



## Specific information levels in relation to fragmentation patterns of shrew mandibles: do fragments tell the same story?



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### ABSTRACT

Archaeological or paleontological remains are often broken and consequently cannot be used as complete specimens, especially for species identification. Consequently, they are poorly studied, even if they could possess species-specific information. Here, we use mandibles of white-toothed shrews and a taphonomic pattern of fragmentation composed of seven pieces to test their validity in species assignment. Using an extant non-ambiguous reference sample of five species, we explore the specific assignments of fragments obtained by a k-NN method of classification, artificially derived from the complete mandible. To describe the form of each piece we use 2D anatomical landmarks and sliding semilandmarks that allow the quantification of objects with no or few true anatomical landmarks. Results show that small fragments still possess species-specific information that is nearly always enhanced when using sliding-landmarks. Moreover, morpho-functional aspects are detected that can affect the species-specific information contained in the fragments.

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### 1. Introduction

Palaeontologists, archaeologists and biologists are regularly confronted with broken or incomplete specimens. Depending on the discipline and its aims, broken or fragmented specimens may be used, but they are frequently discarded from formal analysis. However, if fragments possess specific characteristics, the attribution to a species, genus, or family is sometimes feasible. Such a diagnosis is strongly dependent on the taxon investigated and the associated fragments available. The choice of whether or not to include fragmented material in analyses could create a bias in the results. As a consequence, a potentially large amount of information often remains unexploited.

Studying objects broken due to bad conditions of preservation, linked typically to fossilization or historical deposits, is particularly

problematic in the case of morphometric, and especially geometric morphometric approaches where many variables are needed to describe the form of an object. The first choice is typically to optimize the number of variables and the number of specimens based on what is available and intact, but this is often a restrictive solution. The second choice is to estimate missing data. Although many papers have been written on the subject (e.g. [Couette and White, 2010](#)), an ideal or optimal solution does not exist. An alternative approach will be developed in this paper using 2D sliding-landmark approaches which allow an enhancement of the description of form using fragmented specimens. The method requires complete specimens derived from a correctly diagnosed inter-specific data-set. This data set is then divided into sub-samples following a pattern of fragmentation that is well characterized in the literature or established with archaeological data. Then, specific classifications are performed for each sub-sample, from the complete object to the smallest fragment. These results are then compared to the known specific classification of species in order to evaluate the level of discrimination of the different fragments.

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In this paper we use mandibles of white-toothed shrews belonging to the genus *Crocidura* as our model. They present all characteristics needed for this approach. They are very abundant in archaeological deposits and have a regular and known pattern of fragmentation (Denys, 1985; Andrews, 1990). In addition, they possess a highly uniform shape which makes the allocation of small fragments nearly impossible. Small mammals are very useful in the understanding of palaeo-environments (Weissbrod et al., 2013; Stoetzel et al., 2013; Escudé et al., 2013) and shrews in particular (Stoetzel et al., 2007; Valenzuela et al., 2009). Indeed, the various species of small mammals and their associated ecological niches allow the characterization of climatic trends due to their micro-climatic specificity (Stoetzel et al., 2011, 2013). The exact specific allocation of shrew mandibular fragments recovered from archaeological deposits is therefore of particular interest.

The aim of this study is to calculate and to compare the level of the specific discrimination of these different types of fragments using an extant reference sample. By doing this, we aim to evaluate the utility and the efficiency of using fragmented shrew mandibles. Moreover, a double morphometric approach to describe form is used to compare sliding semilandmarks versus anatomical landmarks. As such this allows us to test and optimize the advantages of different methods based on the absence or scarcity of anatomical landmarks. We predict that sliding semilandmarks will increase the accuracy of the description of form and thus the potential for specific discrimination. Moreover, we predict that this improvement in the description of form will be particularly beneficial for the smallest fragments.

## 2. Material and methods

### 2.1. Material

Teeth and hemi-mandibles are among the best-preserved bones found in archaeological sites, especially in shrews (Butler and Greenwood, 1979) and this is also the case in the archaeological site of the El Harhoura II cave (Stoetzel et al., 2011) where the results of this study have been applied (Cornette, 2011). The preservation can be explained by their solidity and the fusion of the different elements into a single unit. Nevertheless, complete mandibles are an exception and in most cases they are recovered broken in archaeological deposits. The results of fragmentation are not random but follow distinct patterns (Denys, 1985; Andrews, 1990), presumably linked to the mechanical properties of the different parts of the bone.

Our data-set (Table 1) is composed of five species of extant Moroccan white-toothed shrews: the Greater White toothed shrew, *Crocidura russula*, Whitaker's shrew, *Crocidura whitakeri*, the Mauritanian shrew, *Crocidura lusitania*, the Savannah path shrew, *Crocidura viaria*, and the Saharan shrew *Crocidura tarfayensis*. These species are the only ones present in Morocco today (Aulagnier and Thévenot, 1986; Aulagnier, 1987; Hutterer, 1986). The choice of specimens was based on an archaeological application in relation to the El Harhoura II cave, Témara, Morocco (Cornette, 2011). Moreover, this genus is a good model as it is known as being notoriously difficult to identify (Poitevin et al., 1986), also in this geographic area (Vogel et al., 2006). Nevertheless, geometric morphometric approaches have been useful in distinguishing species and even populations in some cases (Sarà, 1990, 1996; Leroy et al., 2004; Cornette et al., 2012, in press). Finally, our sample represents a good reference of both morphologically close and divergent species. Even if the species diagnosis of these five species based on complete bones may be possible, it becomes very difficult based on fragments, and almost impossible when using small fragments.

### 2.2. Methods

We established a typology of broken mandibles allowing us to work with the same piece while being able to use the same landmarks. This typology was created by the study of 609 broken specimens from El Harhoura II cave and comparisons with specimens derived from other taphonomic studies (Denys, 1985; Andrews, 1990). Seven types of fragments were selected that correspond to the most abundant fragments found in archaeological sites (Fig. 1, Table 2) in order to perform Geometric Morphometrics (GM).

Geometric morphometric approaches allow an accurate description of biological objects by partitioning form into shape and size components (Needham, 1950) allowing one to work on the form (including size) or the shape (excluding size) of an object. Several quantitative approaches like Fourier descriptors, anatomical landmarks or sliding semilandmarks (Adams, 2004; Zelditch, 2012) exist and can be coupled to multivariate analyses such as Principal Component Analyses (PCA) or canonical analyses that increase the power of these analyses. All these approaches have given solid results and numerous studies in an archaeological context have been performed (e.g. Bignon et al., 2005; Valenzuela-Lamas et al., 2011; Curran 2012, Stoetzel et al., 2013; Escudé et al., 2008, 2013; Cucchi et al., 2014).

Sliding semilandmarks allow one to describe form where no (or few) anatomical landmarks (as defined by Bookstein, 1991) can be found. Sliding semilandmarks are allowed to slide on the outline until they are positioned optimally relatively to the positions of the corresponding points on the outline of the reference specimen (Bookstein, 1997; Slice, 2007; Mitteroecker and Gunz, 2009; Gunz and Mitteroecker, 2013). In our interspecific study, we chose to use the method minimizing the Procrustes distances (Bookstein et al., 2002; Gunz and Mitteroecker, 2013). This method has proven to be efficient in terms of discriminant morphometric analysis as it completely eliminates variation along the tangent of the curve (Perez et al., 2006). Moreover the alternative method which minimizes bending energy seems to produce a larger shape variance on the same repeated object (Sheets et al., 2006). After sliding, these landmarks can be analysed as homologous landmarks. The number and the position of sliding semilandmarks were decided in relation of complexity of the curvature of the mandible (Mitteroecker and Gunz, 2009; Gunz and Mitteroecker, 2013). Here again, this approach has been successfully applied on a variety of archaeological objects and in different contexts (e.g. Cucchi et al., 2011, Cucchi et al., 2013; Evin et al., 2013; Ros et al., 2014; Cucchi et al., 2014) and also extant species of shrews (Cornette et al., in press).

Each complete left hemi-mandible of the extant species was photographed in lingual view using a Leica Macroscope Z6 coupled to a Leica DFC420 digital six mega pixel camera. Sixty landmarks were placed on the complete mandibles; fourteen anatomical landmarks and forty-six sliding semilandmarks (Fig. 2). The teeth were not taken into account as they have special constraints related to the age of the specimen and are often absent or loose.

All landmarks and sliding semilandmarks were manually digitized using the TPSdig2 software package (Rohlf, 2010a). The whole data set (COMP) was divided in seven sub-samples following the patterns of fragmentation observed in archaeological deposits (Fig. 1). Each fragment possesses anatomical landmarks and sliding semilandmarks (Fig. 2). For anatomical landmarks, general Procrustes analyses (GPA) (Rohlf and Slice, 1990) were performed on each fragment separately, followed by PCA. Shape visualisations along the PC axes were performed using multivariate regressions (Monteiro, 1999). PCA allow one to reduce the dimensionality of the data set (Baylac and Friess, 2005) and 90% of shape variability was

**Table 1**

Geographical origins of the extant reference sample. Abbreviations for institutions: (A) Museum National d'Histoire Naturelle, (B) Department of Ecology and Evolution of the University of Lausanne and (C) University of Barcelona.

Species	N°	Inst	Country	Species	N°	Inst	Country	Species	N°	Inst	Country
<i>C. lusitania</i>	1989–28 <sup>a</sup>	A	Senegal	<i>C. russula</i>	F_ALO_9	C	Spain	<i>C. russula</i>	SB19_199 <sup>a</sup>	A	Morocco
<i>C. lusitania</i>	1982–966	A	Senegal	<i>C. russula</i>	F_ALO_10	C	Spain	<i>C. russula</i>	SB24_198 <sup>a</sup>	A	Morocco
<i>C. lusitania</i>	1981–1112 <sup>a</sup>	A	Senegal	<i>C. russula</i>	F_ALO_11	C	Spain	<i>C. russula</i>	MAR1 <sup>a</sup>	A	Morocco
<i>C. lusitania</i>	1982–967 <sup>a</sup>	A	Senegal	<i>C. russula</i>	F_ALO_12	C	Spain	<i>C. russula</i>	MAR2 <sup>a</sup>	A	Morocco
<i>C. lusitania</i>	1982–968	A	Senegal	<i>C. russula</i>	F_ALO_13	C	Spain	<i>C. russula</i>	MAR3 <sup>a</sup>	A	Morocco
<i>C. lusitania</i>	1982–969	A	Senegal	<i>C. russula</i>	F_ALO_14	C	Spain	<i>C. tarfayensis</i>	7807 <sup>a</sup>	B	Morocco
<i>C. lusitania</i>	1982–971	A	Senegal	<i>C. russula</i>	F_ALO_15	C	Spain	<i>C. tarfayensis</i>	7808 <sup>a</sup>	B	Morocco
<i>C. lusitania</i>	1982–972	A	Senegal	<i>C. russula</i>	F_ALO_16	C	Spain	<i>C. tarfayensis</i>	7809 <sup>a</sup>	B	Morocco
<i>C. lusitania</i>	1982–973	A	Senegal	<i>C. russula</i>	F_ALO_17	C	Spain	<i>C. tarfayensis</i>	7812 <sup>a</sup>	B	Morocco
<i>C. lusitania</i>	1982–974	A	Senegal	<i>C. russula</i>	F_ALO_18	C	Spain	<i>C. tarfayensis</i>	1981–1313	A	Morocco
<i>C. lusitania</i>	1982–975	A	Senegal	<i>C. russula</i>	F_ALO_19	C	Spain	<i>C. viaria</i>	2616_19 <sup>a</sup>	B	Morocco
<i>C. lusitania</i>	1984–667 <sup>a</sup>	A	Senegal	<i>C. russula</i>	F_ALO_20	C	Spain	<i>C. viaria</i>	2617_21 <sup>a</sup>	B	Morocco
<i>C. lusitania</i>	1985–1648 <sup>a</sup>	A	Senegal	<i>C. russula</i>	F_ALO_21	C	Spain	<i>C. viaria</i>	2618_23 <sup>a</sup>	B	Morocco
<i>C. lusitania</i>	1992–558 <sup>a</sup>	A	Senegal	<i>C. russula</i>	F_ALO_22	C	Spain	<i>C. viaria</i>	2619_25 <sup>a</sup>	B	Morocco
<i>C. lusitania</i>	1992–559 <sup>a</sup>	A	Senegal	<i>C. russula</i>	F_ALO_23	C	Spain	<i>C. viaria</i>	2620_27 <sup>a</sup>	B	Morocco
<i>C. lusitania</i>	1992–561 <sup>a</sup>	A	Senegal	<i>C. russula</i>	F_ALO_24	C	Spain	<i>C. viaria</i>	1972–760 <sup>a</sup>	A	Senegal
<i>C. lusitania</i>	1992–560 <sup>a</sup>	A	Senegal	<i>C. russula</i>	F_ALO_25	C	Spain	<i>C. viaria</i>	1992–542 <sup>a</sup>	A	Senegal
<i>C. russula</i>	2636 <sup>a</sup>	B	Morocco	<i>C. russula</i>	F_ALO_27	C	Spain	<i>C. viaria</i>	1992–546 <sup>a</sup>	A	Senegal
<i>C. russula</i>	2639 <sup>a</sup>	B	Morocco	<i>C. russula</i>	F_ALO_28	C	Spain	<i>C. viaria</i>	1992–550 <sup>a</sup>	A	Senegal
<i>C. russula</i>	2637_13 <sup>a</sup>	B	Morocco	<i>C. russula</i>	F_ALO_29	C	Spain	<i>C. viaria</i>	1992–551 <sup>a</sup>	A	Senegal
<i>C. russula</i>	2638_15 <sup>a</sup>	B	Morocco	<i>C. russula</i>	F_ALO_30	C	Spain	<i>C. viaria</i>	1992–553 <sup>a</sup>	A	Senegal
<i>C. russula</i>	2640_17 <sup>a</sup>	B	Morocco	<i>C. russula</i>	F_ALO_31	C	Spain	<i>C. viaria</i>	1994–1059 <sup>a</sup>	A	Senegal
<i>C. russula</i>	F_ALO_1	C	Spain	<i>C. russula</i>	F_ALO_32	C	Spain	<i>C. viaria</i>	1994–1060 <sup>a</sup>	A	Senegal
<i>C. russula</i>	F_ALO_2	C	Spain	<i>C. russula</i>	F_ALO_33	C	Spain	<i>C. viaria</i>	1994–1061 <sup>a</sup>	A	Senegal
<i>C. russula</i>	F_ALO_3	C	Spain	<i>C. russula</i>	JM2_201 <sup>a</sup>	A	Morocco	<i>C. viaria</i>	1994–1062 <sup>a</sup>	A	Senegal
<i>C. russula</i>	F_ALO_4	C	Spain	<i>C. russula</i>	JM5_200 <sup>a</sup>	A	Morocco	<i>C. viaria</i>	1994–1063 <sup>a</sup>	A	Senegal
<i>C. russula</i>	F_ALO_5	C	Spain	<i>C. russula</i>	OY3_487 <sup>a</sup>	A	Morocco	<i>C. whitakeri</i>	1894–2033 <sup>a</sup>	A	Morocco
<i>C. russula</i>	F_ALO_6	C	Spain	<i>C. russula</i>	RE5_202 <sup>a</sup>	A	Morocco	<i>C. whitakeri</i>	1981–1312 <sup>a</sup>	A	Morocco
<i>C. russula</i>	F_ALO_7	C	Spain	<i>C. russula</i>	SB11_197 <sup>a</sup>	A	Morocco	<i>C. whitakeri</i>	1981–1314	A	Morocco

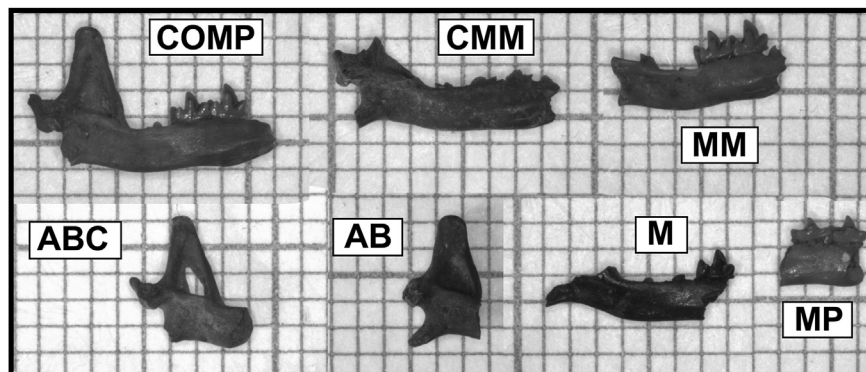
<sup>a</sup> Right and left mandibles are both included.

retained for classification analyses. Sliding semilandmarks were selected using TPSutil (Rohlf, 2010b), and TPSrelw (Rohlf, 2010c) was used to perform the sliding process. For each fragment the sliding process was performed independently. PCA were performed on each divided data set (corresponding to the seven patterns of fragmentation previously established) and shape visualisations were performed. Here, again, 90% of shape variability was retained for the classification analysis.

Because size has an important contribution to species recognition for live specimens and skulls of white-toothed shrews, size represented by the logarithm of the centroid size (the square root of the sum of squared distances of the set of landmarks from their centroid) was added as a variable for both anatomical landmarks and sliding semilandmark data sets. Using the logarithm of centroid size permits to normalise the distribution of the data. However, to improve the method, the same analyses were also performed on

shape alone. Knowing the importance of size in this data set, correct classifications will likely be lower when using shape data only, but comparisons of anatomical landmarks versus sliding semilandmarks will be particularly relevant.

To avoid potential biases in the discriminant analyses (Huberty, 1975; Baylac and Friess, 2005; Mitteroecker and Bookstein, 2011; Evin et al., 2013) especially with small groups and large numbers of variables, we performed a pattern recognition using the K-nearest neighbours algorithm (k-NN) that is less sensitive to the dimensionality of the data (Ripley, 1996; Venables and Ripley, 2002; Baylac and Friess, 2005). k-NN algorithms is a method of classification (supervised machine learning) that permits to assign a given object to classes using its K-nearest neighbours (Ripley, 1996). In our case, this simple and robust approach classifies each object of our mandible dataset using the proximity (here the Euclidian distances of the phenotype of mandibles) using classes



**Fig. 1.** Examples of the seven types of fragmented mandibles found in archeological material of El Hahoura II cave used for creating the pattern of fragmentation. See also Table 2 for anatomical descriptions.

**Table 2**  
Anatomical localisation and description of the seven fragments.

Groups	Anatomical localisation
COMP	The most complete piece, including the ascending branch (except the angular process, systematically absent) and the main part of the body of the mandible except the region situated near the incisors which is typically broken.
CMM	The same as “COMP”, but without the coronoid process.
MM	The body of the mandible from the third molar to the first one.
ABC	The ascending branch including the articular condyle.
AB	The ascending branch excluding the articular condyle.
M	The part of the mandibular body situated under the second and the third molar.
MP	The part of the mandibular body situated under the first and the second molar.

(here our five species) of its nearest neighbours found in the mandible dataset. Here, we used  $k = 1$  which gives the best results after testing from  $k = 1$  to  $k = 5$ . So, each fragment of mandible is assigned to the species of its nearest neighbour after a leave-one-out cross validation. Results of k-NN classification of well classified specimens for each fragment and for shape and form using sliding semilandmarks and anatomical landmarks were compiled and then global percentages of correctly classified specimens and fragments were calculated as well as the percentage for each specific results by fragment and the occurrence of results exceeding or equal to 80% extracted for histogram.

Finally, in order to demonstrate the efficiency of the method of classification in an archaeological context, we performed a test as an example using archaeological material of one archaeological level of the El haroura II cave (Stoetzel et al., 2011; Cornette, 2011) using sliding semilandmarks. The material used for the test is composed of eight fragments of mandibles belonging to the fragmentation pattern “M” and eighteen for the fragment “COMP” (Fig. 1) that represent the two extreme patterns of fragmentation (i.e. the smallest and the largest fragment). They belong to the Middle Palaeolithic (Aterian) and more precisely to level 8 of the El Harhoura cave (see Stoetzel et al. for details). Each archaeological fragment was then pooled with its corresponding artificially fragmented extant reference. The sliding step and PCA were then performed for the two datasets and the centroid size calculated following the previously described method. We kept 90% of the

shape variation and added the logarithm of the centroid size to perform the k-NN classification. Next, k-NN method ( $k = 1$ , as for the reference specimens) was used to attribute the archaeological material to an extant species.

All statistical analyses were performed using the software R (R Development Core Team, 2014), using the specialised library for morphometrics “R-morph” (Baylac, 2014), and the statistical libraries “MASS” (Venables and Ripley, 2002), “class” (Venables and Ripley, 2002) and “ade4” (Dray and Dufour, 2007).

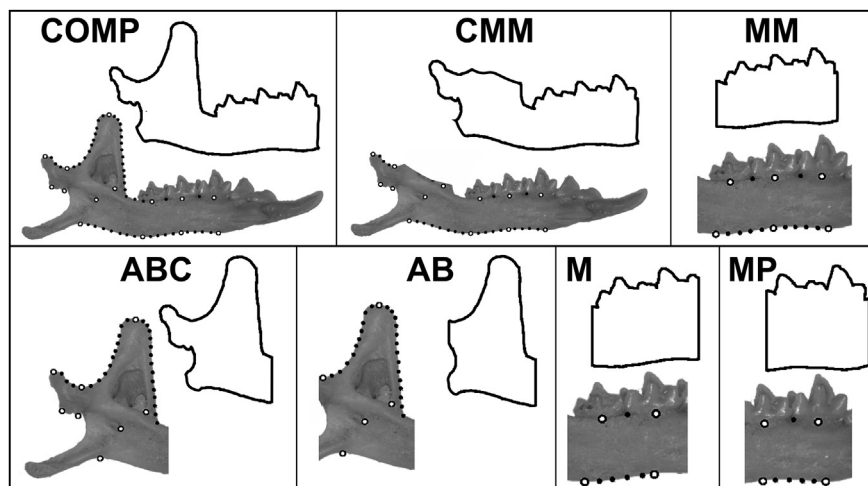
### 3. Results

#### 3.1. Form space for both sliding semilandmarks and anatomical landmarks

With more than 80% for each fragment, the classification level was very high for both methods (Fig. 3; Table 3). In addition, the differences between the two methods were minor, although some differences could be noticed. When comparing the global results of specific classifications (Fig. 3; Table 3) for each fragment based on the two methods (anatomical landmarks and sliding semilandmarks), two results were obtained. First, there were fragments whose specific classification was slightly increased by the use of sliding semilandmarks, like “ABC” and “MP”. Secondly, “MM” and “COMP” obtained a better classification when anatomical landmarks were used. The biggest difference between the two methods was found with the small fragments “ABC” where differences are around 3%. Correct classifications exceeding or equal to 80% (Table 4) are represented in Fig. 4.

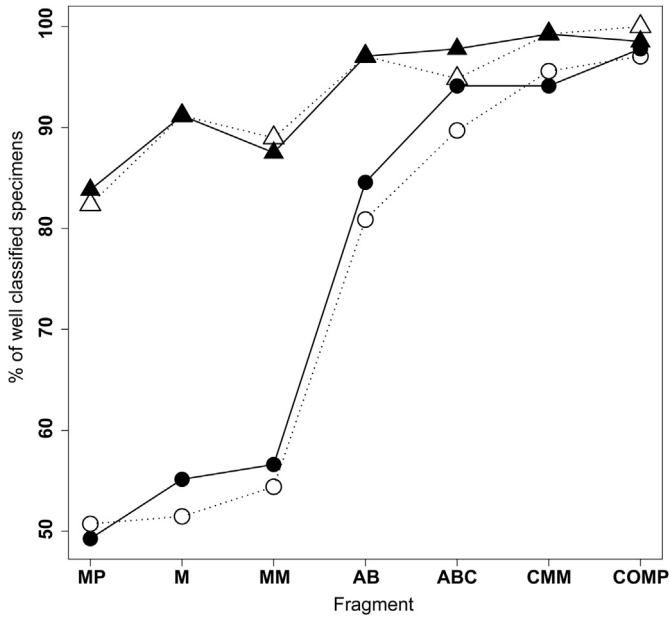
#### 3.2. Shape space for both sliding semilandmarks and anatomical landmarks

Results were significantly different from those obtained above. First, as expected, the correct classification rate was markedly lower in this case (Fig. 3) especially for “MP”, “M” and “MM” fragments. Secondly, sliding semilandmarks offered a better classification than the anatomical landmarks, except for the fragment and “MP” and “CMM”. The biggest difference was found for the fragments “M”, “AB” and “ABC” and reached up to 4.5% in the case of the latter fragment. Sliding semilandmarks offer markedly better results when taking into account classifications exceeding or equal to 80% (Table 4, Fig. 4).



**Fig. 2.** Localisation of anatomical landmarks (white points) and sliding semilandmarks (black points) on the complete mandible “COMP” and divisions of “COMP” dataset into fragments “ABC”, “AB”, “CMM”, “MM”, “M” and “MP”. Outlines correspond to the pattern of fragmentation previously established, see also Fig. 1.





**Fig. 3.** Comparison of the overall proportion of correctly classified specimens using anatomical landmarks (white circles and triangles) and sliding semilandmarks for each fragment (black circles and triangles). Circles represent the results for shape and triangles for form. Results obtained with sliding semilandmarks for shape (black circles) are presented in ascending order of correct classification.

3.3. Results regarding fragments and species

3.3.1. Species

*C. viaria*, *C. russula* and *C. lusitania* were well classified when using form data, irrespective of the use of anatomical landmarks or sliding semilandmarks (Fig. 5). *C. lusitania* is less well identified using shape data, however. *Crociodura tafayensis* is better detected by anatomical landmarks using form data and *C. whitakeri* showed the opposite pattern with sliding semilandmarks. These two species, *C. whitakeri* and *C. tarfayensis* result in the lowest classification rates, but can be well classified with sliding semilandmarks

(Table 3). *C. whitakeri* is completely discriminated with fragments “COMP”, “ABC” and “AB” using form data and with fragments “COMP” and “ABC” for shape data. *C. tarfayensis* is completely discriminated with fragment “CMM” using form data. For anatomical landmarks, *C. whitakeri* is only detected with fragment “COMP” for both form and shape data sets and *C. tarfayensis* is completely discriminated with “COMP” and “CMM” using form data.

3.3.2. Fragments

The best classification results using sliding semilandmarks or anatomical landmarks were obtained for fragments in which parts or the whole ascending ramus of the mandible was present, as in “ABC”, “COMP”, “AB” and “CMM” (Fig. 3; Table 3). Conversely, the worst results pertained to the mandibular body and involved fragments “M”, “MP”, and “MM. Interestingly, the presence of the articular condyle increases the level of classification but does not reach the classification rate obtained with coronoid process. But interestingly, sliding semilandmarks describing the coronoid do not offer a better classification than anatomical landmarks alone (Figs. 3 and 6 ABC).

3.3.3. Results of the test on archaeological material

k-NN classification for the eight archaeological fragments “M” give suggests the presence of seven *C. russula* and one *C. tarfayensis*. Results for the eighteen archaeological fragments “COMP” suggest the presence of 13 *C. russula*, two *C. whitakeri* and three *C. tarfayensis*.

4. Discussion

4.1. Sliding semilandmarks versus anatomical landmarks

Surprisingly, even the smallest fragments retained a high potential for specific identification with anatomical or sliding semilandmarks and especially when using form data as was predicted. However, the best results were obtained when using semilandmarks. In our study the two smallest fragments obtained more than 80% of good classification, which is rather high. Sliding

**Table 3**

Number of well classified fragments for each species as well as the overall proportions per species and per fragment. Results are presented for analyses on both shape and form and for analyses using only anatomical landmarks as well as sliding semilandmarks.

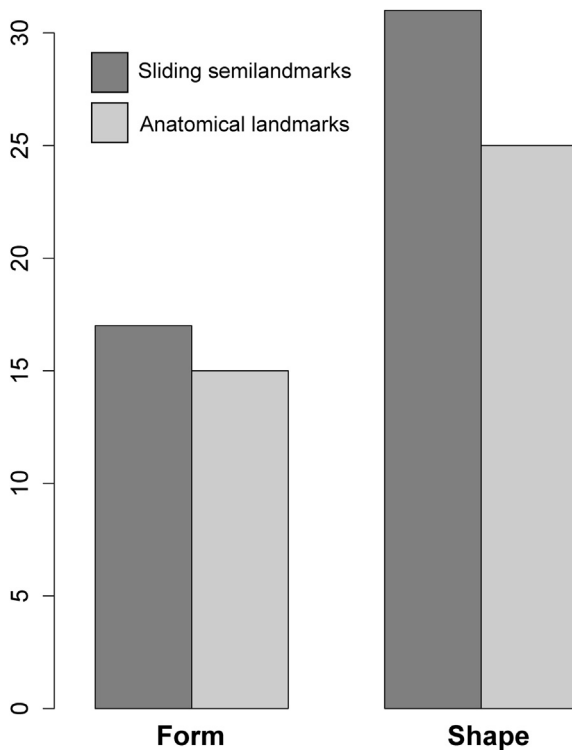
	Sliding semilandmarks-form						Anatomical landmarks-form					
	<i>C. lusitania</i> N = 26	<i>C. russula</i> N = 64	<i>C. tarfayensis</i> N = 9	<i>C. viaria</i> N = 32	<i>C. whitakeri</i> N = 5	% Well classified	<i>C. lusitania</i> N = 26	<i>C. russula</i> N = 64	<i>C. tarfayensis</i> N = 9	<i>C. viaria</i> N = 32	<i>C. whitakeri</i> N = 5	% Well classified
COMP	26	63	8	32	5	98.53	26	64	9	32	5	100.00
CMM	26	64	9	32	4	99.26	26	64	9	32	4	99.26
MM	24	58	3	32	2	87.50	24	59	4	32	2	88.97
MP	24	55	2	32	1	83.82	24	49	5	32	2	82.35
M	26	59	5	32	2	91.18	25	61	5	32	1	91.18
ABC	26	62	8	32	5	97.79	26	61	7	32	3	94.85
AB	26	61	8	32	5	97.06	26	62	8	32	4	97.06
% well classified	97.80	94.20	68.25	100.00	68.57		97.25	93.75	74.60	100.00	60.00	
	Sliding semilandmarks-Shape						Anatomical landmarks-Shape					
COMP	24	64	8	32	5	97.79	24	64	7	32	5	97.06
CMM	23	62	7	32	4	94.12	24	63	7	32	4	95.59
MM	5	43	2	27	0	56.62	3	45	3	23	0	54.41
MP	9	38	1	19	0	49.26	5	40	0	24	0	50.74
M	7	43	3	22	0	55.15	4	39	4	23	0	51.47
ABC	25	60	8	30	5	94.12	23	59	6	32	2	89.71
AB	24	54	7	26	4	84.56	24	49	6	27	4	80.88
% well classified	64.29	81.25	57.14	83.93	51.43		58.79	80.13	52.38	86.16	42.86	

**Table 4**  
Proportion of well classified specimens by species for each fragment.

	Sliding semilandmarks-form					Anatomical landmarks-form				
	<i>C. lusitania</i>	<i>C. russula</i>	<i>C. tarfayensis</i>	<i>C. viaria</i>	<i>C. whitakeri</i>	<i>C. lusitania</i>	<i>C. russula</i>	<i>C. tarfayensis</i>	<i>C. viaria</i>	<i>C. whitakeri</i>
COMP	100.00 <sup>a</sup>	98.44 <sup>a</sup>	88.89 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>
CMM	100.00 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	80.00 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	80.00 <sup>a</sup>
MM	92.31 <sup>a</sup>	90.63 <sup>a</sup>	33.33	100.00 <sup>a</sup>	40.00	92.31 <sup>a</sup>	92.19 <sup>a</sup>	44.44	100.00 <sup>a</sup>	40.00
MP	92.31 <sup>a</sup>	85.94 <sup>a</sup>	22.22	100.00 <sup>a</sup>	20.00	92.31 <sup>a</sup>	76.56	55.56	100.00 <sup>a</sup>	40.00
M	100.00 <sup>a</sup>	92.19 <sup>a</sup>	55.56	100.00 <sup>a</sup>	40.00	96.15 <sup>a</sup>	95.31 <sup>a</sup>	55.56	100.00 <sup>a</sup>	20.00
ABC	100.00 <sup>a</sup>	96.88 <sup>a</sup>	88.89 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	95.31 <sup>a</sup>	77.78	100.00 <sup>a</sup>	60.00
AB	100.00 <sup>a</sup>	95.31 <sup>a</sup>	88.89 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	96.88 <sup>a</sup>	88.89 <sup>a</sup>	100.00 <sup>a</sup>	80.00 <sup>a</sup>
COMP	92.31 <sup>a</sup>	100.00 <sup>a</sup>	88.89 <sup>a</sup>	100.00 <sup>a</sup>	100.00 <sup>a</sup>	92.31 <sup>a</sup>	100.00 <sup>a</sup>	77.78	100.00 <sup>a</sup>	100.00 <sup>a</sup>
CMM	88.46 <sup>a</sup>	96.88 <sup>a</sup>	77.78	100.00 <sup>a</sup>	80.00 <sup>a</sup>	92.31 <sup>a</sup>	98.44 <sup>a</sup>	77.78	100.00 <sup>a</sup>	80.00 <sup>a</sup>
MM	19.23	67.19	22.22	84.38 <sup>a</sup>	0.00	11.54	70.31	33.33	71.88	0.00
MP	34.62	59.38	11.11	59.38	0.00	19.23	62.50	0.00	75.00	0.00
M	26.92	67.19	33.33	68.75	0.00	15.38	60.94	44.44	71.88	0.00
ABC	96.15 <sup>a</sup>	93.75 <sup>a</sup>	88.89 <sup>a</sup>	93.75 <sup>a</sup>	100.00 <sup>a</sup>	88.46 <sup>a</sup>	92.19 <sup>a</sup>	66.67	100.00 <sup>a</sup>	40.00
AB	92.31 <sup>a</sup>	84.38 <sup>a</sup>	77.78	81.25 <sup>a</sup>	80.00 <sup>a</sup>	92.31 <sup>a</sup>	76.56	66.67	84.38 <sup>a</sup>	80.00 <sup>a</sup>

<sup>a</sup> Indicates results equal to or exceeding 80%.

semilandmarks clearly allowed an optimization of classification for some small fragments (Fig. 6) and for some species that are difficult to distinguish, like *C. tarfayensis* or *C. whitakeri*. The increased shape description provided by sliding semilandmarks allowed us to consider regions of bones devoid of anatomical landmarks, yet possessing specific information. The contrary was observed in some anatomical regions possessing a high variability but which did not help in specific classification like the coronoid process (Fig. 6). Nevertheless, these precise descriptions allowed the recognition of bio-mechanically important zones providing insights into jaw function and potentially diet.

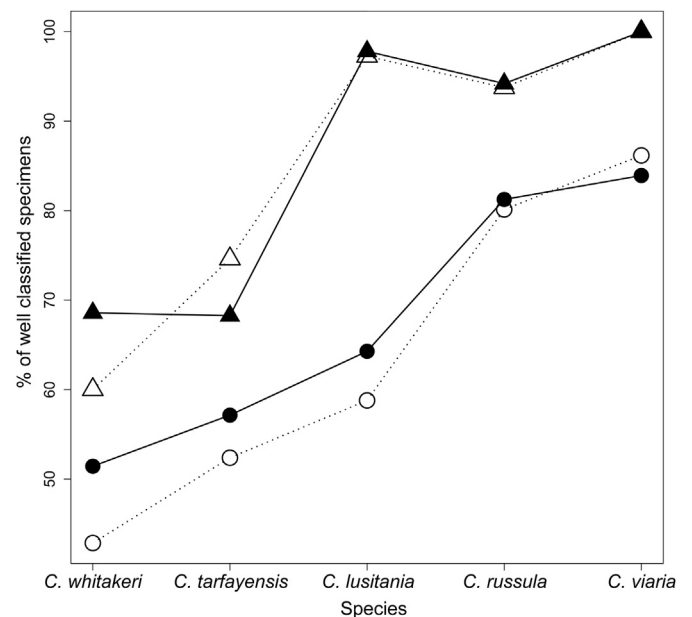


**Fig. 4.** Comparison of global percentage of correctly classified specimens using anatomical landmarks (white circles and triangles) and sliding semilandmarks (black circles and triangles) for each species. Circles represent the results excluding size and triangles including size. Results obtained with sliding semilandmarks excluding size (black circles) are presented in ascending order.

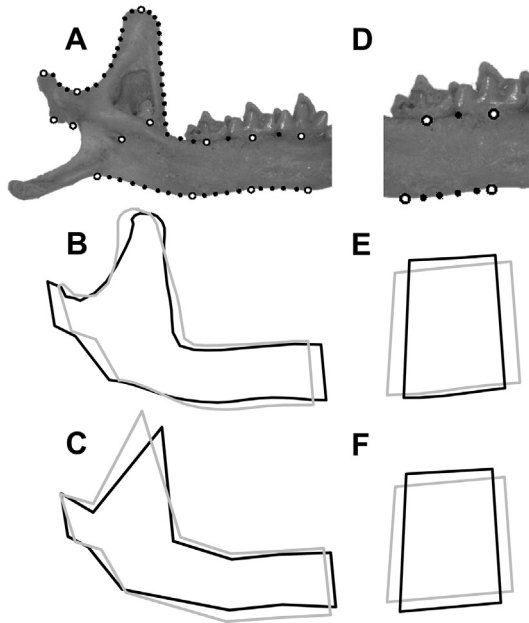
#### 4.2. Functional implications

The coronoid process of shrews is a good example of an important source of intra-specific shape variability directly linked with functional activity (Badyaev and Foresman, 2004; Cornette et al., 2012, 2013, in press). However, this anatomical region may reduce the specific–specific information contained in the fragment as they respond to functional constraints independent of species–specific information as in *C. tarfayensis*, for example. Thus, the results of our classification are not increased by the use of sliding semilandmarks on this zone (Fig. 6) despite providing a more accurate description.

On the other hand, functional differences can also be species specific and may constitute an important source of discrimination. This is particularly well demonstrated by *C. whitakeri* which was better discriminated when the coronoid process and articular condyle were included. This suggests that for further similar approaches an exhaustive analysis of shape using sliding semilandmarks could be beneficial. The functional signal contained in



**Fig. 5.** Histogram of occurrences of exceeding or equal to 80% of well classified specimens by species for each fragment (Table 4). Results are given for both form and shape using sliding semilandmarks (dark grey) and anatomical landmarks (light grey).



**Fig. 6.** Illustration of two emblematic examples where sliding semilandmarks could not increase the classification rate for “COMP” (A, B) and, on the contrary, increase the classification rate for “M” (D, E) compared to anatomical landmarks (A, C) and (D, F). The high morpho-functional signal contained within the coronoid process could explain this result.

elements like the mandible could also provide useful indirect palaeo-environmental information. As has been demonstrated by Cornette et al. (2012, 2013, in press) differences in form may reveal functional patterns linked for example to bite force which in turn may be related to the feeding habits of a species. This functional variable is known to be associated with food consistency (Young et al., 2007). In this context hypotheses on the prey consumed, derived from functional morphological patterns, may help to describe palaeo-environments.

#### 4.3. Further applications

The archaeological application presented in this paper highlights the advantages of using small fragmented material. Indeed, in this example we observe that *C. russula* is the dominant species but that two others species are also present at the site, *C. tarfayensis* and *C. whitakeri* at the Aterian period. In order to describe a historical fauna composed of predominantly fragmented material relative to an extant morphological reference sample, the experimental approach proposed here could be followed. In this case even small fragments should be measured as they may contain significant amounts of species-specific information. Misidentifications become particularly evident when all extant fragments are compared with the complete reference sample. This permits to eliminate pieces with a low proportion of good specific classification. For archaeological applications, pooling results of specific reassignments of all archaeological fragments could yield an informative global list of the extinct fauna at a given site (Cornette, 2011). As a precaution, such a faunal list should be examined according to the methodological limits associated with the method of classification and the reference data. Thus one should bear in mind that such a list is based on the phenotypic proximities between a fossil and an extant reference and does not prove a non-ambiguous species assignment.

Another possible application could be the detection of a particular species or group among abundant broken archaeological material. Here again, the same protocol with an extant reference

sample, as used in this study, should be applied. However in this case a choice of fragments should be performed in order to maximize the reassignment of the species of interest. Moreover, an optimisation of the reassignment of one species (or more) could be achieved by choosing the optimal method, either anatomical or sliding semilandmarks. The correlated effect may, however, be a decrease in the level of assignment of other species.

This study should be regarded as a first example and should be repeated for other samples involving other taxa and bone fragments, as this method is particularly dependent on the reference material used. The reference material should be as exhaustive as possible in order to increase the level of classification. In our case, the low numbers of the rare species *C. whitakeri* and *C. tarfayensis* in our reference sample may have limited the interpretation of some of the fragments. Also, both species are morphologically very similar (Vogel et al., 2006). Nevertheless, our specific reassignments of fragments separated them efficiently and permitted to formulate hypotheses on palaeo-environmental specific compositions.

Another limit of the method is that all archaeological fragments will be obligatorily assigned to an extant group. Indeed, if the reference sample is not complete at the specific level or if archaeological fragments belong to another species, extinct or not, the fragment will be misidentified. In any case a complete extant reference sample is highly recommended. Consequently, this limitation requires one to apply this method in the context of a known reference sample meaning that archaeological remains should obligatorily belonging to an extant species of the reference or an unambiguously identified extinct species.

#### 5. Conclusions

Assuming that this approach offers a global appraisal of the palaeo-environmental specific composition based on phenotypic similarities with extant species, our study showed that sliding semilandmarks clearly increase the correct classification of species, especially with small fragments. Our method demonstrated the usefulness of maintaining such fragments into the analyses because they still possess interesting shape specific information. Moreover, a functional signal is detected by this approach and has to be taken into account in taxonomic analyses. Applying this method in others cases will permit to compare its efficiency for other bones or taxa. Our results strongly encourage the further studies of fragmentation of biological objects in an archaeological context.

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