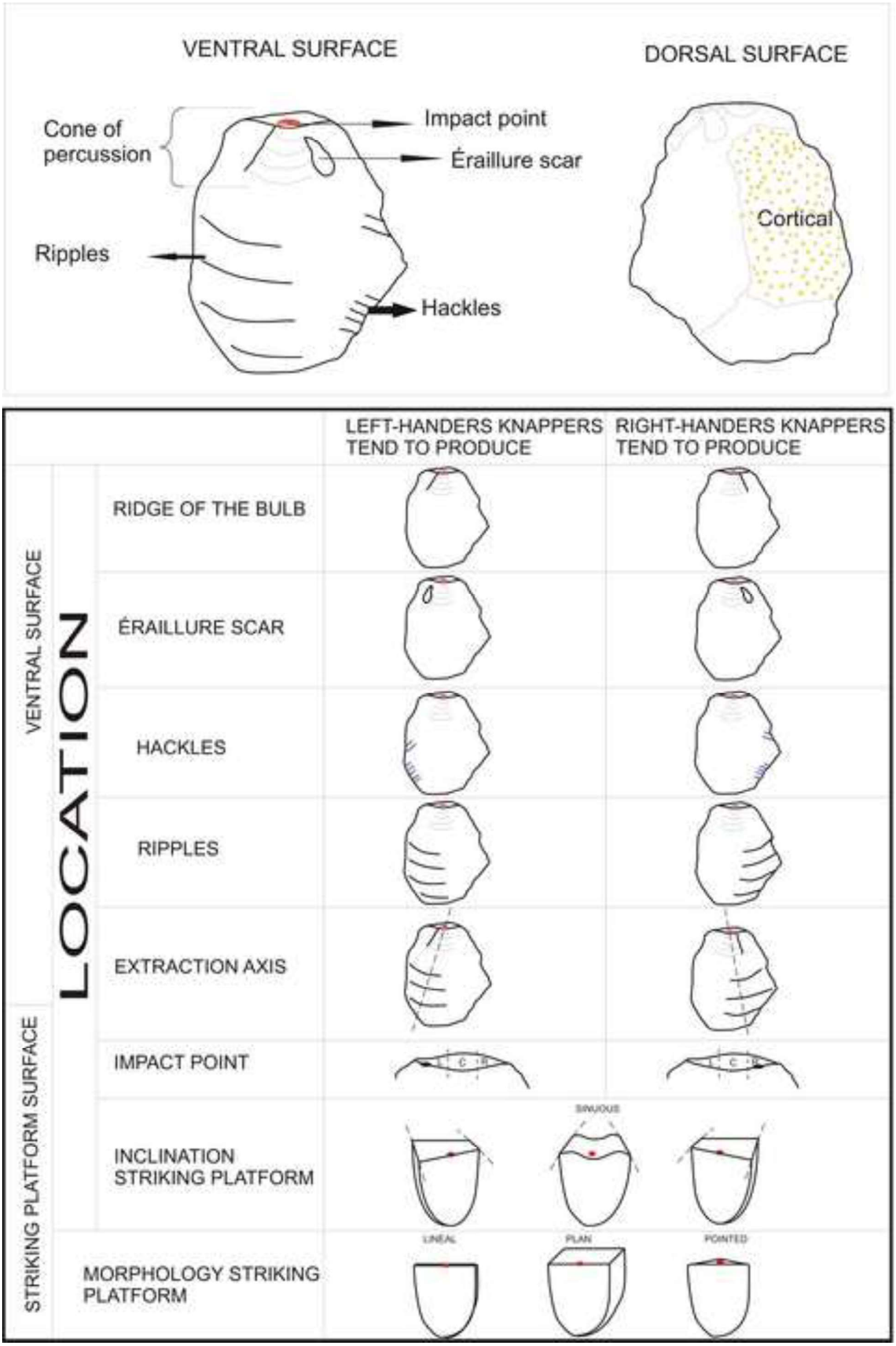
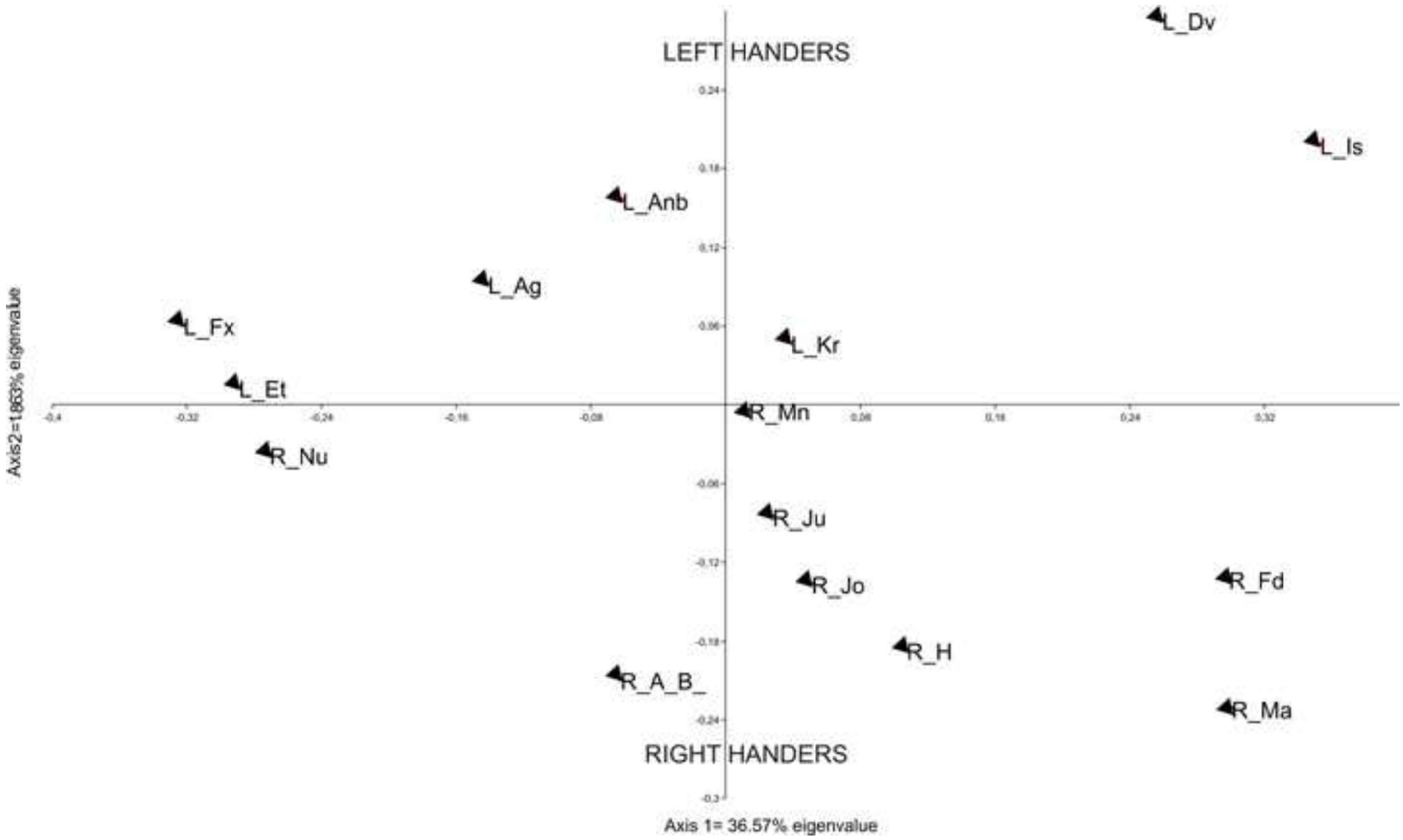


Figure


LEFT HANDERS
RIGHT HANDERS
L_Dv
L_Is
L_Anb
L_Ag
L_Fx
L_Et
L_Kr
R_Mn
R_Nu
R_Ju
R_Jo
R_Fd
R_H
R_A_B_
R_Ma
Axis 1= 36.57% eigenvalue
Axis2=1863% eigenvalue

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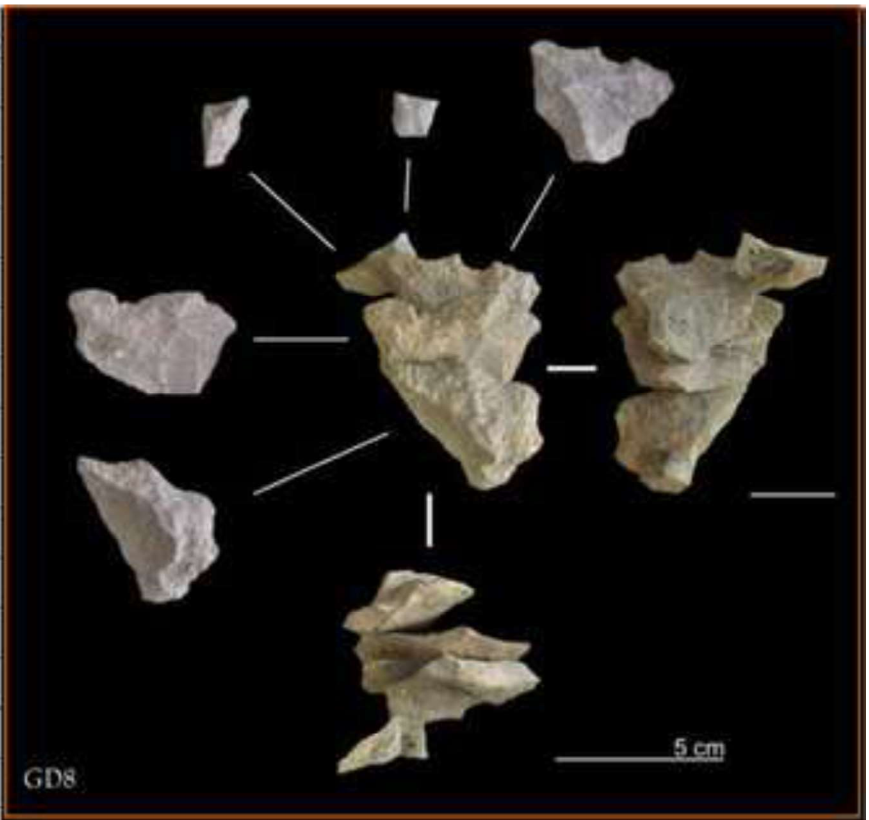
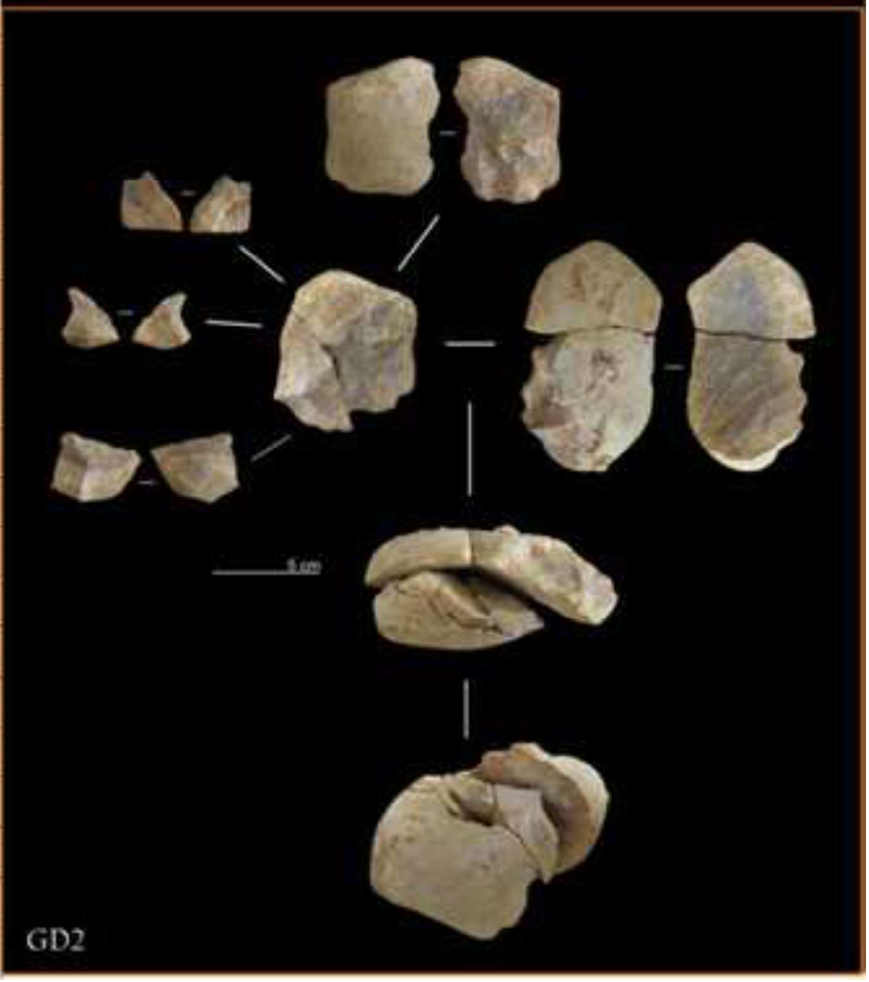
Refit group	Num. pieces
GD1	2
GD2	4
GD3	2
GD4	2
GD5	2
GD6	2
GD7	2
GD8	4
GD9	3
GD10	3
GD11	3
GD12	2
GD13	2
GD14	2
GD15	2
GD16	3
GD17	2
GD18	2
GD19	2
GD20	2
GD21	2
GD22	2
GD23	2
GD24	2
GD25	2
GD26	2
GD27	2
GD28	2
GD29	5
GD30	2
GD31	3
GD32	2
GD33	2
GD34	2
TOTAL	80





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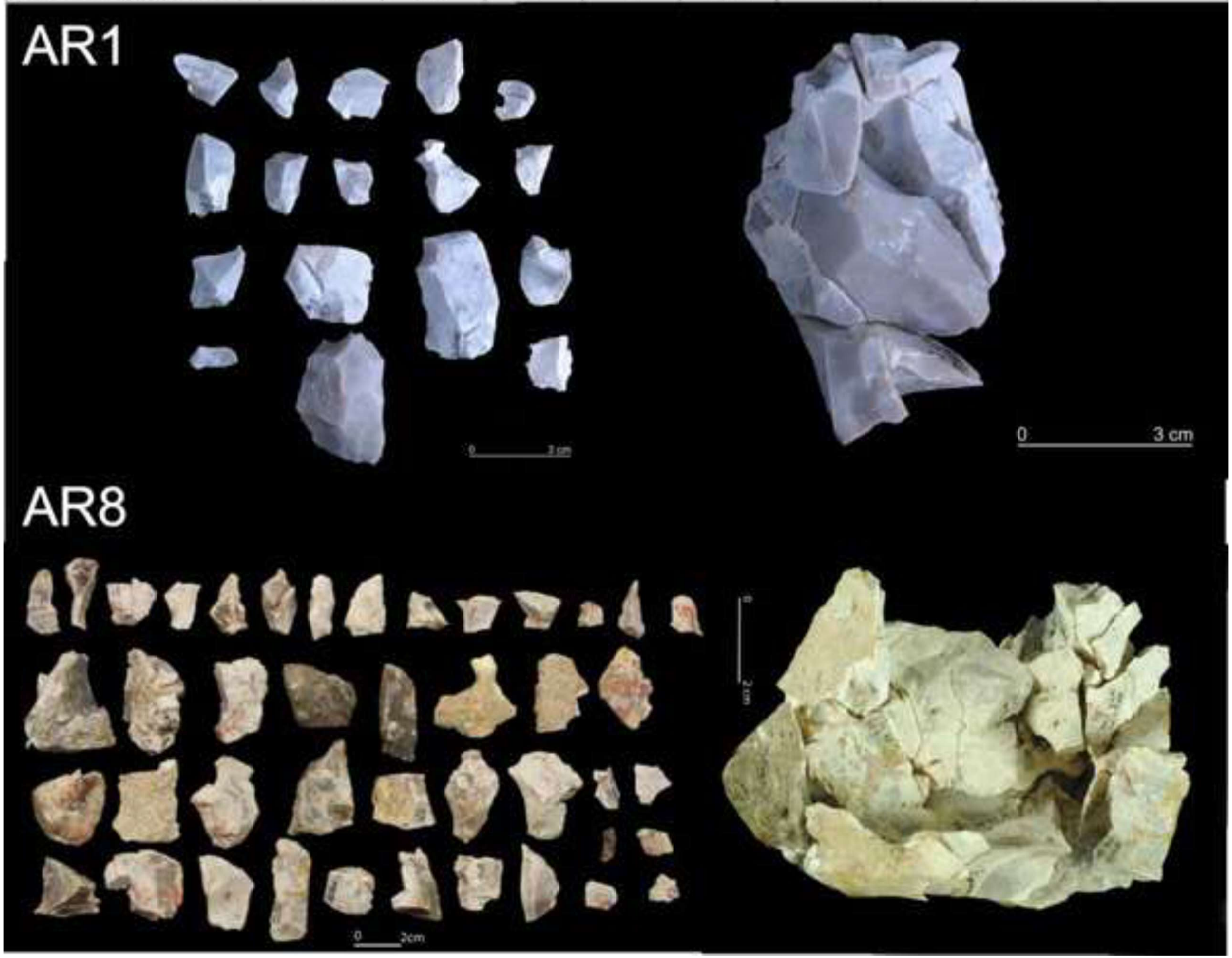
Level	Ja	M							Total
Refit group	AR1	AR2	AR3	AR4	AR5	AR6	AR7	AR8	116
Num. pieces	21	7	5	7	10	12	18	36	



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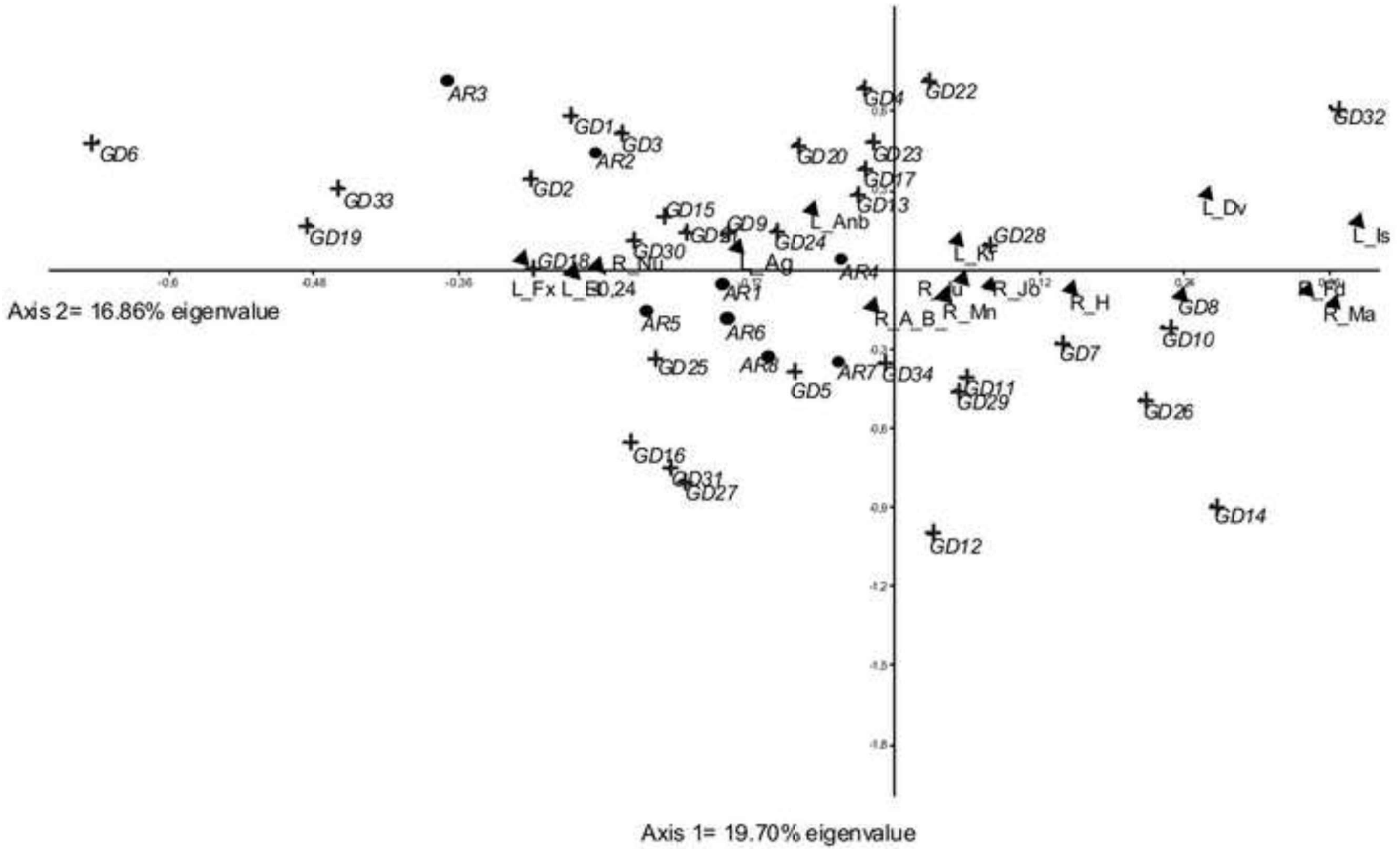

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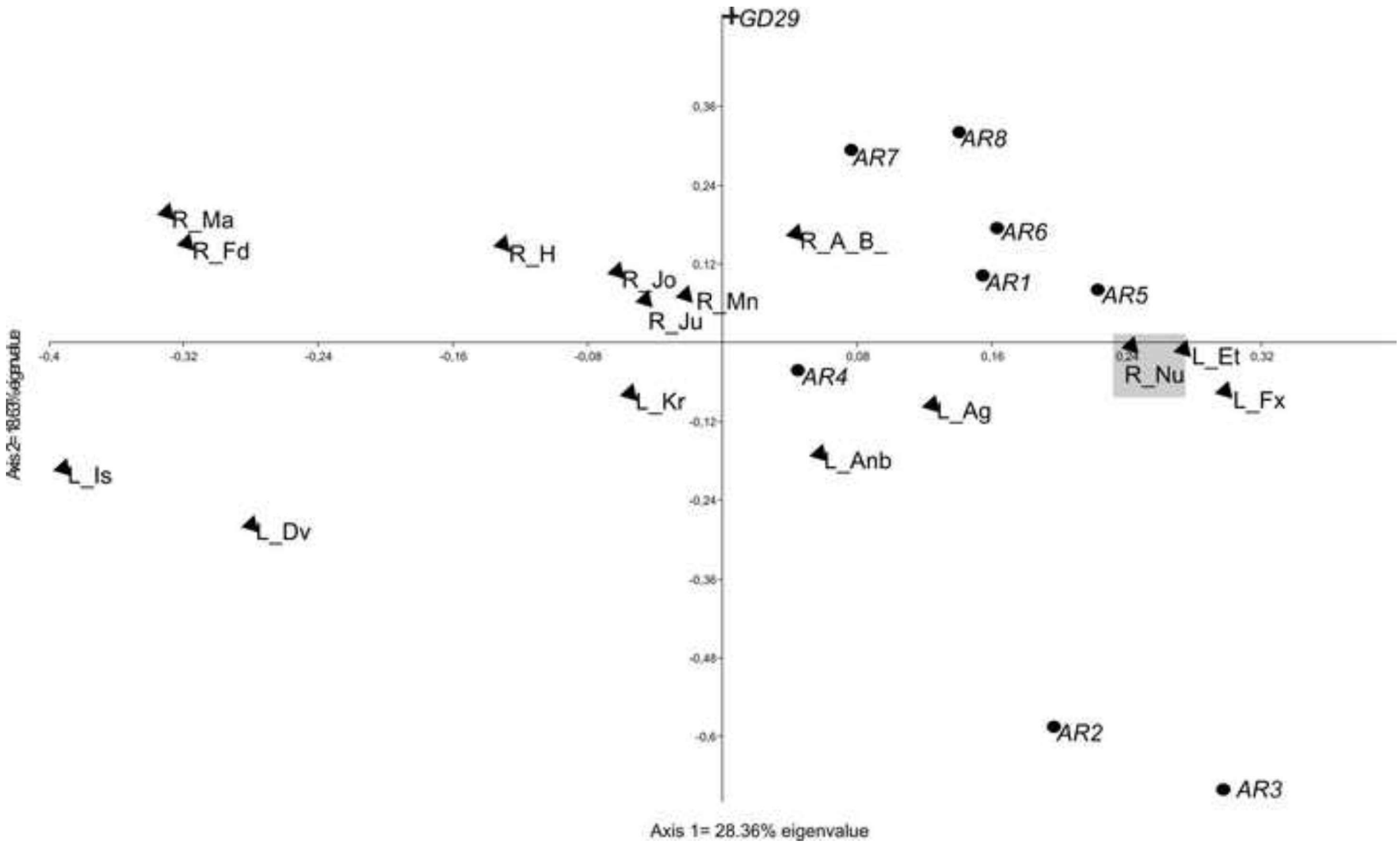

Figure
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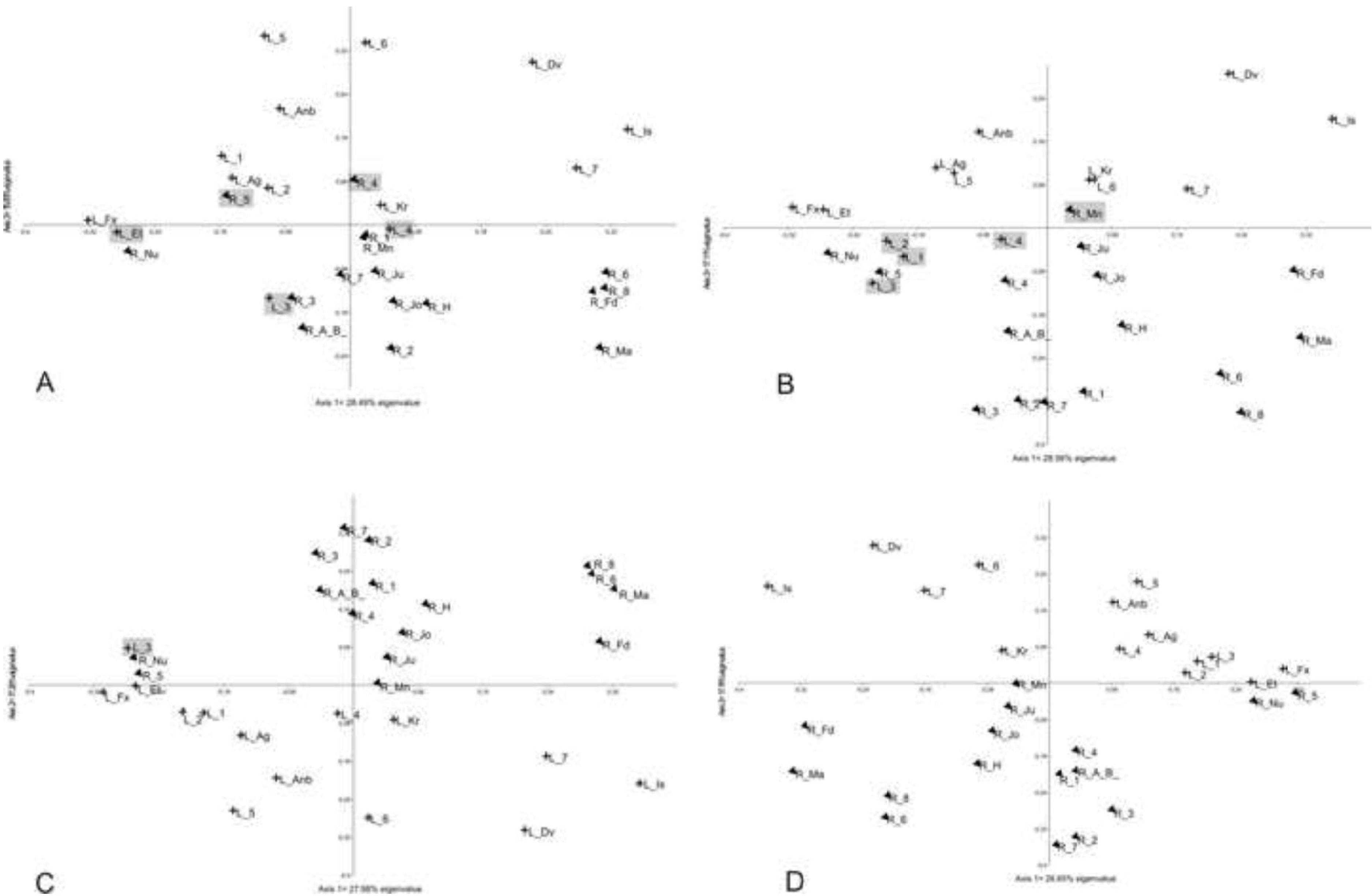

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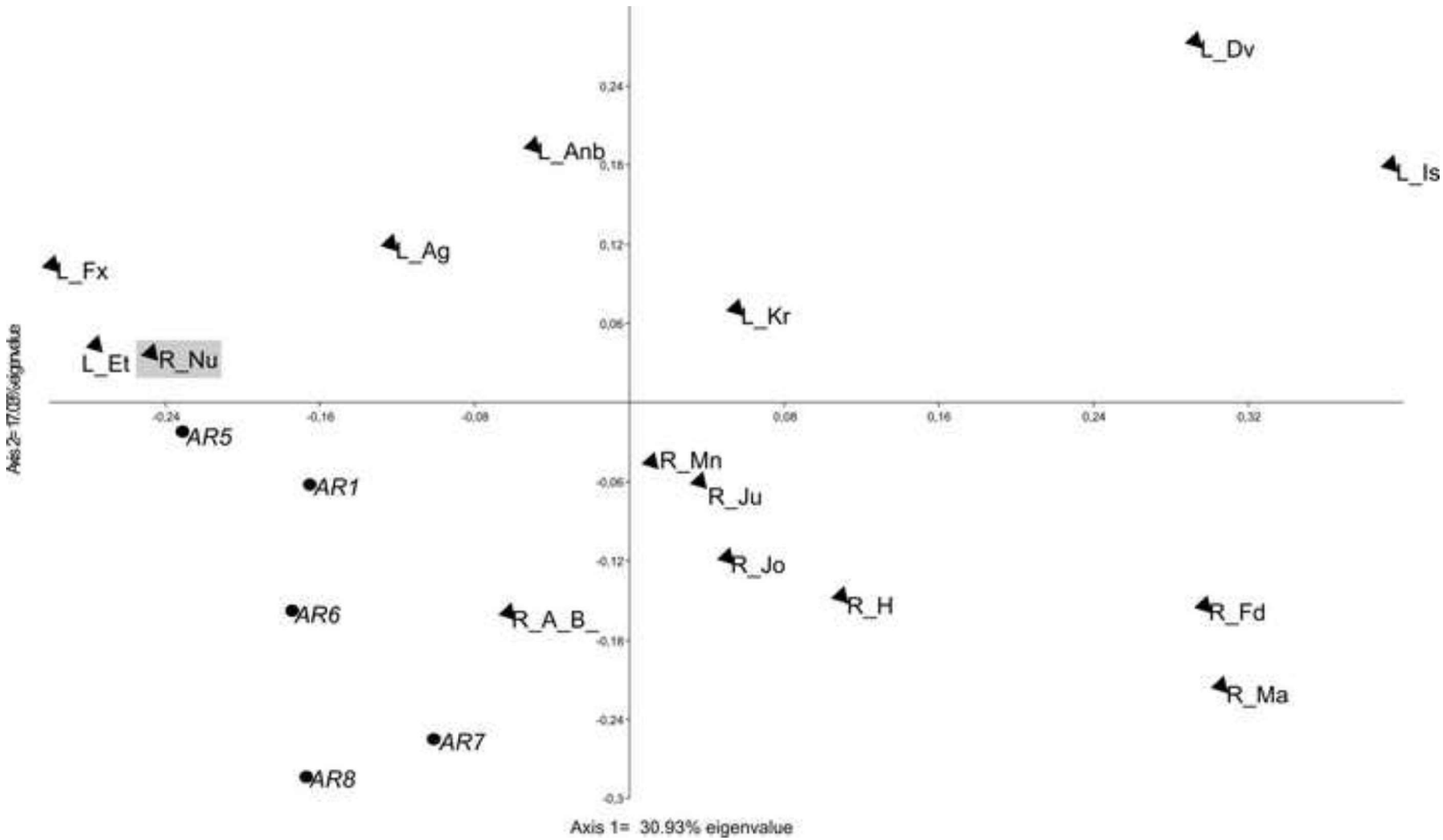
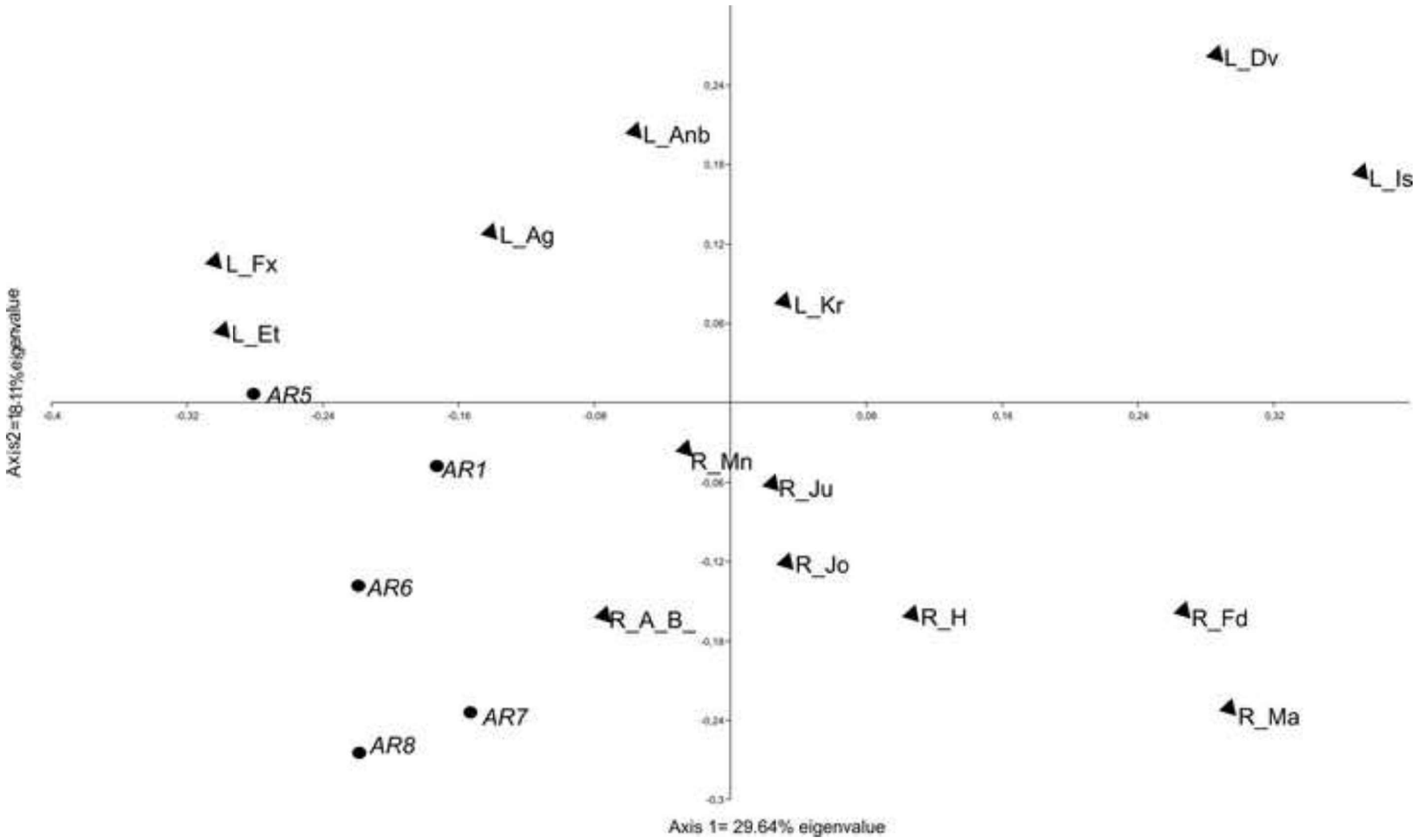


Figure


L_Dv
L_Anb
L_Is
L_Ag
L_Fx
L_Kr
L_Et
AR5
R_Mn
AR1
R_Ju
R_Jo
AR6
R_A_B_
R_H
R_Fd
AR7
R_Ma
AR8
Axis 1= 29.64% eigenvalue
Axis2=18.11%eigenvalue