The cranial base and related internal anatomical features in Homo neanderthalensis and Homo sapiens

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Abstract
The cranial anatomy of Homo neanderthalensis and Homo sapiens is well documented in the paleoanthropological and medical literature. However, there are few high-quality visual guides of their comparative morphology. We give here a detailed description of the anatomy of two important fossil specimens, La Chapelle-aux-Saints 1 and abri Pataud 1, based on high-resolution imaging data with each specimen representing the respective morphologies of H. neanderthalensis and H. sapiens. We describe the comparative morphology of external, endocranial, and internal characteristics of the cranium, with a focus on the petrous and tympanic portions of the temporal bone. This descriptive approach shows differences between our specimens, including in positions of cerebral components relative to cranial structures and patterns of dural sinus drainage. Numerous external and internal differences in the shape of the petrous temporal are also described, including its articulation with the tympanic bone and the orientation of the petrotympanic crest. The presence of a large protuberance between the osseous Eustachian tube orifice and carotid foramen in H. neanderthalensis suggests that the levator veli palatini muscle took origin more laterally than the dilator tubae arm of the tensor veli palatini muscle, a feature shared with H. sapiens. The overall pattern that emerges is one in which two species have undergone large-scale evolutionary changes in a functionally critical region. Such differences necessitate high-quality visualization and consideration of both internal and external morphology.

KEYWORDS
human evolution, internal cranial anatomy, nasopharynx

1 | INTRODUCTION

While external morphological characteristics of the skull are well documented for human fossil species, there is less information on internal data. Specific character studies do exist, but they are not contextualized relative to other adjacent anatomical structures (e.g., Balzeau & Radovčić, 2008; Harvati, 2003; Heim, 1974; Márquez et al., 2014; Martínez et al., 2006; Rosas et al., 2014; Schwartz & Tattersall, 1996; Stoessel et al., 2016). In the context of this special issue about “the evolution, development, and functional morphology of the nasopharynx and its boundaries,” we wanted to provide a detailed description of the basic external, endocranial, and internal characteristics of the skull, with a focus on the inferior part of the temporal bone. We compare the anatomy of a fossil attributed to Homo neanderthalensis, La Chapelle-aux-Saints 1, with an Upper Paleolithic Homo sapiens, the skull from l’Abri Pataud (Figure 1). There has
been ongoing debate regarding the phylogenetic status of “Neandertals” and “modern humans.” However, as Neandertals are morphologically distinct from modern humans and this study focuses on those differences, we approach H. sapiens and H. neanderthalensis as two separate morphospecies. This descriptive article will serve as a synthetic anatomical framework for researchers studying the cranial base, the brain anatomy as reflected by the endocranial cast or internal cranial features such as the temporal bone pneumatization or the semi-circular canals. We consider jointly those anatomical traits and discuss the specificities of the two analyzed specimens. We have two objectives here: (a) to give a high-quality imaging and a detailed anatomical description of external and internal traits of the cranial base together with detailed illustrations of all the analyzed features and (b) to go beyond the well-documented apomorphies of H. neanderthalensis and H. sapiens to identify new specificities in the way external, endocranial, and internal characteristics of the skull and of the brain are integrated together.

2 | MATERIALS

La Chapelle-aux-Saints 1 is a quite complete skull (Figure 1a) from the bouffia Bonneval site at La Chapelle-aux-Saints, Corrèze, France (Boule, 1909). It is from an adult male belonging to H. neanderthalensis. Pataud 1 is a complete skull (Figure 1b) coming from the site of l’abri Pataud in les Eyzies-de-Tayac-Sireuil, Dordogne, France that is dated between 28,000 and 26,000 cal. BP (Movius Jr & Vallois, 1959; Villotte et al., 2015). It belongs to a young adult woman and is attributed to H. sapiens.

We used micro-CT datasets of those two original fossils housed in the collection of the National Museum of Natural History, in the Musée de l’Homme, Paris, France. The fossils were scanned at the imaging facility of this institution, the AST-RX platform. The resolution for the micro-CT dataset of La Chapelle-aux-Saints 1 was of 23.5 μm (0.0235 mm) and of 110 μm (0.11 mm) for Pataud 1.

3 | METHODS

We used the micro-CT datasets to reconstruct high-resolution 3D models. The model of the skull was obtained through a global and automatic segmentation of the micro-CT data with Avizo 7. We then used endomaker (Profico et al., 2020) to obtain automatically the reconstruction of the endocast from the 3D model of the skull. In addition, we segmented manually the temporal bone pneumatization and the semi-circular canals to obtain 3D models of those features. The 3D models of the skull, endocast, temporal bone pneumatization, and semi-circular canals were visualized together in Avizo 7 at different levels of transparency. Images of these respective structures were exported in isolation from Avizo in identical orientations. We used a drawing filter in Photoshop Elements to transform the 3D views in simplified traits drawings to help for the visualization of the many traits to be labeled on the different views. Then the different images of the structures were overlayed on one another. The approach is purely descriptive. The left side of the La Chapelle-aux-Saints 1 and the right side of the Pataud 1 specimens were preferred because of their better preservation relative to the contralateral side. Those images are shown in Figures 2 and 3.

4 | DESCRIPTIVE ANATOMY AND COMPARISON BETWEEN SPECIES

Figure 2 shows several views in the same infero-lateral orientation of all the anatomical features of the cranial base and related internal structures in the H. neanderthalensis fossil La Chapelle-aux-Saints 1. Figure 3 illustrates the same features in an Upper Paleolithic H. sapiens fossil from the Abri Pataud. Table 1 lists all the anatomical features that are labeled in Figures 2 and 3. All the represented anatomical features are present in H. neanderthalensis and H. sapiens but their expression and the respective organization between exocranial features and the anatomical structures of the brain or of internal cranial features, such as the temporal bone pneumatization and the semi-circular canals, exhibit differences.

We synthesize below the observed variations (Figures 2 and 3) in the context of the documented variation between the two analyzed species.

4.1 | External temporal bone morphology

The temporal bone in H. neanderthalensis and H. sapiens is relatively high in lateral view compared to other hominin species, and even to other primates.

![Image](https://example.com/image.png)
Some differences are visible here between the two analyzed specimens (Figures 2a,b and 3a,b) and reflect differences that may be widely recognized between their two respective species. The zygomatic process has a more inferior position and an inclined orientation in *H. neanderthalensis* compared to *H. sapiens*. Posteriorly, the articular eminence that borders the mandibular fossa (2) is flatter in *H. neanderthalensis* (Martinez et al., 2006). The external auditory meatus (8) has a more circular shape and is bordered inferiorly by thicker bone in *H. neanderthalensis*. This thickening leads to a coronally oriented petrotympanic crest (Harvati, 2003; Minugh-Purvis et al., 2000; Vallois, 1969) while *H. sapiens* exhibits a more sagittally oriented crest instead taking origin at the

![Figure 2](image-url). Infra-lateral views of all the anatomical features of the left part of the cranial base and related internal structures in the *Homo neanderthalensis* fossil La Chapelle-aux-Saints 1; (a) drawing of the exocranial surface with the limits of the bones and the labeled anatomical features; (b) 3D reconstruction of the exocranial surface with the same labels as in (a); (c) drawing of the endocranial surface with the limits of the cerebral lobes and the course of cerebral sulci in orange, the imprints of the venous sinuses and the meningeal system in red and the labeled anatomical features; (d) 3D reconstruction of the endocranial surface with the same labels as in (a) and the frontal lobe extension colored in purple, the temporal lobe extension colored in blue, the parietal lobe extension colored in yellow, the occipital lobe extension colored in green; (e) drawing of the exocranial surface, with bone sutures shown in orange, superposed by the endocranial surface, the temporal bone pneumatization and the semi-circular canals; (f) 3D reconstructions of the endocranial surface, of the temporal bone pneumatization and of the semi-circular canals. The anterior part of the fossil is on the left side of the images.
FIGURE 3  Infero-lateral views of all the anatomical features of the right part of the cranial base and related internal structures in the *Homo sapiens* fossil Pataud 1; (a) drawing of the exocranial surface with the limits of the bones and the labeled anatomical features; (b) 3D reconstruction of the exocranial surface with the same labels as in (a); (c) drawing of the endocranial surface with the limits of the cerebral lobes and the course of cerebral sulci in orange, the imprints of the venous sinuses and the meningeal system in red and the labeled anatomical features; (d) 3D reconstruction of the endocranial surface with the same labels as in (a) and the frontal lobe extension colored in purple, the temporal lobe extension colored in blue, the parietal lobe extension colored in yellow, the occipital lobe extension colored in green; (e) drawing of the exocranial surface, with bone sutures shown in orange, superposed by the endocranial surface, the temporal bone pneumatization and the bony labyrinth; (f) 3D reconstructions of the endocranial surface, of the temporal bone pneumatization and of bony labyrinth. The anterior part of the fossil is on the right side of the images.
anterior boundary of the mastoid process (12). Further, *H. sapiens* is apomorphic among hominins because of a more anteriorly inclined mastoid process (12) with an anterior margin of the process that is vertical while the posterior margin is angled forward (Schwartz & Tattersall, 1996). The mastoid process (12) of *H. neanderthalensis* is bordered medially by a larger mastoid notch (13) and the juxtamastoid process (14) forms an eminence that extends inferiorly below the level of the mastoid apex in lateral view (e.g., Heim, 1974; Trinkaus, 1983). In *H. sapiens*, the mastoid process is often larger and better individualized while the juxtamastoid process is smaller. *H. sapiens* is unique among hominoids in having a styloid process (10) that lies laterally, with the stylomastoid foramen (11) at its base (Schwartz & Tatersall, 1996). In the case of Pataud 1 (Figure 3b), the styloid process is missing but the pit in which it once sat (10) is still visible. Just posteriorly, the stylomastoid foramen lies at the anterior edge of the mastoid notch (11) or digastric groove.

The osseous Eustachian tube orifice (6) in both *H. sapiens* and *H. neanderthalensis* lies in close proximity to the confluence of the petrous bone, squamous temporal, and inferolateral edge of the greater sphenoid wing (only expressed as a sphenoid spine among *H. sapiens*). *H. neanderthalensis* exhibits an enlarged protuberance between the carotid foramen (9) and bony Eustachian tube orifice (6), at the location of the levator veli palatini muscle origin (7) (Huang et al., 1997). This trait is absent among *H. sapiens*. However, the location of this protuberance in *H. neanderthalensis* suggests that the levator veli palatini muscle took origin more laterally than the dilator tubae arm of the tensor veli palatini muscle. This positional configuration between the respective dilator tubae and levator origins has been described, based on comparative dissection, as a trait found only among living humans (Dean, 1985) but it appears to have also been present among *H. neanderthalensis*. It is thus likely that the common ancestor of *H. sapiens* and *H. neanderthalensis*...
possessed such an anatomical configuration. See Pagano et al. (n.d.) for a full description of this bony structure and its implications.

4.2 Endocranial morphology

Concerning the dural venous sinuses, Schwartz and Tattersall (1996) reported that H. neanderthalensis lack a groove for the superior petrosal sinus. However, this feature is visible in La Chapelle-aux-Saints 1 (23) but this feature remains rare in H. neanderthalensis. There would be a higher incidence of the petrosquamous sinus in H. neanderthalensis compared to H. sapiens (Rosas et al., 2014), even if the feature is absent in the fossil shown here. In both species, the more frequent pattern for the drainage of sinuses in the posterior part of the brain includes two lateral sinuses (22) that spread on each side in the sigmoid sinus (21). The right lateral (or transverse) sinus and the right sigmoid sinus are often larger than on the left side in association with a left occipital petalia (Rosas et al., 2014). This observation would deserve a specific study to have more details on the potential correlation between those brain and venous traits. The sphenoparietal sinus is frequent and large in H. neanderthalensis and less visible in H. sapiens. A percentage of 14% of occurrence has been reported on a sample of recent H. sapiens endocasts (Grimaud-Hervé et al., 2004). The whole set of imprints for the cerebral circulation system, particularly for the middle meningeal system (MMS below), is different between H. neanderthalensis and H. sapiens (Saban, 1982; Grimaud-Hervé et al., 2004). The MMS is much reduced in H. neanderthalensis, with often an anterior ramus (19), that arises from the anterior branch (17), and that is as developed as the posterior ramus (18). There are only a few ramifications and very rare anastomoses in H. neanderthalensis. Those characteristics are clearly visible on La Chapelle-aux-Saints 1 (Figure 2c,d). In H. sapiens, there is a clear dominance of the anterior (19) and middle rami (20) as illustrated by Pataud 1 (Figure 3c,d). This middle or obelic ramus of the anterior branch of the MMS may split in many meningeal vessels that can present multiple anastomoses. The MMS is in the continuation of the middle meningeal artery. This last enters the skull through the foramen ovale (1) and forms on the endocranial surface a relief that corresponds to the common tract of the MMS (16) in H. neanderthalensis and H. sapiens.

On the endocranial surface, the general structure of the brain is similar between the two specimens. We observe the same sulci that delimit the different lobes but also anatomical areas. This general configuration is shared within the genus Homo (Ponce de León et al., 2021). For example, the third frontal convolution (24; Balzeau et al., 2014) appears to have a similar structure with a horizontal branch of the Sylvian fissure—or anterior ramus of the lateral fissure—(25) and a vertical branch of the Sylvian fissure—or ascending ramus of the lateral fissure—(26). The relative position of the frontal bone and frontal lobe is slightly different in the two species. Indeed, the inferior course of the coronal suture has a more anterior position relative to the infero-posterior part of the frontal lobes, that is, the posterior limit of the third frontal convolution—in H. neanderthalensis. In La Chapelle-aux-Saints 1, the position of the vertical branch of the Sylvian fissure (26) is close to the inferior extension of the coronal suture (Figure 2a,c). In Pataud 1, this sulcus has a more anterior position compared to the suture (Figure 3a,c). This relative disposition implies also that the inferior course of the precentral sulcus has a different position, being more posteriorly located relative to the coronal suture in La Chapelle-aux-Saints 1 than in Pataud 1. The Sylvian valley that is the space anterior to the lateral (or Sylvian) sulcus (33) is larger in H. neanderthalensis than in H. sapiens. This is related to a larger distance between the inferior extension of the third frontal convolution (24) and the anterior part of the temporal lobe, see for example the relative position of the temporal pole (34) that is the more anterior point of the lobe. This difference in the general organization of the infero-lateral disposition of the frontal lobes relative to the posterior limit of the frontal bone deserves some attention. Indeed, we identify two different patterns in H. neanderthalensis and H. sapiens that complicate the simple dichotomy proposed between a primitive state for early hominins and a shared “human-like” morphology for some H. erectus and later hominins.

**FIGURE 4** Lateral views of the bony labyrinth of La Chapelle-aux-Saints 1 in (a) and Pataud 1 in (b). The labyrinths are aligned according to the planes of their lateral semicircular canal. The ampullar line (APA, blue line) is more vertically inclined and the inferior component of the sagittal labyrinthine index is increased (SLII, red lines) in La Chapelle-aux-Saints 1 compared to Pataud 1.
(Ponce de León et al., 2021). In *H. sapiens*, the inferior surface of the temporal lobe (39) would be larger and the cerebellar lobes (43) are also larger (Rosas et al., 2014), particularly for their medial extension (Weaver, 2005) and maybe more asymmetric (Zhang & Wu, 2021).

### 4.3 Internal temporal bone morphology

The temporal bone pneumatization is more variable and may have a larger extension in *H. sapiens*, particularly in the larger mastoid process and occasionally in the squamous temporal. The pneumatization is mainly restricted to the petromastoid areas in *H. neanderthalensis* and shows a limited bilateral variation and a reduced specific variation (Balzeau & Radović, 2008). Clear differences are documented in the shape of the semi-circular canals (read for example, Spoor et al., 2003 for a detailed presentation on the topic) and of the ossicles (Gómez Olivencia et al., 2018; Stoessel et al., 2016). The main differences for the morphol- ogy of the labyrinth are that the posterior canal has a more inferior position in *H. neanderthalensis* than in *H. sapiens*, resulting in a larger distance for SLII (Figure 4), and that the ampullar line is more vertically inclined (Figure 4). We cannot comment here on the relation between these structures which are not entirely preserved in the two fossils, this subject will certainly merit a specific study in the future. However, besides the numerous differences in dimensions and shape of all the internal features of the temporal bone, *H. neanderthalensis* and *H. sapiens* are said to have similar auditory capacities according to the analysis of estimated sound power transmission inside the outer and middle ear and the resulting bandwidth (Conde-Valverde et al., 2021). This result has been interpreted in terms of potentially similar speech capacities. In addition, we have recently identified a shared anatomical substrate on the endocranial surface possibly linked to language and common to *H. neanderthalensis* and *H. sapiens* (Mounier et al., 2020). These observations and previous results highlight the complex evolution of anatomical traits related to language skills (Albessard-Ball & Balzeau, 2018). They also illustrate that the anatomical traits observed in *H. sapiens* are not always apomorphic relatively to other hominin species.

### 5 CONCLUSIONS

The anatomy of *H. neanderthalensis* and *H. sapiens* is well documented in the paleoanthropological and medical literature. However, a complementary approach of external and internal features is rare and has been facilitated by recent development in imaging methodologies. We attempted here to give a detailed description of the basic external, endocranial, and internal characteristics of the skull, with a focus on the lower part of the temporal bone, as well as a discussion of the relative expression of the features outside and inside the skull. This purely descriptive approach shows clear differences between our two selected specimens that are globally visible between the two species, including a different position of the brain relative to the skull in the infero-lateral area of the frontal bone and frontal lobe or numerous external and internal differences in the shape of the petrous temporal.

This article shows the interest in combined studies of external, internal, and endocranial traits to better evaluate the anatomical specificities of fossil hominin species but also to discuss the implication in terms of functions and behaviors. Future research will have to include more specimens and several other species and consider in greater details the integration of external, internal, and intracranial traits.

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### AUTHOR CONTRIBUTIONS

**Antoine Balzeau:** Conceptualization (equal); formal analysis (equal); funding acquisition (lead); investigation (equal); methodology (equal); software (lead); supervision (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal).

**Anthony Pagano:** Conceptualization (equal); formal analysis (equal); funding acquisition (supporting); investigation (equal); methodology (equal); project administration (equal); resources (equal); software (supporting); supervision (equal); validation (equal); visualization (equal); writing – original draft (supporting); writing – review and editing (equal).

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