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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 *Homo neanderthalensis* suggests that the *levator veli palatini* muscle took origin more laterally than the *dilatator tubae* arm of the *tensor veli palatini* muscle, a feature shared with *Homo 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.

Key words: internal cranial anatomy; human evolution; Nasopharynx

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. 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 lower 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. This descriptive paper 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 canal. We consider jointly those anatomical traits and discuss the specificities of the two analyzed specimens. We have two objectives here: 1) to give a detailed anatomical description of external and internal traits of the cranial base together with detailed illustrations of all the analyzed features and 2) 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.

MATERIALS

La Chapelle aux Saints 1 is a quite complete skull from the bouffia Bonneval site at La Chapelle-aux-Saints, Corrèze, France. It is from an adult male belonging to *H. neanderthalensis*. Pataud 1 is a complete skull coming from the site of l’abri Pataud in les Eyzies-de-Tayac-Sireuil, Dordogne, France that is dated between 28000-26000 cal. BP (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 microCT dataset of La Chapelle aux Saints 1 was of 23.5 microns, and of 110 microns for Pataud 1.

METHODS

We used the micro CT datasets to reconstruct high-resolution 3D models. The model of the skull was obtained 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. Different complementary images of these respective structures were exported in the same orientation. We used a drawing filter in Photoshop Elements to transform the 3D views in traits drawings to help for the visualization of the many traits to be labelled on the different views. 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 1 and 2.

DESCRIPTIVE ANATOMY AND COMPARISON BETWEEN SPECIES

Figure 1 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 2 illustrates the same features in an Upper Paleolithic *H. sapiens* fossil from the Abri Pataud. Table 1 list all the anatomical features that are labelled on Figures 1 and 2. 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 some differences.

<insert around here Table 1, figures 1 and 2, ideally it would be perfect that fig 1 and 2 would be displayed in full page size on two adjacent pages>

We synthesize below the observed variations (Figs. 1 and 2) in the context of the documented variation between the two analyzed species.

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 (Schwartz, Tattersall, 1996). Some differences are visible here between the two analyzed specimens (Figs 1a,b and 2a,b) but those differences are also clear between the two 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* (Martínez 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 (Vallois, 1969, Minugh-Purvis et al., 2000, Harvati, 2003) while *H. sapiens* exhibits a more sagittally oriented crest instead taking origin at the 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 2003). 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, Tattersall, 1996). In the case of Pataud 1 (Fig. 2b), 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 the *dilatator 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. (this issue) for a full description of this bony structure and its implications.

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. 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, 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, 2004). The middle meningeal system 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 few ramifications and very rare anastomoses in *H. neanderthalensis*. Those characteristics are clearly visible on La Chapelle-aux-Saints 1 (Fig.1c and d). In *H. sapiens*, there is a clear dominance of the anterior (19) and middle rami (20) as illustrated by Pataud 1 (Fig.2c and 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 middle meningeal system (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 Leon 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, i.e. 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 (Fig. 1a,c). In Pataud 1, this sulcus has a more anterior position compared to the suture (Fig. 2a,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 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 relatively to the posterior limit of the frontal bone deserves some attention. Indeed, we identify two different patterns in *H. neanderthalensis* and *H. sapiens* that complicates the simple dichotomy proposed between a primitive state for early hominins and a shared “human-like” morphology for some *H. erectus* and later hominins (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 and Wu, 2021).

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 and Radovčić, 2008). Clear differences are documented in the shape of the semi-circular canals (Spoor *et al.*, 2003) and of the ossicles (Stoessel *et al.*, 2016; Gómez-Olivencia *et al.*, 2018). 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 and Balzeau, 2018). They also illustrate that the anatomical traits observed in *H. sapiens* are not always apomorphic relatively to other hominin species.

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 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 paper shows the interest of 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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Table 1: Detailed legend of the anatomical features that are represented on Figures 1 and 2

Exocranial features (red arrows and number 1 to 15 on Figs. 1, 2 a, b)	Imprints of the cerebral circulation system on the endocast (shown in red on Figs. 1, 2 c and d)	Endocranial features (red arrows and numbers on Figs. 1, 2 c)
1: Foramen ovale	16: Common tract of the middle meningeal system	24: Third frontal convolution
2: Mandibular fossa	17: Anterior branch of the middle meningeal system (MMS)	25: Horizontal branch of the Sylvian valley
3: Entoglenoid tubercle	18: Posterior branch of the middle meningeal system	26: Vertical branch of the Sylvian valley
4: Petrotympanic fissure	19: Bregmatic ramus of the anterior branch of the MMS	27: Inferior frontal sulcus
5: Sphenoid spine	20: Obelic ramus of the anterior branch of the MMS	28: Second frontal convolution
6: Osseous Eustachian tube orifice	21: Sigmoid sinus	29: Precentral sulcus
7: <i>Levator veli palatini</i> muscle origin	22: Lateral sinus	30: Ascending frontal gyrus
8: External auditory meatus	23: Superior petrosal sinus	31: Central sulcus
9: Carotid foramen		32: Parietal lobe
10: Styloid and vaginal processes		33: Lateral sulcus
11: Stylomastoid foramen		34: Temporal pole
12: Mastoid process		35: Superior temporal sulcus
13: Mastoid notch		36: Middle temporal sulcus
14: Juxtamastoid process		37: Inferior temporal sulcus
15: Occipitomastoid crest		38: Fourth temporal sulcus
Sutures are shown in orange (on Figs. 1, 2 a, b and e)		39: Temporal lobe
Bone names are written in orange (on Figs. 1, 2 a)		40: Temporo-occipital fissure
		41: Occipital lobe
		42: superior occipital sulcus
		43: Cerebellar lobe

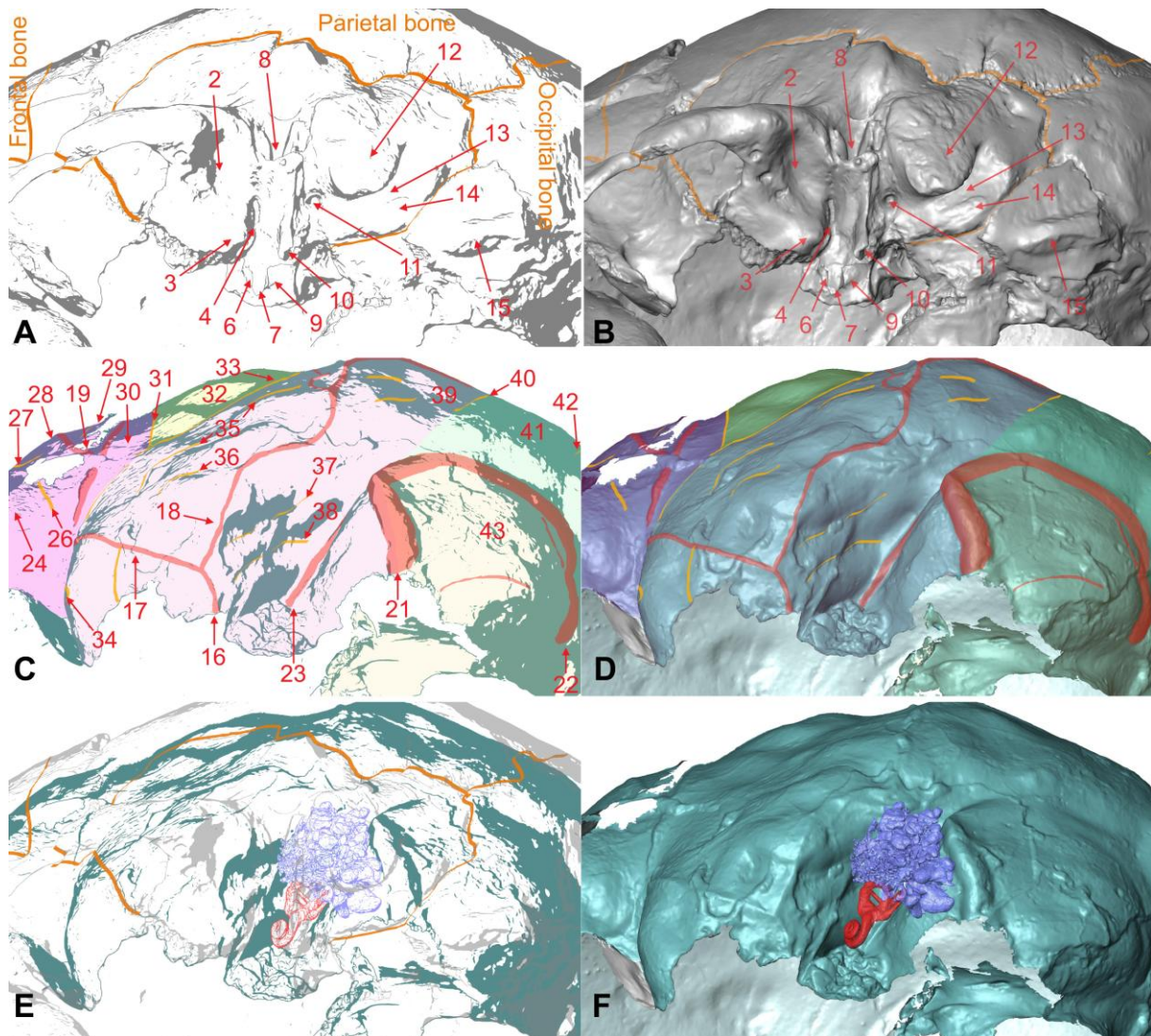


Figure 1. infero-lateral views of all the anatomical features of the left part of the cranial base and related internal structures in the *Homo neanderthalensis* fossil La Chapelle aux Saints 1; a: drawing of the exocranial surface with the limits of the bones and the labelled anatomical features; b: 3D reconstruction of the exocranial surface with the same labels than 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 labelled anatomical features; d: 3D reconstruction of the endocranial surface with the same labels than 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 transparency to the endocranial surface, to the temporal bone pneumatization and to 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.

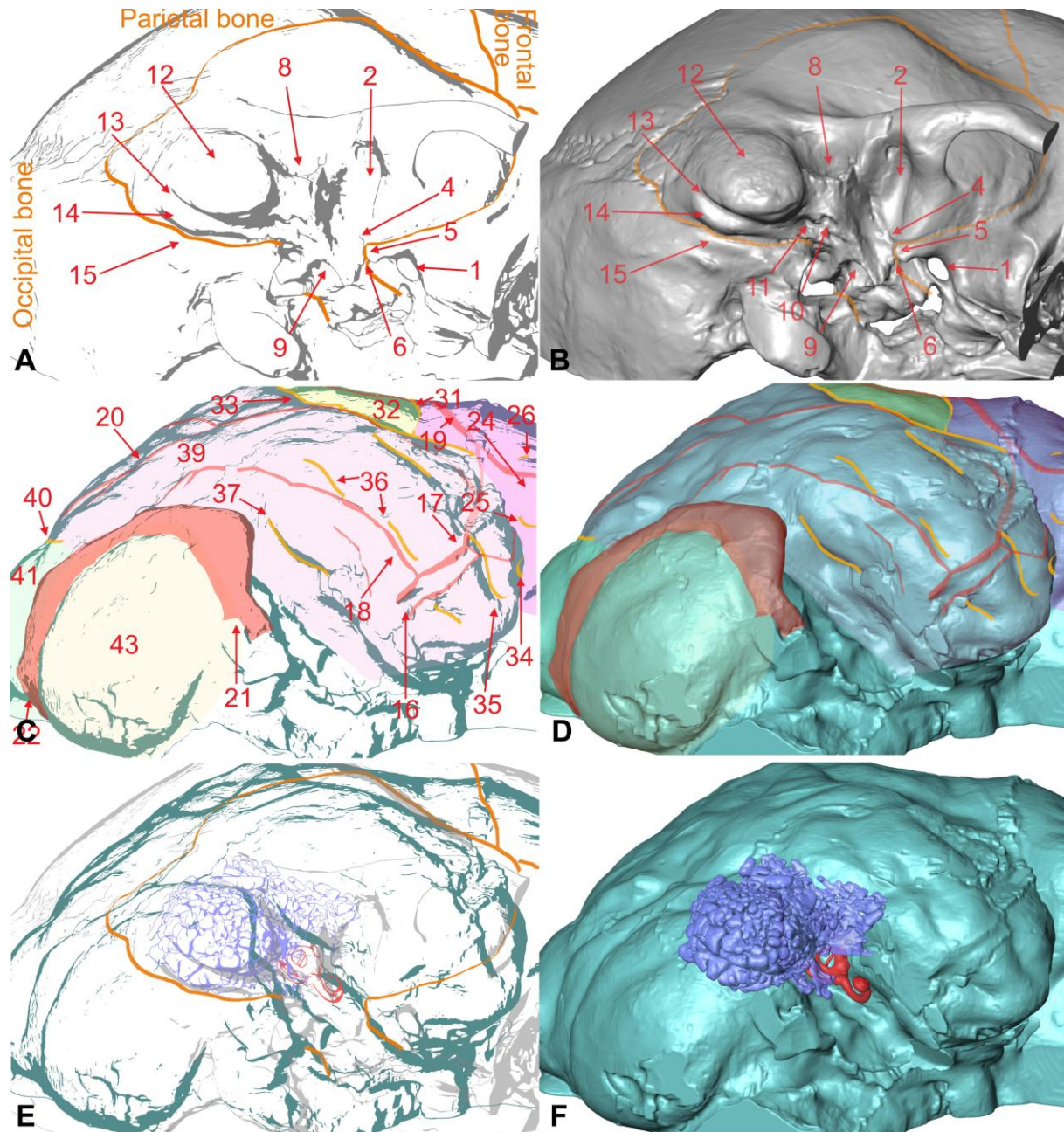


Figure 2. infero-lateral views of all the anatomical features of the right part of the cranial base and related internal structures in the *Homo sapiens* fossil Pataud 1; a: drawing of the exocranial surface with the limits of the bones and the labelled anatomical features; b: 3D reconstruction of the exocranial surface with the same labels than 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 labelled anatomical features; d: 3D reconstruction of the endocranial surface with the same labels than 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 transparency to the endocranial surface, tu the temporal bone pneumatization and to 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 right side of the images.

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