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# Investigating histomorphological variations in human cranial bones through ontogeny

*Enquête sur les variations histomorphologiques des os crâniens humains au cours de l'ontogenèse*

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### ABSTRACT

Through ontogeny, human cranial vault bones undergo differentiation in terms of their shape, size and tissue maturation. This differentiation is visible at both the macroscopic and microscopic levels. Preliminary data from a histological and compartmentalisation exploratory analysis of individuals with different ages suggest differences in the modelling and remodelling patterns through ontogeny. Child vault bones are primarily composed of avascular lamellar bone (largely vascularised), late juvenile or adolescent bones present the largest extension of mineralised areas (highly remodelled) and the lowest vascularisation (diploe is highly reduced), and the adult present highly vascularised bone in which the diploe is again largely extended. During childhood, the existence of an avascular lamellar bone promotes the sealing of the cranium bones surfaces whereas adult vault bones seem to become opened ectocranially due to the remodelling. We discuss the possibility that both effects could be related with the head thermoregulation.

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### RÉSUMÉ

Au cours de l'ontogenèse, les os de la voûte crânienne humaine subissent une différenciation en termes de forme, de taille et de maturation de tissu. Cette différenciation est visible, non seulement au niveau macroscopique, mais aussi au niveau microscopique. Les données préliminaires d'une analyse exploratoire histologique et de la compartmentalisation d'individus d'âges différents suggèrent des différences dans les schémas de modelage et de remodelage au cours de l'ontogenèse. Les os de la voûte crânienne de l'individu infantile sont composés principalement d'os lamellaire (largement vascularisé), les os du juvénile

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ou de l'adolescent présentent la plus large extension de zones minéralisées (os très remodélés) et la plus faible extension de vascularisation (le diploé est très réduit), et l'adulte présente un tissu osseux très vascularisé, dans lequel le diploé est aussi très développé. Pendant l'enfance, l'existence d'os lamellaire avasculaire favorise le scellement des surfaces des os du crâne, tandis que les os de la voûte des adultes semblent s'ouvrir ectocraniallement, en raison du remodelage. Nous discutons de la possibilité que les deux effets soient liés à la thermorégulation de la tête.

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## 1. Introduction

As part of the axial skeleton, the skull is considered one of the most important skeletal structures, the growth of which is closely associated with the development of the brain and sense organs. Similar to rest of the skeleton, skull growth is a sequential and ordered process that configures size and shape of bones through ontogeny (Scheuer and Black, 2000). As it is well known, the lower part of the neurocranium (i.e., the basicranium or the cranial base) is derived from mesoderm cells (used as a mould to build different bone morphologies during endochondral ossification, Karaplis, 2008). In contrast, the calvaria or cranial vault (the upper part of the neurocranium) and the major part of the viscerocranum (i.e., bones that constitute the face) course intramembranous ossification (osteoid substance is laid down directly over mesenchyme cells; Lewis, 2007; Scheuer and Black, 2000). Although the intramembranous ossification process of cranial bones has been embryologically well studied, the growth of the vault bones encompasses a more complex process that is not fully understood, and several important aspects, including bone tissues organisation in cranial bones, remain unknown (Bartsikas, 2002; Hillier and Bell, 2007; Percival and Richtsmeier, 2013; Trammell, 2012). During ontogeny, bone tissues are biomimeticised early while bones begin to increase in size and take shape according to their cranial morphological configuration. After the first mineralisation (constituting the trabecular or embryonic-like bone, de Ricqlès et al., 1999), bone tissues are reconfigured within the periosteum (situated in the ectocranial and endocranial surfaces) and the endosteum (the surface of the diploe cavities) (Francillon-Vieillot et al., 1990; Lieberman, 2011) such that the bone becomes thicker and radially enlarged from ossification centres. During this process (i.e., modelling, first named growth remodelling by Enlow, 1963), active periosteal and endosteal membranes replace old structures (younger tissues), depositing new bone via accretion and/or reabsorbing it in the complementary surface (Enlow, 1963, Enlow and Hans, 1996; Lieberman, 2011; McFarlin, 2006). The modelling of cranial bones is accompanied by an increase in the brain size, which provokes their passive movement via primary displacement and relocation (Aguila and Enlow, 1998; Enlow and Hans, 1996; Francillon-Vieillot et al., 1990) until they contact one another at cranial sutures (Enlow and Hans, 1996). The sutures are formed by a fibrous connective tissue derived from the mesenchyme that exhibits the same behaviour as an ossification growth site, and the sutures grow until the brain reaches its final size (Hall, 2005; Lana-Elola et al.,

2007; Mishina and Snider, 2014; Moriss-Kay and Wilkie, 2005; Opperman, 2000). Sometimes, sutures present accessory ossification centres that generate isolated bones (sutural or wormian bones, Di Ieva et al., 2013). Remodelling, unlike modelling, replaces old bone by new one (Bayliss et al., 2011; Enlow, 1963; Martínez-Maza et al., 2006; McFarlin, 2006). A specialised type of cells, termed osteoclasts, and osteoblast, which are coordinated to constitute the basic multicellular units (BMUs), multiply after chemical or mechanical stimulations and begin to reabsorb bone, those causing irregular perforations called resorption spaces (RS). Then, finely laminated bone is centripetally deposited, enclosing blood capillary and nerves, constituting a secondary osteon (SO). The number of SOs within a bone section is related to mechanical loading in long bones and is usually used for age estimation (Robling and Stout, 2008). However, due to the absences of such mechanical influences (comparable to long bones) in the vault bones, the true role of SOs in these bones continues to be discussed (Hillier and Bell, 2007; Trammell, 2012).

Despite the profuse number of investigations regarding the cranium microstructure and histology using noninvasive-nondestructive analytical protocols, such as scanning electron microscope (SEM) (Kraniović et al., 2009; Martínez-Maza, 2007; Martínez-Maza et al., 2006, 2011, 2013; Mowbray, 2005), computed tomography (CT) (Anzelmo et al., 2014), micro-computed tomography ( $\mu$ CT) (Rühli et al., 2007) and synchrotron absorption-based  $\mu$ CT (Sanchez et al., 2012), conventional histological techniques used to assess bone tissue through bone thin sections (e.g., Enlow, 1968), could aid in better understanding human cranium ontogeny and the evolution of the cranium (Bartsikas, 2002; Martínez-Maza et al., 2006). The present study focused on the histological analysis of cranial vault bones, in which we explored the microstructure of the frontal, parietal and occipital bones of three individuals from the same osteoarchaeological collection with different ages (child, adolescent and young adult). Our primary objectives in this preliminary study of vault bones histology were (i) to analyse the tissue typologies and their spatial configurations, (ii) to study the compartmentalisation and spatial distribution of the mineralised and non-mineralised areas of each bone section, and (iii) to discuss possible implications of these variations from an ontogenetical perspective.

## 2. Materials and methods

Following the methodology proposed in Cambra-Moo et al. (2012, 2014), in which we analysed sections of tibia

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