Postnatal changes in the growth dynamics of the human face revealed from the bone modelling patterns

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INTRODUCTION

The skull is an anatomically complex system, which has been a focal point for studies in vertebrate biology for more than a century. It presents unique opportunities to examine the role of the multiple, intricate developmental processes involved in the craniofacial morphology and in the evolutionary origin of the hominid cranium. Understanding the development of the skull can be achieved through the study of the growth dynamics of their skeletal elements considering the Moss’ functional matrices theory (Moss and Young 1960; Moss 1962; Moss, 1970 c, d; Moss and Salentjin, 1969) and the Enlow’s counterpart principle (Enlow et al 1969; Enlow and Hans, 1996). According to this theoretical framework, the human craniofacial skeleton results from the interactions of their different components that are influenced by both internal (e.g. hormonal and genetic factors; e.g. Enlow and Hans, 1996; Moss, 1960) and external stimuli (soft tissue growth, dental maturation, biomechanical factors; e.g. Moss and Young, 1960; 1997a,b,c,d; Moss and Young, 1960; Moss and Rankow, 1968; Atchley and Hall, 1991; Enlow and Hans, 1996; Lieberman et al., 2002; Klingenberg et al., 2003). The growth of the skeletal elements involves changes in their size and shape as well as their relative position within the craniofacial system in order to maintain the proper bone alignment, function and proportionate growth (e.g. O’Higgins et al., 1991; Enlow and Hans, 1996; McCollum, 1999). During the human development, these skeletal elements from the neurocranium, viscerocranium and mandible are intimately associated to the functional spaces (cranial, orbital, nasal, and oral cavities) and the soft tissues in which they are embedded (e.g. brain, muscles, connective tissues) (Moss and Young 1960; Moss, 1962; 1997a; Enlow and Hans, 1996).

The skull grows through two simultaneous and interrelated processes: growth modelling and growth displacements of the skeletal elements. Growth modelling consists in the coordinated activity of two cellular groups, osteoblasts forming bone on one surface and...
osteoclasts removing bone in the opposite surface (Enlow, 1962; Bloom and Fawcett, 1994; Enlow and Hans, 1996). This mechanism results in the increase in size of the bone and the growth movement in the direction of the forming bone surfaces also termed cortical drift (Enlow, 1962; 1963; Enlow and Harris, 1964). As a consequence of the bone modelling growth, the skeletal components are displaced into the craniofacial system with coordinated and passive movements -the primary and secondary displacements- as well as rotations (for a detailed description of these movements see Björk, 1969; Moss and Young, 1960; Moss, 1970; Bjork and Skieller, 1972; 1976; Enlow and Hans, 1996).

In the last century, Enlow showed that the activity of osteoblasts and osteoclasts is recorded in the bone surface (last formed bony lamellae) as fields of growth activity, bone formation and resorption fields (Enlow, 1963; Enlow and Hans, 1996). The distribution of these growth fields –the bone modeling pattern– is species-specific and its interpretation following the craniofacial biology principles provide data on the growth dynamics of the craniofacial skeletal components during human ontogeny (e.g. Enlow and Harris, 1964; Mauser et al., 1975; Kurihara et al., 1980; Enlow and Hans, 1996; McCollum, 2008). According to these studies, the prenatal craniofacial system shows a general growth as indicated by the bone deposition surfaces (Mauser et al., 1975; Enlow and Hans, 1996; Radlanski and Klarkowski, 2001). Bone resorption activity is first reported in the mandibular corpus and ramus around 8,5th-9th prenatal weeks (Radlanski and Klarkowski, 2001; Mauser et al., 1975; Enlow and Hans, 1996) indicating a lateral growth of the mandibular corpus and a posterior relocation of the ramus (Mauser et al., 1975; Enlow and Hans, 1996). In the postnatal period, the human facial skeleton is depository until 3 months of age, when bone resorption surfaces appear in the nasoalveolar clivus (Kurihara et al., 1980; Enlow and Hans, 1996; McCollum, 2008). From 2 to 14 years old, resorbing activity spread out over the nasomaxillary region although the extension and the location of resorbing fields change.
throughout ontogeny indicating changes in the growth dynamics associated to downward growth of the human face (Kurihara et al., 1980; McCollum, 2008). Postnatal changes in the bone modeling activity are also observed in the human mandible (Enlow and Harris, 1964; Kurihara et al., 1980; Hans et al., 1995). At 2 years old, bone resorption fields appear for the first time in the alveolar region of the buccal symphyseal region. From this age to 14 years old, resorption extends towards the basal area of the symphyseal region and/or through the anterior area of the mandibular corpus (Kurihara et al., 1980). During this postnatal period, the mandibular ramus shows a complex modelling pattern indicating a posterior growth of the mandible and its anterior displacement (Enlow and Harris, 1996). These studies analysed facial skeleton growth up to 14 years old but the bone modelling activities during the adulthood period remains almost unstudied. The aging craniofacial skeleton and mandible show morphological changes related to their horizontally increase in size of the maxilla and the mandible and to their increase in height of the anterior face (e.g. Behrents, 1985; Forsberg et al., 1991; Bishara et al., 1994; Enlow and Hans, 1996; Bondevik, 1995; Doual et al., 1997; West and McNamara, 1999; Akgül and Toygar, 2002; Albert et al. 2007; Williams and Slice, 2010; Tsiopas et al., 2011). In the present study, we analyse the postnatal growth dynamics of the craniofacial skeleton comparing juvenile and adult specimens. We observe that adult and juvenile specimens show different bone modelling patterns, adults presenting an increase of bone formation surfaces in the maxilla and mandible that explains the horizontal and vertical changes observed in aging craniofacial skeleton.

In addition, we explore how modelling activities of the facial skeleton and mandible regions are related during the ontogeny. As mentioned above, the skeletal components growing within the craniofacial complex system interact with each other keeping a functional and structural balance whereas they increase in size during development (Enlow and Hans, 1996; Moss and Young, 1960; Moss, 1962). Correspondences between different anatomical
parts of the skull have been demonstrated by morphometric analyses (see Bastir et al., 2006). However, previous studies on the craniofacial growth through the analysis of modelling activities have focused on particular facial or mandibular regions, except for Enlow’s reference work on craniofacial morphology in individuals up to 14 years old (Enlow, 1982, revised in Enlow and Hans, 1996). In the present study, we hypothesize that ontogenetical changes of the bone modelling also reflect the relationships between the facial and mandible skeleton to maintain the functional and physiological balance of the craniofacial system. Results obtained in this work will allow us to hypothesize how these relationships could be involved in the morphology of the human skull.

MATERIAL AND METHODS

The sample analysed in this study comprises twelve human skulls of known age and sex divided into two subgroups: 6 specimens in the subadult group and 6 specimens in the adult group (Table 1). All specimens belonged to the Anthropological Collection of the University of Coimbra (Portugal). Individuals with malformations, traumatisms, or alveolar bone resorption caused by tooth loss during life were excluded.

Obtaining the bone modeling pattern requires the microscope analysis of the bone surface to identify bone formation and resorption fields. The best preserved half part of both facial skeleton and mandible was employed in the analyses. We have used a non-destructive methodology that involves the replication of the bone surface and the microscope analysis of these replicas (Martinez-Maza et al., 2010; see also Bromage, 1989). Specimens were first cleaned with 60% alcohol applied with a smooth hair brush to eliminate any particles adhering to the microrelief of the bone. Second, the negative impressions of the periosteal bone from the facial skeleton and the mandible were made using a low-viscosity silicone (Exaflex injection type 3 low viscosity; DVD Dental, SA, Spain). Negative impressions were
made independently from anatomical regions of the facial skeleton (glabella, superciliar arch, nasal bones, naxomaxillary region, zygomatic bone) and the mandible (buccal and lingual side of the symphysis, mandibular corpus, and ramus) to fit the microscope's size limitations and to facilitate the manipulation during observation. Once silicone was cured, the negative cast was removed from the bone surface and delimited with a retaining wall elaborated with a silicone Optosil P plus and Optosil Xantopren (DVD Dental SA, Spain). Finally, positive replicas of each anatomical region were generated using the polyurethane resin Feropur (Feroca, SA, Spain). Replicas were then coated with gold (sputter coater SC510 BIORAD) prior to observation under a reflected light microscope (Olympus BX51TRF microscope equipped with an Olympus DP11 digital camera) using a 20 X objective (Martinez-Maza et al., 2010). To facilitate the localization of the remodeling microfeatures of the bone surface, a grid of 5X5 mm squares was drawn on the surface of the gold-coated replica using a sharp permanent pen. Each square was referred to by a coordinate (x,y) starting on the inferior left square (1,1). This grid and the outline of the anatomical region were drawn on a paper to record the data from the microscope.

The microscope analysis of the replicas from the periosteal bone surfaces allowed us to identify and map the fields of growth modeling activities following the criteria provided by Martinez-Maza et al. (2010; see also Bromage, 1989). Briefly, bone forming surfaces are characterized by mineralized collagen fibre bundles produced by osteoblasts (Figure 1a; Boyde, 1972; Bromage, 1989; Martinez-Maza et al, 2006; Martinez-Maza et al., 2010) and bone resorbing surfaces showed Howship’s lacunae produced by the osteoclasts (Figure 1b; Boyde, 1972; Bromage, 1989; Martinez-Maza et al., 2010). Bone surface also showed eroded surfaces characterized by several marks associated to the manipulation of the skulls such as trampling, tool marks, fissures or writing marks, where neither bone formation nor resorption features could be identified. From these data, modelling patterns for each individual were
drawn. Following previous works, generalized modeling patterns for the subadult and the adult groups were established through the identification of intraspecific similarities in the bone modeling field distribution of each anatomical region of the facial skeleton and mandible (Enlow and Hans, 1996; Bromage, 1989; Rosas and Martinez-Maza, 2010; Martinez-Maza et al., 2011).

RESULTS

Schematic bone modeling maps of subadult and adult specimens analysed in this study are represented in Figures 2 and 3. Individual patterns show bone modeling fields with variable size and shape, irregular boundaries, and patchy distribution. Even though different specimens show eroded surfaces lacking information, histological data recorded from the facial and mandibular regions have allowed us to elaborate generalized bone modeling patterns for adults and subadults (Figure 4). A detailed description of the modeling fields identified in the facial skeleton and the mandible is provided. Finally, we compare the generalized bone modeling patterns of subadult and adult groups.

Facial skeleton: subadult specimens

The upper region of the facial skeleton (glabella and superciliary arch) is mainly depository. Small resorption fields are only found in the superciliary arch-glabella contact area close to the frontonasal suture in individuals 101 and 218, and in the inferior area of the superciliary arch of specimen 100A. In the nasal bones, depository surfaces are present in all specimens but in 126 and 100A, which present resorptive fields close to the pyriform aperture. The nasomaxillary region shows high variability in the distribution of modeling fields respect to other facial regions. This region displays predominantly resorptive surfaces in the maxillary bone and depository surfaces in the nasal or frontal processes in individuals 218
and 101. This last specimen also presents small bone formation fields in the canine fossa region close to the infraorbital foramen and in the lateral margins of the nasal aperture. Specimen 100 shows bone resorption both in the nasomaxillary bone and in the nasal process, while tiny depository surfaces are found close to the frontonasal suture and two fields in the alveolar region of the maxilla. Specimens 284 and 126 show similar patterns characterized by bone formation fields in the nasal process, in the lateral margins of the nasal aperture, in the zygomaticomaxillary suture, and small depository fields in the canine fossa area. On the contrary, specimen 100A shows mainly depository surfaces both in the nasal process and in the maxillary bone, while resorptive surfaces are found close to the lacrimal area, in the lateral margins of the nasal aperture, in the canine fossa area, and in the zygomaticomaxillary suture. The zygomatic bone in all specimens displays primarily depository surfaces but three specimens show bone resorption activity in the orbital margin of the frontal process either close to the glabella (specimen 100) or extending from the zygomaticomaxillary suture to the level of the infraorbital foramen (specimens 126 and 100A).

**Facial skeleton: adult specimens**

The bone modeling map of the upper facial region is characterized by bone formation surfaces. Both the glabella and the superciliar arch regions are entirely depository in specimen 52, whereas specimens 92, 98, 144, and 342 show bone resorption fields in the glabella and in the area between the glabella and superciliar arch and even in the frontonasal suture (individuals 92 and 144). The remaining specimen (46) shows eroded bone surfaces in most of the glabella and superciliar arch regions but small resorption fields are identified in the glabella-superciliar arch region, and tiny bone formation fields can be identified in the frontomaxillary suture and in the upper region of the superciliar arch. The nasal bones are characterized by bone formation surfaces. This region is entirely depository in specimens 46 and 342, while in specimens 144 and 52 small resorptive fields are observed close to the
pyriform aperture and in the frontonasal suture area (specimen 144). On the contrary, specimens 92 and 98 show predominantly bone resorption fields of variable size. The nasal process of the nasomaxillary bone is also characterized by bone formation surfaces occupying the whole area in specimens 98 and 342, while specimens 46, 92, 52, and 144 show small resorption fields in the area between the frontal process and the maxillary body, and distributed from the orbitary lateral margin to the lateral margin of the nasal aperture. The specimen 144 also displays resorptive surfaces along the lateral orbital margin. The studied specimens display a highly similar distribution of the growth fields in the maxilla. This facial region is predominantly depository with bone resorption fields extending from the infraorbital foramen to the canine alveolus (46, 92, 98, 342, and 52). Small resorbing surfaces are also observed close to the nasal process in specimens 46, 52, 144 and 92, in the zygomatic nasomaxillary suture (specimens 46 and 92), and in the lateral-inferior margin of the nasal aperture (specimens 144 and 52). On its part, the zygomatic bone shows some variability, being mainly depository in specimens 46, 98, 52 and 342, while in specimens 92 and 144 bone formation is reduced to the infraorbital foramen area. Resorption fields are observed in the zygomatic maxillary suture in individuals 46, 92 and 98, also along the inferior margin of the bone zygomatic to the temporal zygomatic suture in 92 and 98, and in the area extending from the zygomatic maxillary suture to the infraorbital foramen level in specimen 46. The specimen 92 displays bone resorption activity along the lateral orbital margin to frontozygomatic suture. In this suture a resorption field is also observed in the specimen 144.

*Mandible: subadult specimens*

Among subadults, bone modeling activity is preserved in the mandibles of specimens 284 and 126, whereas specimens 101, 100A, 126, and 100 present a combination of eroded surfaces and modeling fields with variable size and distributed along different mandibular
regions. In the symphyseal region, specimens 284 and 126 display predominantly bone formation fields from the alveolar process to the inferior symphyseal border, whereas the specimen 100A shows small depository fields in the mental fossae at the level of the central incisives. All specimens show bone resorption fields in the alveolar process of the buccal side. Small resorptive fields are also observed above the mental protuberance and at the level of the canine in specimens 101 and 100A and in the mental fossae in individuals 100, 126, and 218. The lingual side of the symphyseal region is characterized by depository fields distributed both in the alveolar process and in the basal component in specimens 284, 126, and 101, whereas depository fields of variable size are observed in the lingual alveolar process of specimens 218 and 100, in the sublingual fovea of 100 and 100A, and in the inferior border of specimen 100. Resorptive fields are restricted to the alveolar process of specimen 218, the sublingual fovea of specimens 101 and 284, and the inferior border of specimen 284.

Subadult mandibular corpus is characterized by depository surfaces in the buccal side and resorbing surfaces in the lingual side. However, some resorbing fields are found in the buccal side in the alveolar process at the level of the second premolar in specimens 100A and 284, and in the basal component in the anterior region of the corpus of specimen 101, close to the mandibular foramen in specimens 101 and 126, in the posterior region of the corpus in the oblique line area of specimens 284 and 100A, and in the inferior region as a stripe of small resorptive fields extending from the symphyseal region to the ramus of specimens 100A. On its part, specimen 100 shows a high degree of erosion, but preserves resorption surfaces in the alveolar process at the level of the incisives and the canine and close to the anterior border of the ramus. At the lingual side, the sublingual fossa is characterized by bone resorption fields in the premolar and molar area in specimens 218, 101, and 284 and in the molar region of specimens 100 and 100A. Conversely, all specimens display depository surfaces in the anterior area of the sublingual fossa at the level of the lateral incisives and the canines, from
the alveolar process to the mylohyoid line. The submandibular fossa is also characterized by
depository fields in specimens 101, 284, 100, and 100A, while erosion precluded obtaining
histological data from specimen 218. The lingual side of specimen 126 show a particular
modeling pattern characterized by bone formation surfaces in the sublingual fossa, whereas
the submandibular fossa is predominantly resorptive with depository fields at the level of the
first premolar and second molar.

In the mandibular ramus, the buccal side is predominantly depository in specimens
218, 101, 284, and 126, whereas in specimens 100 and 100A this region is characterized by
bone resorption surfaces. The bone formation activity in the specimens 218, 101, 284, and
126 is distributed as large (284 and 126) or small (218 and 101) fields throughout the buccal
side of the ramus. Among them, specimens 101, 284, and 126 display resorbing fields in the
anterior border of the ramus, the coronoid process and the condyle neck, and also, in the
specimen 284, bone resorption fields extend as a diagonal stripe from the coronoid until the
angle of the ramus. The remaining two specimens -100 and 100A- are characterized by
resorbing surfaces although bone formation is observed in the area between the coronoid
process and the condylar neck, and, in the specimen 100A, close to the angle of the mandible.
In the lingual side of the ramus, bone resorption activity predominates. Resorption fields
appear in the area between the anterior border and the endocoronoid crest of specimens 218,
284, 100, and 126, along the posterior region from the condyle neck to the angle of the ramus
in individuals 218, 101, and 126, and in the area associated to the pterigoideus internus from
which extend to the mandibular corpus in all specimens except in specimen 100. Depository
surfaces are observed close to the mandibular foramen between the condyle and the coronoid
in specimens 218, 101, 284, and 126, and in the corpus-ramus contact area of specimens 101,
284, and 126. Three specimens -284, 100, and 126- also display small depository fields below
the mandibular foramen and in the mylohyoid groove.
Mandible: adult specimens

The symphyseal region shows resorptive fields in the alveolar component of the buccal side of specimens 46, 92, and 144, whereas specimens 52, 98, and 342 display predominantly bone formation fields. The basal component of this region is always depository, although specimen 342 also presents small resorbing fields at the mental fossa. Similarly, the lingual side is characterized by depository surfaces in the alveolar process, but specimens 46, 52, 98, and 144 also show small resorptive fields. The lingual basal component of the symphysis mainly displays bone formation fields with resorptive fields in the mental spine and in the digastric fossa regions. In specimens 52, 92, 98, and 144 resorptive activity is also identified in the sublingual fossa.

The mandibular corpus is predominantly depository. In its alveolar component, bone resorption activity is just found at the level of the canine of specimen 46, the premolar of 92, and the molar regions of specimens 92 and 98. On the other hand, the basal component of the corpus displays small resorptive fields close to the mental foramen area in specimens 46 and 342, in the contact region between the mandibular corpus and the ramus in specimens 46, 92, 98 and 144, and as a large stripe of resorptive fields along the inferior region of the corpus from the premolar area to the ramus in specimens 98 and 144. In the lingual side of the corpus, specimens 46, 52, and 342 display depository surfaces in the anterior region of the sublingual fossa extending from the symphyseal region to the premolar region. Small depository surfaces are also identified in the molar region close to the mylohyoid line of all specimens but 342, and in the alveolar component of specimens 92, 98, and 144. The premolar-molar region of the sublingual fossa of all individuals is characterized by bone resorption fields. The submandibular fossa displays depository surfaces along the mylohyoid line area and throughout the molar area in specimens 46, 98, and 342. Small depository surfaces are also identified in the anterior part of the submandibular fossa in specimens 46,
92, 98, and 342. A large field of bone resorption activity is observed in the anterior area of this fossa at the level premolar level in specimen 46, whereas small fields are identified in the first molar level in 144 and 342 and in the area extending from the symphyseal region to the ramus in specimen 98.

The adult mandibular ramus shows bone resorption surfaces in the buccal side of specimens 46, 52, 92, and 144, whereas specimens 98 and 342 are characterized by depository surfaces. On the one hand, resorbing activity is identified in the coronoid area in specimens 46, 92, 98, 144 and 52, in the condyle neck in 46, 92, 98, and 52, along the area running parallel to the posterior border in 46, 92, 52 and 342, in the angle of the ramus in 144 and 52, and close to the inferior border in 46, 98, 144, and 52. On the other hand, depository surfaces are observed in the coronoid area in specimens 98 and 342, in the mandibular notch area in 92, 98, and 342, in the condylar neck in 98, 52, and 342, along the area running parallel to the posterior border in specimen 98, and in the gonial region of specimen 342. The lingual side of the adult ramus displays predominantly bone formation activity. Bone resorption activity is located in the area between the anterior border and the endocoronoid crest in all specimens, in the neck of the condyle of specimens 46, 92 and 98, in the area parallel to the posterior border of specimens 46, 92, 98, and 144, and small resorptive fields in the mandibular notch area in 46, 92, 52, and 342. All specimens also display resorbing surfaces in the area associated to the pterigoideus internus and in the corpus-ramus contact area.

The generalized bone modelling patterns for subadult and adult groups (Figure 4) are obtained through the identification of intraspecific similarities in the bone modelling field distribution of each anatomical region from the facial skeleton and mandible (Enlow and Hans, 1996; Bromage, 1989; Rosas and Martinez-Maza, 2010; Martinez-Maza et al., 2011). The subadult face generalized pattern shows bone formation fields in the upper (glabella and
superciliar arch) and middle face (nasal bones and frontal apophysis of the maxillary bone), whereas bone resorption fields extends throughout the lower face (maxillar bone) and the frontal process of the zygomatic bone. In the subadult mandible, the buccal side is characterized by depository surfaces but resorption fields are identified in the alveolar component of the symphyseal region, the coronoid region and the condyle neck. In the lingual side, the anterior region of the mandible and the mandibular notch area are depository whereas the molar region in the submandibular and the sublingual fossae is resorptive.

In adults, the generalized pattern of the facial skeleton is predominantly depository but bone resorption activity, comparing with subadult pattern, is reduced to small fields in the glabella, in the frontal apophysis of the maxillary bone and in the frontal apophysis of the zygomatic bone (orbital margin). The resorbing activity of the lower face extends from the canine fossa and along the inferior border of the zygomatic bone. The adult mandible shows in the buccal side resorption activity in the alveolar component of the symphyseal region, along the inferior region of the corpus, and a large field in the corpus-ramus contact area that extends from the inferior margin to the coronoid region. The condylar neck and the mandibular angle region show small resorptive fields. Unlike subadult specimens, the lingual side is characterized by bone formation surfaces. The symphyseal region shows small resorptive fields in the digastric fossa and mental spine region. In the lingual mandibular corpus, the resorption activity is located in the molar region of the submandibular fossa and extends by the coronoid region. A large resorptive field is identified in the gonial region and close to the condyle neck.

**DISCUSSION**

In the present study, we have examined the postnatal growth dynamics of the human facial skeleton and mandible through the analysis of the bone growth modeling activity. The
bone modeling patterns from subadult and adult specimens show differences in the
distribution of growth fields that demonstrate postnatal changes in bone growth dynamics.
Integration of the modelling data from the different anatomical elements informs us about the
general growth dynamics of the whole skull and its relationships with ontogenetic postnatal
changes of the craniofacial system.

**Bone growth dynamics in the subadult face and mandible**

The modelling pattern of the face and the mandible from the subadult specimens
established here is similar to the pattern described by Enlow (1982). On the one hand, the
facial skeleton is characterized by depository surfaces in the upper (supraorbital region) and
middle face (orbital and nasal regions) and bone resorption fields in the lower face
(nasomaxillary region). According to this map, the upper and the middle face grow in a lateral
and forward direction, whereas the zygomatic region grows laterally and is relocated
posteriorly in agreement with the resorbing surfaces present at the orbital margins. The lower
face shows complex growth dynamics related with the preservation of a functional nasal
cavity. As reported by Enlow (1982), resorption in the nasomaxillary region occurs
simultaneously to bone formation in the posterior region of the face (specifically in the
craniofacial sutures) and in the nasal cavity floor and palate. Consequently, the lower face
results in a downward or vertical growth of the maxilla, the formation of the *canine fossa*, a
depression on the external surface of the maxillary bone, and the increase in height of the
nasal cavity (Kurihara et al., 1980; Enlow and Hans, 1996; McCollum and Ward, 1997).

On the other hand, the mandible pattern is characterized by depository surfaces in the
symphyseal region and the anterior corpus, whereas the posterior region of the corpus and the
ramus show complex modelling patterns. According to these data, the mandible shows a
forward growth associated to the deposition in the symphysis and the corpus, as well as to the
lengthening of the posterior region of the corpus. At the same time, the ramus and the molar
region of the corpus show a main lateral growth, whereas the condyle and coronoid regions
show a forward growth with a posterior relocation of the ramus. Interestingly, the lingual side
of the corpus shows an opposite pattern to that proposed by Enlow (1982) –resorption in the
sublingual fossa and the region anterior to the mandibular foramen, and formation in the
submandibular fossa– suggesting a marked lateral growth of the molar region in the
mandibular corpus and ramus. Other differences regarding the extension of the resorbing
surfaces in the buccal side of the ramus could be considered artefacts due to the variability of
the distribution of modelling fields observed in the human mandible (Enlow and Harris, 1964;
Kurihara et al., 1980; Hans et al., 1995). It is also worth mentioning that the symphyseal
region presents a human-specific resorption field in the alveolar component of the buccal side
related to the dental movements and the mental growth, and being involved in the
development of the human chin (Enlow and Hans, 1996).

Variability in the distribution of the modelling fields is mainly observed at the anterior
lower face and at the mandibular ramus. Differences in the distribution and the extension of
the resorption fields of the anterior face agrees with the modelling data provided by Kurihara
et al. (1980) for humans up to 14 years old, but disagrees with the mainly-depository anterior
lower face observed by McCollum (2008). As annotated by Kurihara et al. (1980) and later by
McCollum (2008), variability in the modelling maps from this facial region could be due to
morphological variations associated to differences in geographic origin. Variability in the
mandible ramus involves the extension and the location of the resorption fields in the
coronoid and the condyle neck, due to lateral adjustments while growing upward and
relocating posteriorly. Besides these two main areas, variability is also observed in the buccal
symphyseal region -previously reported by Kurihara et al (1980)- and in the mandibular
corpus -opposite to the general pattern established here, individual 126 submandibular fossa pattern resembles to that established by Enlow and Hans (1996)-.

**Bone growth dynamics in the adult face and mandible**

We have established for the first time, to our knowledge, the bone modelling pattern of the face and the mandible from adult humans. The facial pattern is mainly depository with resorption surfaces restricted to the nasal region, the canine fossae, and the inferior margin of the zygomatic region. General growth directions from this pattern indicate a lateral, downward and forward growth of the whole adult face. Like in subadult specimens, the nasomaxillary region shows complex growth dynamics associated to the functional spaces such as the nasal and the oral cavities (Moss, 197x). Bone resorption in the nasal region could be associated with the increase in high of the nasal aperture (CITA) and the forward projection of this region (CITA). Although there is no data about the nasal floor and palate for adult specimens, the modelling map obtained in our study and the morphometric data obtained in previous works (CITAS) allow us to hypothesize that the lower face shows a downward and forward growth of the maxilla associated to the increase of the nasal cavity. Resorbing surfaces in the anterior nasomaxillary region of the adult face are restricted to the area of the canine fossae, likely related to its development.

In the adult mandible, the symphysis and the anterior region of the corpus are mainly depository with resorbing surfaces restricted to the alveolar component of the buccal side of the symphysis, resembling the pattern of subadult specimens. Slight differences are found in the lingual side of the symphysis which show resorption fields in sites associated to muscle attachment (gastricus, genioglossus, geniohyoideus and the anterior part of the mylohyoideus muscles). The pattern of the posterior region of the corpus and the ramus highly differs from the subadult patterns established in the present and previous works (Enlow and Hans, 1996;
Kurihara et al., 1980). In the adults, resorption extends to cover, in the buccal side, the posterior region of the corpus and the anterior region of the ramus, and, in the lingual side, the submandibular fossa of the corpus, and the coronoid region and the lower half (gonial area) of the ramus. This map indicates a forward growth direction of the symphysis and a lateral growth of the molar region of the corpus, whereas the anterior region of the ramus grows in a posterior and medial direction. The posterior region of the ramus experiments complex growth dynamics characterized by a lateral growth of the gonial area, a medial growth of the mandibular notch area, and a lateral and medial growth of the condyle area. These growth directions indicate that the lower part of the ramus is taking a vertical position while the upper area increases in width and grows backwards.

The modelling pattern of the facial skeleton and the mandible varies less in adult than in subadult specimens. Variability is observed in the extension of the resorption fields of the anterior nasomaxillary region and the mandibular ramus, as observed in subadults. As proposed by Kurihara et al. (1980) and McCollum (2008) for subadult specimens, we hypothesize that these variations could respond to individual differences in functional or morphological characteristics (Kurihara et al., 1980; Enlow and Hans, 1996).

Postnatal changes in the growth dynamics of the human face

According to the data obtained in the present study, the facial skeleton and mandible from both subadult and adult specimens show a general downward and forward growth, in agreement with Enlow and Hans (1996). However, bone modelling patterns differ among both age groups, showing a marked spatial gradient, from a anterior region of the maxilla where most changes concentrate to the almost constant facial regions in the proximity of the neurocranium. Interpretation of these ontogenetic changes would benefit from an integrative perspective taking into consideration how the different skeletal components within the
craniofacial system interact to maintain the functional and structural balance whereas they increase in size during the postnatal development (Enlow and Hans, 1996; Moss and Young, 1960; Moss, 1962).

During the subadult stage, the facial skeleton experiences a downward growth and a forward displacement, together with the lengthening of the maxilla. This growth and displacement of the facial block is accompanied by an upward maxillary rotation (airorhynchy) due to the higher bone growth in the craniofacial sutures that attach the midface to the basicranium than in the anterior region of the maxilla (Björk and Skieller, 1976; Bromage, 1989; McCollum and Ward, 1997). This rotation of the premaxilla would be countered by a downward rotation through compensatory resorption activity in the external surfaces of the anterior region of the maxilla (Björk, 1968; Björk and Skieller, 1976; 1983; see also Bromage, 1989; McCollum and Ward, 1997 and references there in). The resulting downward facial growth vector contributes to the relative orthognathy in humans (Bromage, 1989). Simultaneously, the whole mandible is displaced forward and downward to compensate the displacements of the maxilla and to maintain the occlusal plane (Moss, 197x; Enlow and Hans, 1996). The forward displacement of the face becomes balanced through the growth of the posterior region of the mandibular corpus, whereas the vertical growth is compensated by the increase in height of the ramus and, particularly, the condyle (Enlow and Hans, 1996). During this displacement, the mandibular corpus increases in width at the anterior region, whereas the molar region and the ramus show a lateral drift. The lateral drift and the vertical growth of the ramus have been related to the growth of the basicranium as a way to keep the mandible in contact with the neurocranium through the temporomandibular joint.

With adulthood, the modelling pattern changes reflecting the biological changes that take place with maturation. Most important changes occur in the anterior region of the face,
where the resorbing surfaces that occupy most of the immature nasomaxillary region become restricted to the canine fossae whereas formation occupy the remaining surface. This modelling pattern would indicate a direct forward growth of the nasomaxillary complex during adulthood opposite to the primary displacement that takes place in immatures. Modelling changes run parallel to the fusion of the craniofacial sutures and the end of the brain growth that occur around 18 to 20 years after birth (Madeline and Elster, 1995; Björk, 2007). Considering that the posterior growth of the face in immature individuals occur by bone formation at the craniofacial sutures (Enlow and Hans, 1996), the fusion of these sutures and the subsequent arrest of the bone growth in the area would limit the growth of this posterior region of the facial skeleton. Thus, the modelling pattern and the biological constraints indicate that the facial growth in the adult stage is restricted to the anterior region and suggest a forward growth of the whole facial skeleton with an increase in the height of the nasal region.

The mandible also responds to these developmental changes, as reflected in its modelling pattern. Ontogenetic changes concentrate in the *ramus*, a region that increases in height at a rate similar to the nasomaxillary region, resulting in a increase of the nasal cavity while it maintains the occlusal plane. The *ramus* also grows laterally and medially to keep the vertical position and the contact with the neurocranium through the temporomandibular joint (Enlow and Hans, 1996). As the neurocranium and basicranium stops growing in the adult stage, the distance between the mandible fossae becomes established and the condyles would adapt to this distance changing the growth of the condyles and maintaining a functional position.

Changes in the modelling pattern of the face and the mandible during adulthood have been related to the necessity of increasing the volume of the oral and nasal cavities to cope the physiological requirements of the organism. It has been suggested that growth and
development of the craniofacial complex is related to the nasal respiratory function (Hall, 2005; Chinn et al., 2006; Weinstein, 2008; Gungora and Turkkahramanb, 2009). The coordinated development of the respiratory system and body size is likely a factor that could influence the facial growth particularly for the nasomaxillary complex and the mandible (see Bastir, 2008 and references therein). In addition, the craniofacial growth is also related to size, shape, and energetics of the entire body (Bastir, 2008). In this line, the forward growth of the anterior face that occurs during the adulthood would reflect that the neurocranium has stop growing but the body still grows together with all its physiological requirements.

In conclusion, our results demonstrate postnatal changes in the growth dynamics of the facial skeleton and the mandible. We hypothesize that these changes are related to biological events occurred in the craniofacial system such as the fusion of the craniofacial sutures, or the reaching of the adult size of the brain and the neurocranium. Thus, in the adults, a new relationship among skeletal elements of the skull emerges but the face needs to continue growing, increasing the nasal and oral cavities in order to maintain a functional and structural balance.

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**Table 1.** List of the *Homo sapiens* specimens from the Anthropological Collection of the University of Coimbra (Portugal) analysed with Reflected Light Microscopy.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Age (years old)</th>
<th>Age group</th>
<th>Sex</th>
</tr>
</thead>
<tbody>
<tr>
<td>101</td>
<td>12</td>
<td>Subadult</td>
<td>Female</td>
</tr>
<tr>
<td>218</td>
<td>10</td>
<td>Subadult</td>
<td>Female</td>
</tr>
<tr>
<td>284</td>
<td>17</td>
<td>Subadult</td>
<td>Female</td>
</tr>
<tr>
<td>100</td>
<td>7</td>
<td>Subadult</td>
<td>Male</td>
</tr>
<tr>
<td>100A</td>
<td>11</td>
<td>Subadult</td>
<td>Male</td>
</tr>
<tr>
<td>126</td>
<td>8</td>
<td>Subadult</td>
<td>Male</td>
</tr>
<tr>
<td>52</td>
<td>38</td>
<td>Adult</td>
<td>Female</td>
</tr>
<tr>
<td>144</td>
<td>29</td>
<td>Adult</td>
<td>Female</td>
</tr>
<tr>
<td>342</td>
<td>28</td>
<td>Adult</td>
<td>Female</td>
</tr>
<tr>
<td>46</td>
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<td>Adult</td>
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<tr>
<td>92</td>
<td>27</td>
<td>Adult</td>
<td>Male</td>
</tr>
<tr>
<td>98</td>
<td>24</td>
<td>Adult</td>
<td>Male</td>
</tr>
</tbody>
</table>
**FIGURE LEGENDS**

**Figure 1.** Bone formation (left) and resorption (right) surfaces identified in the sample of *Homo sapiens* analysed in this study. Image on left shows a bone formation surface from the buccal side of the mandibular corpus region (specimen 126), which is characterized by collagen fiber bundles. Image on right shows a bone resorption surface from the maxilla (specimen 218) characterized by Howship’s lacunae. Scale bar: 100 µm.

**Figure 2.** Schematic bone modeling patterns from the specimens of the subadult group. Black colour: bone formation surfaces; grey colour: bone resorption surfaces.

**Figure 3.** Schematic bone modeling patterns from the specimens of the adult group. Black colour: bone formation surfaces; grey colour: bone resorption surfaces.

**Figure 4.** Generalized bone modeling patterns from subadult and adult humans. Stippling areas represent bone deposition and grey areas represent bone resorption. Black arrows show the direction of growth by bone formation and white arrows the direction of growth by bone resorption.

**Figure 5.** Figure shows the growth vectors inferred from the generalized bone modeling patterns from subadult and adult humans. Black arrows show the direction of growth by bone formation and white arrows the direction of growth by bone resorption.