Bone remodelling in Neanderthal mandibles from the El Sidro´n site (Asturias, Spain)

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Skull morphology results from the bone remodelling mechanism that underlies the specific bone growth dynamics. Histological study of the bone surface from Neanderthal mandible specimens of El Sidro´n (Spain) provides information about the distribution of the remodelling fields (bone remodelling patterns or BRP) indicative of the bone growth directions. In comparison with other primate species, BRP shows that Neanderthal mandibles from the El Sidro´n (Spain) sample present a specific BRP. The interpretation of this map allows inferences concerning the growth directions that explain specific morphological traits of the Neanderthal mandible, such as its quadrangular shape and the posterior location of the mental foramen.

Keywords: bone remodelling pattern; histology; morphology; growth

1. INTRODUCTION

Morphological studies of the Neanderthal craniofacial system have led us to hypothesize that their anatomical features are a consequence of the specific distribution of bone growth fields [1,2]. Bones grow through the remodelling mechanism that involves the coordinated activity of osteoblasts—forming bone—and osteoclasts—resorbing bone—[3]. Through this mechanism bones change their size, shape and relative position, maintaining the functional balance of the craniofacial system and meeting the requirements of the soft tissues and the external and internal stimuli [3,4]. As a result, craniofacial elements show a particular distribution of the remodelling fields, known as the bone remodelling pattern (BRP), which reflects the bone growth dynamics. Understanding these dynamics is basic to knowing the craniofacial morphology and the evolutionary significance of the species-specific features in extinct and extant primates [1,2,5]. Each species presents a specific BRP associated with its particular craniofacial growth processes and morphology [(3,5–8); see revision in Martinez-Maza et al. [9]]. In the present contribution, we show the first BRP of Homo neanderthalensis mandibles obtained after the analysis of the El Sidro´n site (Spain; [10,11]). The bone growth dynamics inferred from this BRP explain different apomorphic features of these Neanderthal mandibles, such as their quadrangular shape, the position of the mental foramen and the retromolar space [10].

2. MATERIAL AND METHODS

Fossil remains analysed in this study are detailed in table 1. All specimens belong to the El Sidro´n sample of H. neanderthalensis [11], dated at about 49 000 years [12]. Two of the specimens (mandibles 1 and 2) did not preserve histological information on the bone surface, which was masked by chemical preservatives. Palaeohistological analysis was based on Martinez-Maza et al. ([13]; see also [5]). Briefly, high-resolution replicas of the bone surface were obtained using a low-viscosity silicone (negative replica) and a polyurethane resin (positive replica). Replicas were gold metallized and analysed with a reflected light microscope and scanning electron microscope to identify bone remodelling activities. Bone forming surfaces (BForSs) showed mineralized collagen fibre bundles produced by osteoblasts, while bone resorbing surfaces (BResSs) showed Howship’s lacunae left by osteoclasts (figure 1). BRPs for all specimens are available in the electronic supplementary material.

3. BONE REMODELLING PATTERN OF THE NEANDERTHAL MANDIBLE FROM THE EL SIDRO´N SAMPLE

A generalized BRP for the mandible of the El Sidro´n H. neanderthalensis sample was obtained through the identification of intraspecific similarities in the BRP of the mandibular regions (figure 2). Only two coronoid (SDR-009 and mandible 3) and gonion regions (SDR-011 and SD-650a) could be compared, while unique representatives of the condyle region (SD-30) and mandibular corpus (mandible 3) were used to complete this generalized map. Histological information and thus the generalized BRP are associated with the adult stage.

The buccal side of the mandibular corpus showed a large BForS extending from the anterior part of the mandibular corpus to the mandibular ramus, while a large BResS was observed close to the mental foramen, at the level of the first molar. In addition, small BResSs were located in the alveolar component at the level of the P4/M1, in the basal area at the level of the P3, and close to the ramus. The lingual side of the mandibular corpus showed a large BResS at the level of the P2 (both at the alveolar component and the sublingual fossa), and a BResS at the level of the M2. Two BForSs were located in the mylohyoid line at the level of the P3/P4 and the M2. The mandibular ramus showed a large BForS in the buccal side, while BResSs was located in the upper part of the masseteric fossa and in the coronoid process. The lingual side displayed a BForS from the endocoronoid ridge to the level of the mandibular foramen, in the gonial angle, and in the ramus–corpus area. In addition, a BResS strip was observed between the anterior border and the endocoronoid crest, and two small BResSs were found in the mandibular foramen and at the inferior border of the ramus.

4. DISCUSSION

In the present study, we have obtained for the first time, to our knowledge, histological data on the Neanderthal mandibles from the El Sidro´n sample, which...
show a specific BRP, different from other primate species (Figure 2). Bone growth directions inferred from this pattern can be associated with apomorphic features previously identified in the adult Neanderthal mandibles from the El Sidron site [10]. The mandibular corpus shows a lateral growth mainly involving the molar region. This growth direction has been described in all primates analysed to date, but interspecific differences have been observed in the BRP.

The mandibles of *Australopithecus* and *Paranthropus* [5], *Macaca mulatta* [3], *Pan troglodytes* [14] and *Procolobus verus* [15] show BForSs at both buccal and lingual surfaces, and lateral growth occurs by different buccal/lingual bone growth rates. Conversely, the El Sidron sample resembles other *Homo* species, being very similar to *Homo heidelbergensis*, both presenting BResS at the sublingual and submandibular fossae, while in *Homo sapiens* BResS is restricted to the sublingual fossa. The El Sidron specimens present specific features related to the extension of BResS from the P4 to the M2, while in *H. heidelbergensis*, it extends through the M1 to the M3 and the mandibular ramus (Figure 2). Considering the growth dynamics proposed for *H. sapiens* and *H. heidelbergensis* [3,8], we suggest an intensive lateral relocation at the molar region of the mandibular corpus. A similar lateral growth of the corpus has been proposed for the foetal and early postnatal stages of Neanderthal mandibles [2]. The results obtained in this work have led us to hypothesize that lateral growth could be associated with a wide symphysis and the characteristic quadrangular shape of the Neanderthal mandibles. However, the BRP of *H. heidelbergensis* has been associated with the divergence of the mandibular arcade [8].

El Sidron mandibular corpus shows small BResS at the buccal side that could reflect the intraspecific variations as observed in *H. sapiens* [3], *H. heidelbergensis* [8] or *P. verus* [15]. Further research is necessary to characterize BRP variability and to evaluate the influence of external (e.g. mechanical forces) and internal (e.g. hormonal factors) stimuli. However, until new histological data become available, we have included this buccal BResS within the generalized BRP and related it to the posterior location of the mental foramen and the characteristic retromolar space of the Neanderthals. The posterior position of the mental foramen, achieved during the M2 eruption, can be owing to a mesial drift of a relatively small dentition rather than to a posterior displacement of the foramen itself [16]. In this sense, the BResS close to the mental foramen in the El Sidron adult mandible could indicate the influence of dietary stresses [17] as the mandibular corpus grows laterally during this postnatal stage. Furthermore, the associated molar mesial drift could be involved in the emergence of a large retromolar space, although previous analyses cautioned about considering the retromolar space as a Neanderthal derived trait [18].

Table 1. List of the Neanderthal specimens from El Sidron (Spain) analysed in this study.

<table>
<thead>
<tr>
<th>specimen</th>
<th>preserved area</th>
<th>age</th>
</tr>
</thead>
<tbody>
<tr>
<td>mandible 1 (SDR-005 + SDR006)*</td>
<td>mandible</td>
<td>adult</td>
</tr>
<tr>
<td>mandible 2 (SDR-007 + SDR-008 + SDR-014)*</td>
<td>left hemimandible</td>
<td>adult</td>
</tr>
<tr>
<td>mandible 3 (SD-1217 + SD-1218)</td>
<td>left hemimandible</td>
<td>adult</td>
</tr>
<tr>
<td>SDR-009</td>
<td>left coronoid apophysis</td>
<td>adult</td>
</tr>
<tr>
<td>SDR-011</td>
<td>gonion</td>
<td>adult</td>
</tr>
<tr>
<td>SD-650a</td>
<td>left gonion region</td>
<td>adolescent/adult</td>
</tr>
<tr>
<td>SD-30</td>
<td>right condyle</td>
<td>adolescent/adult</td>
</tr>
<tr>
<td>SD-1081</td>
<td>left mylohyodeal groove region</td>
<td>adult</td>
</tr>
</tbody>
</table>

*No histological data were obtained from the specimens.

Figure 1. Bone surface microfeatures: (a) Howship lacunae related to bone resorbing surfaces; (b) mineralized collagen fibres related to bone forming surfaces. Images of specimen SD-650a taken with scanning electron microscope (voltage 25.0 kV; high-vacuum).
Regarding the mandibular ramus, our results show a BRP in the lingual side characterized by BForS with a particular BResS in the endocoronoid area, similar to the patterns of *H. heidelbergensis* [8], *H. sapiens* and *M. mulatta* [3], *Australopithecus* and *Paranthropus* [5], but different from *P. troglodytes* [14] and *P. verus* [15], which show BForS in the endocoronoid area. Nevertheless, small BForSs were observed close to the edge of the coronoid border in the lingual side. On the contrary, the buccal side shows a specific BRP—with a BResS in the masseteric fossa—different from the patterns of all primate species presently analysed, which show BResSs in the upper half of the ramus. The BRP of the El Sidrón ramus could reflect a specific growth characterized by the lateral growth of the coronoid region and the medial growth of the masseteric fossa (figure 2). These growth dynamics suggest that the coronoid region could be not associated with the posterior relocation of the ramus and the elongation of the mandibular corpus, unlike other primate species (e.g. [3,5,8]). However, Ponce de Leon & Zollikofer [2] proposed that the foetal and early postnatal ramus show BResS in the buccal side, while our histological data show BForS in the Neanderthal adult ramus. If both growth dynamics were correct, these ontogenetic differences could indicate that relocation of the ramus and elongation of the mandibular corpus occur early in the ontogeny. Comparative study of the BRP shows that adult *H. heidelbergensis* displays a BForS in the anterior border [8], which could indicate that in the Neanderthal lineage the elongation of the corpus stops before the adult stage. On the other hand, the buccal side of the ramus shows a BResS associated with the flat masseteric fossa described in the El Sidrón sample [10]. Nevertheless, this BResSs as well as the two BResS of the coronoid could reflect remodelling activities resulting from the mechanical forces as described for *P. verus* [15].

Overall, this histological study shows that the mandibles from the El Sidrón Neanderthal sample have a specific BRP. Although the interpretation of this map provides the bone growth dynamics of the adult mandible, this study shows how they are related to the Neanderthal features previously identified. Inter-specific comparison has shown that certain mandibular regions shared a similar BRP with *Homo* species [3] and particularly with adult specimens of *H. heidelbergensis* [8]. We propose further palaeohistological analysis of different ontogenetic stages in order to describe intraspecific variation and to understand the developmental changes that explain the craniofacial morphology of Neanderthals.

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