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COMMENTARY

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# Unfused transverse foramen of the atlas vertebra in the Neandertal lineage fossils

**Asier Gómez-Olivencia**[1,2,3] | **Mikel Arlegi**[4,5] |
**Juan José Valenzuela-Fuenzalida**[6] | **Mathias Orellana-Donoso**[6,7] |
**Juan Luis Arsuaga**[2,8] | **Juan A. Sanchis-Gimeno**[9]

[1]Departamento de Geología, Universidad del País Vasco-Euskal Herriko Unibertsitatea (UPV/EHU), Leioa, Spain
[2]Centro UCM-ISCIII de Evolución y Comportamiento Humanos, Madrid, Spain
[3]Sociedad de Ciencias Aranzadi, Donostia-San Sebastián, Spain
[4]McDonald Institute for Archaeological Research, Department of Archaeology, University of Cambridge, Cambridge, UK
[5]Histoire Naturelle des Humanités Préhistoriques (HNHP, UMR 7194), PaleoFED, MNHN/CNRS/UPVD, Musée de l'Homme, Paris, France
[6]Departamento de Morfología, Facultad de Medicina, Universidad Andres Bello, Santiago, Chile
[7]Escuela de Medicina, Universidad Finis Terrae, Santiago, Chile
[8]Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, Madrid, Spain
[9]GIAVAL Research Group, Faculty of Medicine, University of Valencia, Valencia, Spain

**Correspondence**
Asier Gómez-Olivencia, Departamento de Geología, Universidad del País Vasco-Euskal Herriko Unibertsitatea (UPV/EHU), Leioa, Spain.
Email: asier.gomezo@ehu.eus

Juan A. Sanchis-Gimeno, GIAVAL research group. Faculty of Medicine. University of Valencia, Spain.
Email: juan.sanchis@uv.es

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## Abstract

In anatomically modern humans, the atlas can display an unfused transverse foramen (UTF) but currently the presence of UTF in the Neandertal lineage is uncertain due to a scarcity of prevalence studies and no exhaustive record of its presence throughout the entire hominin fossil record. In this context, this study aimed to assess the UTF prevalence in Neandertal lineage fossils. In the Neandertal lineage fossil record, UTF was identified in three atlases: a Middle Pleistocene Preneandertal fossil (VC3) from Sima de los Huesos, and the Neandertal specimens Kebara 2 and Krapina 98. These results suggest that UTF may have been present in the hominin lineage since, at least, the Middle Pleistocene. An UTF could have been present in other, older hominin lineages but this remains unclear due to the generally poor preservation of atlases outside the Neandertal lineage fossil record. However, the existence of UTFs in the Neandertal lineage warrants further investigation into the evolutionary and developmental factors underlying this vertebral morphological variation.

KEYWORDS
atlas vertebra, developmental anatomy, fossil hominines, Neandertal, unfused transverse foramen

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## 1 | INTRODUCTION

The first cervical vertebra (C1) or atlas differs from other cervical vertebrae in its anatomy and function (Scheuer & Black, 2000). It consists of an anterior and posterior arch, two lateral masses, and a neural foramen (Drake et al., 2010; White et al., 2011). The lateral masses contain a transverse process (TP) and both superior and inferior articular facets. The superior facets articulate with the occipital condyles, while the inferior facets and the internal surface of the anterior arch articulate with the axis (C2), the second cervical vertebra. Within each TP, there is a transverse foramen (TF) which is the passageway for the vertebral artery (VA) and vertebral veins. Each TF of the atlas allows for the passage of the VA, on its way superiorly to meet the contralateral partner artery to form the basilar artery, which is accompanied by the vertebral veins. In addition, sympathetic fibers join the vertebral nerve/plexus usually from the vertebral ganglion and/or inferior cervical/stellate ganglion. Ventral rami from the upper six cervical spinal levels also connect to the vertebral nerve/plexus carrying somatosensory information (Drake et al., 2010).

The TF of cervical vertebrae has traditionally been described as consisting of three components: (1) the true TP located posteriorly (known as diapophysis), (2) an anterior vestigial costal element or rudimentary cervical rib (referred to as pleurapophysis), and (3) for some authors, a costotransverse bar laterally (Castellana & Kósa, 1999; Cave, 1975; Macalister, 1868; Scheuer & Black, 2000; Starck, 1978). However, the pioneering study made by Allen (1879) on variants of the human atlas, is still acknowledged (Allen, 1879, p. 25): "The anterior part of the TPs of the typical cervical vertebrae is now usually looked on as the homolog of a rib, its extremity being comparable with the body, its point of origin with the head, and the part directly in front of the arterial foramen with the neck of a rib. This part in the atlantal and axial TPs has, however, a somewhat different morphological signification from that of the typical cervical vertebrae."

In anatomically modern humans (AMHs), the atlas ossifies from three primary centers. Each lateral mass develops a center that includes the articular pillar and approximately half of the posterior arch, becoming active during the seventh week of prenatal life. Additionally, the anterior arch has its own ossification center, which becomes active during the first year of life. The TP forms through the fusion of a thick posterior bar, resulting from the lateral extension of the ossification center of the lateral mass, which is already present at the time of birth and a thinner anterior bar that develops from the ventrolateral edge of the articular pillar, which develops later. The posterior bar will fuse to the anterior bar, passing around the position of the VA, forming the TF between the third and fourth year of life. The anterior center of ossification gradually spreads laterally, forming a distinct anterior arch during the third or fourth year of life. Fusion between the anterior arch, which is located along the front portions of the superior articular facet, and each lateral mass at the neurocentral junction occurs around the fifth–sixth year of life (Allen, 1879; Macalister, 1893; Menezes, 2008; Menezes & Fenoy, 2009; Scheuer & Black, 2000). It is known that 7.9% to 10.2% of AMH atlases can display unclosed or unfused transverse foramen (UTF) (Figure 1) (Billmann & Le Minor, 2009; Sanchis-Gimeno et al., 2018; Travan et al., 2015; Wysocki et al., 2003).

Because nearly 10% of AMH may have a UTF, it would be worthwhile to know how this morphological variation fares among other hominin species, especially the closest lineage, the Neandertals. Nonetheless, the prevalence of UTF in the Neandertal lineage is uncertain due to a dearth of prevalence studies and there is no exhaustive record of its presence throughout the entire hominin fossil record or its potential prevalence among fossil specimens. Following on from this, the objective of this study was to determine the presence of the UTF in the Neandertal lineage fossil record.

**FIGURE 1** Caudal view of anatomically modern human (AMH) atlases with fused (left) and unfused (right) transverse foramina.

## 2 | MATERIALS AND METHODS

We reviewed the Preneandertal and Neandertal fossil record in order to assess the absence/presence of UTF. The UTF absence/presence was determined through visual inspection of the original specimens and a comprehensive review of the literature (Table 1). The Neandertal atlas fossil record is relatively abundant and at least 15 atlases from nine sites have been found. The Kebara 2, Krapina 98, Krapina 99, Krapina 100, La Ferrassie 1, La Chapelle-aux-Saints 1, La Quina H5 atlases, and the atlases SD-1643 and SD-1605/1595 from El Sidrón preserve, at least, one complete TP. In the case of Regourdou 1 (Gómez-Olivencia et al., 2013), it is nearly complete. In the case of Feldhofer, Schmitz et al. (2002) describe the presence of a right articular surface of an atlas (NN17) which has not been illustrated, but we assume that it does not preserve the TP. In addition, Preneandertal atlases from the Middle Pleistocene site of Sima de los Huesos (Sierra de Atapuerca, Burgos, Spain) were also studied (Table 1).

## 3 | RESULTS

In the known Neandertal sample there are two specimens that show UTF: Kebara 2 on the left TP and Krapina 98 on the right TP. For the current Neandertal fossil record, we would obtain a maximum prevalence of UTF of 20% (2 individuals out of 10) based on the individuals

**TABLE 1** Neandertal lineage atlas vertebrae fossil record.

| Taxon | Sample (S)/individual (label) | Number of atlases | Number of complete[a] transverse processes (number of atlases with at least one complete) | Notes | Reference(s) |
|---|---|---|---|---|---|
| Preneandertals | Sima de los Huesos (S) | 11 | 3 (2) | | Carretero et al. (1999); Gómez-Olivencia et al. (2007); Gómez-Olivencia and Arsuaga (2024) |
| *Homo neanderthalensis* | Kebara 2 | 1 | 1 | | Arensburg (1991); this work |
| | Krapina 98 | 1 | 1 | | Trinkaus (2016); Palancar, García-Martínez, et al. (2020) |
| | Krapina 99 | 1 | 1 | | Trinkaus (2016) |
| | Krapina 100 | 1 | 1 | | Trinkaus (2016) |
| | La Ferrassie 1 | 1 | 1 | | Heim (1976); Gómez-Olivencia (2013a) |
| | La Chapelle-aux-Saints 1 | 1 | 1 | | Boule (1911–1913); Gómez-Olivencia (2013b) |
| | La Quina H5 | 1 | 0 | Specimen lost (Verna, pers. com.) | Martin (1923) |
| | Neandertal (NN 17) | 1 | 0? | Not illustrated | Schmitz et al. (2002) |
| | Regourdou 1 | 1 | (1) | | Gómez-Olivencia et al. (2013) |
| | Shanidar 1 | 1 | 0? | | Trinkaus (1983) |
| | Shanidar 2 | 1 | 0 | | Trinkaus (1983) |
| | El Sidrón (SD-1643) | 1 | 1 | | Ríos et al. (2015); Palancar, Torres-Tamayo, et al. (2020) |
| | El Sidrón (SD-1605/1595) | 1 | 1 | | Ríos et al. (2015); Palancar, Torres-Tamayo, et al. (2020) |
| | El Sidrón (remaining sample) | At least 2 | 0 | | Palancar, Torres-Tamayo, et al. (2020) |

[a] Complete or nearly complete transverse processes in which it is possible to observe the presence/absence of UTF; Values between () correspond to estimations (nearly complete transverse foramina); N/O = non-observable.

in which it is possible to observe the complete TP/TF. Moreover, we would obtain a minimum prevalence of UTF of 13.3% (2 individuals out of 15), assuming the absence of UTF in the fragmentary TPs in which it has not been possible to perform the observation. For both Kebara 2 and Krapina 98, an UTF only preserves on one TP making this morphology unilateral, but given the preservation of these atlases, it is not possible to rule out that they could be bilateral.

Among the Preneandertals from Sima de los Huesos, a single case of UTF was observed (VC3) among the two atlas specimens preserving at least one complete TF. In the Sima de los Huesos sample a minimum of 11 atlases are represented, but in most of the specimens the TPs are missing (Gómez-Olivencia et al., 2007; Gómez-Olivencia & Arsuaga, 2024). For the current Preneandertal fossil record, we would obtain a maximum prevalence of UTF of 50% (one individual out of two) based on the individuals in which it is possible to observe the complete TP/TF. Moreover, we would obtain a minimum prevalence of UTF of 9.1% (1 individual with UTF out of 11), assuming the absence of UTF in the fragmentary TPs in which it has not been possible to perform the observation.

## 4 | DISCUSSION

We have found the presence of three atlases with UTF in the Neandertal lineage (i.e., Neandertal and Preneandertal) fossil record: VC3 from Sima de los Huesos, Kebara 2 and Krapina 98 (Figure 2) (Billmann & Le Minor, 2009; Sanchis-Gimeno et al., 2018; Travan et al., 2015; Wysocki et al., 2003). The prevalence of UTF among known fossil atlases in Preneandertals (9.1%–50%) and Neandertals (13.3%–20%) would be similar to and/or higher than studied AMH populations (7.9%–10.2%; Wysocki et al., 2003; Billmann & Le Minor, 2009; Travan et al., 2015; Sanchis-Gimeno et al., 2018). However, it should be noted that the relative number of preserved TF in the hominin fossil record in which it is possible to assess the prevalence of

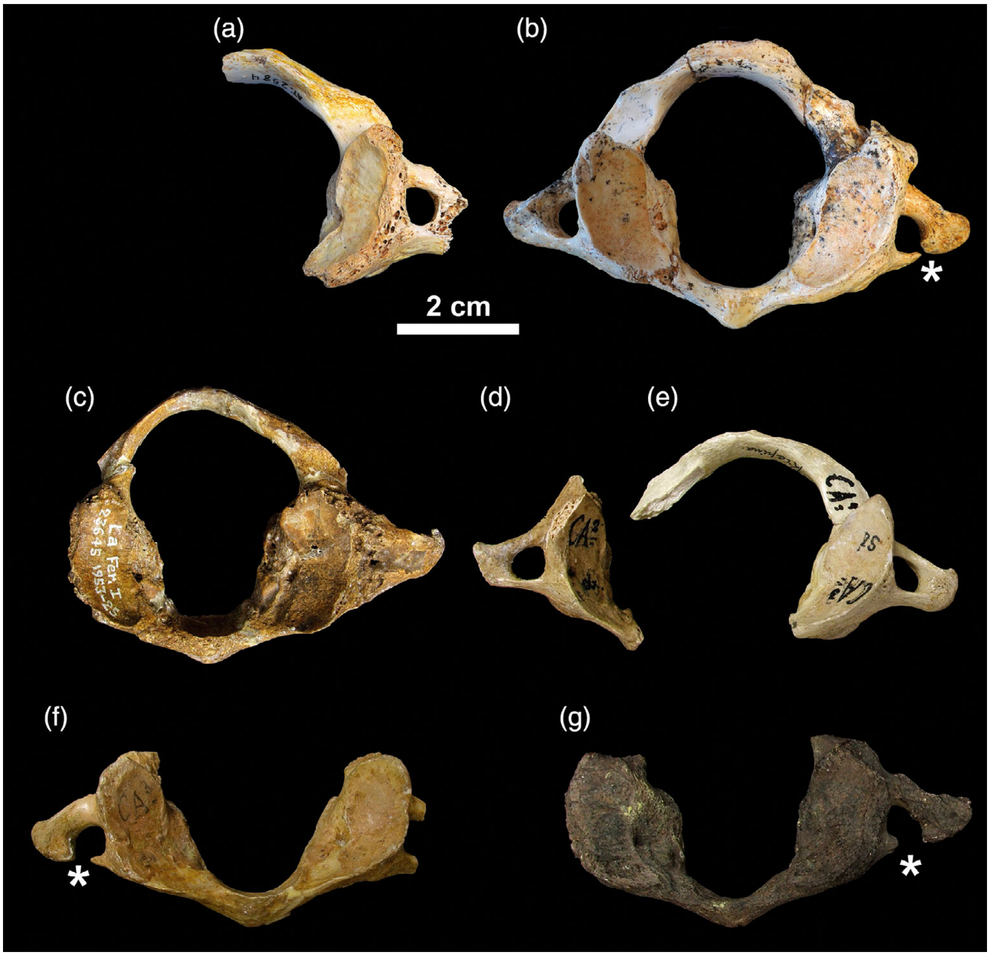

FIGURE 2 Selected fossil hominin atlases of the Neandertal lineage in cranial view with fused and unfused transverse foramina (UTF; marked with an asterisk). Middle Pleistocene atlases from Sima de los Huesos: (a) AT-2584; (b) VC3. Neandertal atlases: (c) La Ferrassie 1; (d) Krapina 99; (e) Krapina 100/101; (f) Krapina 98; (g) Kebara 2.

UTF is relatively low, both in absolute terms and also in relative terms, compared to the total amount of known hominin atlases in the fossil record because vertebrae are generally fragile and preservation is often variable.

The likely anthropic origin for the Sima de los Huesos hominin accumulation (SH; 430–300 ka), located in the Cueva Mayor-Cueva del Silo karst system in the Sierra de Atapuerca (Burgos, Spain) (Arsuaga et al., 2014, 2015, 2024) has yielded evidence of at least 11 atlases. However, only two of them preserve the TPs complete enough for study: (1) the partial atlas AT-2584, which preserves the left lateral mass, and a nearly complete left TP and the posterior arch; and (2) the complete atlas VC3 which preserves both TPs with the left side having an UTF (Carretero et al., 1999; Gómez-Olivencia et al., 2007; Gómez-Olivencia & Arsuaga, 2024). The relatively large number of known partial-to-complete skeletons of Neandertals is due to burial practices (see Pettitt, 2011 for a review) and this could be, at least partially, the reason for the larger record of preserved atlases. There are, however, other factors to be considered, as burial practices do not always ensure the preservation of atlases, which are inherently fragile and prone to damage from fossil diagenetic processes or recovery and identification errors. One example would be the absence of an atlas in Neandertal skeletons found with bones in anatomical articulation such as the individual Tabun C2 (McCown & Keith, 1939).

The presence of UTFs in the atlas of other species of early *Homo* (e.g., *Homo erectus*) and other hominin genera such as *Australopithecus* remains unclear because there has been no prior formal investigation of this variation in their fossil records. In order to address this possibility, we have reviewed the current hominin atlas fossil record (see references in Table 2). The australopithecine atlas fossil record consists of two specimens assigned to *Australopithecus anamensis*, two specimens from Sterkfontein of which one is attributed to *Australopithecus prometheus*, and a single *Australopithecus afarensis* atlas. Finally, there is one atlas from Koobi Fora for which there is uncertainty as to which species the fossil belongs to (either *Paranthropus boisei* or *Homo* sp.). Two partial atlas fragments attributed to *A. anamensis* (c. 4.2 Ma) and representing two different individuals were described by Meyer and Williams (2019a). Both of these fragments preserve the roots of the TF, but the TP is not complete. The Sterkfontein Member 2 from Silberberg Grotto (Sterkfontein Caves) has yielded a near-complete skeleton of *A. prometheus* (StW 573; "Little Foot") with a chronology of 3.67 Ma (Bruxelles et al., 2019; and references therein). This skeleton preserves a complete atlas (Beaudet et al., 2020) which was found together with the cranium, preserving both TPs, and not showing any sign of UTF. Beaudet et al. (2020) also report a partial atlas from Sterkfontein (StW 679; Member 4; between 2.6 and 2.0 Ma; Herries et al., 2013) that preserves the left lateral mass, the complete left TP and a fragment of the posterior arch. The TP does not show any sign of UTF. Lovejoy et al. (1982) published on a partial atlas (A.L.333-83) from Hadar (c. 3.2 million years) attributed to *A. afarensis* preserving the left lateral mass and part of the posterior arch. However, the TP is not complete to assess whether it had an UTF. KNM-ER 1825, dated to 1.7 Ma (Brown, 1995) and possibly belonging to either *Homo* sp. or *Paranthropus boisei* (see Meyer & Williams, 2019b for a complete discussion), is an atlas preserving part of the posterior arch with a left lateral mass preserving a complete TF, though the TP is not complete (Leakey & Walker, 1985).

Regarding the Early Pleistocene *Homo* atlas record, there are two remains: KNM-ER 1808z attributed to *H. erectus* and ATD6-90 assigned to a *Homo antecessor*. KNM-ER 1808z (1.7 Ma; Feibel et al., 1989) is a fragmentary atlas and part of a juvenile *H. erectus* partial skeleton (Walker et al., 1982). It consists of the right lateral mass and part of the posterior arch (Leakey & Walker, 1985). However, it lacks the TPs. The nearly complete adult atlas ATD6-90 from the TD6 level of Gran Dolina (c. 949–772 ka; Sierra de Atapuerca, Burgos, Spain) (Duval et al., 2018) has been assigned to a female individual (Carretero et al., 1999; Gómez-Olivencia et al., 2007). Both of the TPs preserve the roots of the TF but are not complete to assess if they were unfused.

Regarding the Middle Pleistocene *Homo* atlas record, five sites are of importance here: Zhoukoudian, Arago, Sima de los Huesos, Dinaledi Chamber and Lesedi Chamber. The Zhoukoudian Locality 1 (Dragon Hill, People's Republic of China) has yielded a partial atlas (Locus I; level 8/9; c. 600–800 ka) attributed to *H. erectus* missing its left side that shows a deep puncture bite mark on its TP (Boaz et al., 2004 and references therein). As the TP is lacking only its roots are noticeable and therefore it is not possible to ascertain the presence of an UTF. The Caune de l'Arago (Tautavel, Roussillon, France) has yielded an atlas from sublevel Gm (level G; Middle stratigraphic assemblage; c. 450 ka) (de Lumley, 2022; Moigne et al., 2006) attributed to *Homo erectus tautavelensis* (Chevalier & de Lumley, 2022; de Lumley, 2015). This atlas preserves the anterior arch and the left lateral mass with one of the roots of the TP and does not preserve the relevant morphology to assess the presence of an UTF.

The Dinadeli vertebral collection attributed to *Homo naledi* has yielded two atlases (Williams et al., 2017). Specimen U.W. 101–651 preserves the superior right articular facet, a TF that is complete, and part of the posterior arch (Williams et al., 2017; Williams, personal

**TABLE 2** Prevalence of UTF in fossil hominin atlases.

| Taxon | Sample (S)/ individual (label) | Number of atlases | Number of complete[a] transverse processes (number of atlases with at least one complete) | Number or atlases with UTF | Notes | Reference(s) |
|---|---|---|---|---|---|---|
| *Australopithecus anamensis* | ASI-VP-2/219 | 1 | 0 | N/O | | Meyer and Williams (2019a) |
| | ASI-VP-2/220 | 1 | 0 | N/O | | Meyer and Williams (2019a) |
| *Australopithecus prometheus* | StW 573 (“Little Foot”) | 1 | 2 | 0 | | Beaudet et al. (2020) |
| | Stw 679 | 1 | 1 | 0 | | Beaudet et al. (2020) |
| *Australopithecus afarensis* | A.L.333-83 | 1 | 0 | N/O | | Lovejoy et al. (1982) |
| *Homo* sp./ *Paranthropus boisei*[b] | KNM-ER 1825 | 1 | 1 | 0 | | Leakey and Walker (1985) |
| *Homo erectus* | KNM-ER 1808 | 1 | 0 | N/O | | Leakey and Walker (1985) |
| *Homo antecessor* | ATD6-90 | 1 | 0 | N/O | | Carretero et al. (1999) |
| *Homo erectus* | Zhoukoudian (no label) | 1 | 0 | N/O | | Boaz et al. (2004) |
| *Homo erectus tautavelensis* | Arago (A122) | 1 | 0 | N/O | | Chevalier and de Lumley (2022) |
| *Homo naledi* | Dinaledi (U.W. 101-651) | 1 | 1? | 0? (N/O) | | Williams et al. (2017); Williams, personal communication |
| | Dinaledi (U.W. 101-331) | 1 | 0 | N/O | | Williams et al. (2017); Williams, personal communication |
| | Lesedi Chamber (102a-171 and 102a-172) | 1 | 0 | N/O | | Hawks et al. (2017); Williams, personal communication |

[a] Complete or nearly complete transverse processes in which it is possible to observe the presence/absence of UTF.

[b] There is uncertainty as to which species the fossil belongs to, *Homo* sp. or *Paranthropus boisei*; N/O = non-observable.

communication). Specimen U.W. 101–331 does not preserve the relevant morphology to assess the presence of an UTF (Williams et al., 2017; Williams, personal communication). The Lesedi Chamber within the Rising Star cave system has also yielded two atlas fragments, U.W. 102a-171 and U.W. 102a-172, that have been attributed to the LES1 skeleton, and neither preserves the relevant morphology to assess the presence of an UTF (Hawks et al., 2017; Williams, personal communication).

In summary, our research has confirmed the presence of UTF in three atlases belonging to the Neandertal lineage: the Middle Pleistocene Preneandertal VC3 atlas from Sima de los Huesos and two Neandertal atlases (Kebara 2 and Krapina 98). In the case of the Sima de los Huesos Preneandertals it would be one case out of two atlases that preserve the TF (out of a total of 11 atlases represented in this site). In the case of Neandertals, the prevalence of UTF (between 13.3% and 20%) is slightly higher than the prevalence known among AMH populations that have been studied. Assuming that the observed fossil prevalence is representative of the populations from which they are derived, Neandertals (2 atlases with UTF out of 15), Preneandertals (1 atlas with UTF out of 11) and the combined samples (3 atlases out of 26) would not be significantly different from the prevalence published by Billmann and Le Minor (2009) for a large *H. sapiens* population (51 atlases out of 500)

($\text{Chi}^2 = 0.15487$; $p = 0.69$; $\text{Chi}^2 = 0.014484$; $p = 0.90$; and $\text{Chi}^2 = 0.00062725$; $p = 0.98$, respectively). It is important to highlight, however, that the prevalence in the fossil record could be biased due to the fragile nature of the TP, which are only rarely preserved.

Nonetheless, our research suggests that UTF may have been present in the hominin lineage since, at least, the Middle Pleistocene. But, we believe an UTF could have been present in all the hominin lineages and we have simply yet to detect this possibility given the relatively low number of well-preserved atlases outside the Neandertal lineage fossil record.

## AUTHOR CONTRIBUTIONS

**Asier Gómez-Olivencia:** Conceptualization; data curation; formal analysis; investigation; methodology; resources; validation; writing – original draft; writing – review and editing; supervision; funding acquisition. **Mikel Arlegi:** Data curation; formal analysis; investigation; resources; validation; writing – original draft; writing – review and editing; funding acquisition. **Juan José Valenzuela-Fuenzalida:** Formal analysis; investigation; methodology; writing – original draft; writing – review and editing. **Mathias Orellana-Donoso:** Formal analysis; investigation; methodology; writing – original draft. **Juan Luis Arsuaga:** Data curation; resources; validation; writing – review and editing; funding acquisition; supervision. **Juan A. Sanchis-Gimeno:** Conceptualization; formal analysis; investigation; methodology; resources; writing – original draft; writing – review and editing; supervision.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Availability of data, code, and other materials: The studied material is available at the respective museum.

## ORCID

*Asier Gómez-Olivencia* https://orcid.org/0000-0001-7831-3902

*Juan A. Sanchis-Gimeno* https://orcid.org/0000-0002-2599-8474

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