



# Arcuate foramen: “Anatomical variation shape or adaptation legacy?”

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## Abstract

**Purpose** The groove of the vertebral artery on the posterior arch of the atlas (*sulcus arteriae vertebralis*) may become a complete or partial osseous foramen: the arcuate foramen. The presence of a complete or partial arcuate foramen is a rare anatomical variant described in a minority of patients and it seems to be associated with vertigo, vertebro-basilar insufficiency, posterior circulation strokes, and musculoskeletal pain. As the number and morphology of cervical vertebrae is highly preserved, we questioned about its significance from an evolutionary point of view. We thus investigated through an extensive literature review if the arcuate foramen is a pure anatomical variation shape or if it might represent an adaptation legacy.

**Methods** We observed five atlas of an extinct species, the Late Pleistocene Mammoths (*M. primigenius*), and we compared them with five atlas of a closely related existent species, the African elephant (*L. africana*).

**Results** All the mammoths' atlas had an arcuate foramen through which the vertebral artery passed before turning anteriorly and becoming intradural. This foramen was not present in elephants' atlas, where only a groove was observed, such as in the majority of patients.

**Conclusion** We would like to raise the hypothesis that this peculiar morphology of mammoths' atlas might have contributed, in association with other factors, to their precocious extinction and that the arcuate foramen might represent a disadvantage in the evolutionary process, with a low prevalence in humans being the result of a natural selection.

**Keywords** Atlas · Arcuate foramen · Mammoth · Elephant · Extinction · Evolution · Cervical vertebra · Vertebral artery · Groove

## Introduction

The arcuate foramen (AF) is an osseous foramen present at the place of the classical groove for the vertebral artery (*sulcus arteriae vertebralis*) on the posterior arch of the atlas.

It is a well-described anatomical variant [17, 27, 39] and it was first reported in 1879 [3]. Many etiological hypotheses have been advanced to explain the presence of AF. It may completely or partially encircle the suboccipital nerve, the vertebral venous plexus, and the vertebral artery

existing from the transverse foramen and turning anteriorly to become intradural (atlantic portion or V3). Its morphology is thus highly variable and it may be uni or bilateral [19, 43]. Only a small percentage of patients' variable from 4% [32, 34] to 17% [4, 9, 13, 16, 19] has been reported as having a true canal for the vertebral arteries in the posterior arch of the atlas and this finding is generally not related with sex [7, 16, 19, 27, 36]. This anomaly is called under different anatomical designations: arcuate foramen, foramen arcuale, perpendicular foramen, retroauricular foramen, posterior foramen, or Kimmerle's anomaly. In our surgical experience, we operated patients of every age and they rarely presented a complete or a partial AF (about 0.5% of our surgical cohort, unpublished data). The number and morphology of cervical vertebrae in mammals are remarkably preserved during evolution and changes seem to be associated with deleterious pleiotropic effects and thus to evolutionary constraints [42]. Therefore, these anatomical variations might represent a legacy or an adaptive evolution within the same species.

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We had the opportunity to examine the Atlas of an extinct species, the Late Pleistocene mammoths (*M. primigenius*) and we compared them to the Atlas of a very close related existing species, the African elephant (*Loxodonta africana*), searching for the presence of an AF. We thus wondered if the extinction of the AF may be just considered a simple anatomical variant or better a step of evolution adaptation legacy.

## Methods

### Ethic statement

The local ethics committee of the Bretonneau Hospital approved this study. All necessary permits were obtained for the described study, which complied with all relevant regulations.

### Specimens

We analysed five dried atlas of Late Pleistocene mammoths (*M. primigenius*) of unknown age and sex from private collection (Weill collection, numbers 1–5, Alençon, France) and 5 (3 females, 2 males) atlas of *L. africana* from the collection of Comparative Anatomy, Mammals and Birds of the Natural History Museum Paris (MNHN-ZM-AC 1–3 and 4, 5; Paris, France). After a careful inspection, these vertebrae were examined for the existence of an osseous bridge or exostosis behind each superior articular process of the atlas, thus transforming the groove of the vertebral artery into a complete or partial foramen.

## Results

All five atlas of Late Pleistocene mammoths showed a bony bridge starting from the posterior surface of the superior articular process. Every sample presented a bilateral AF and the ossification was complete (Fig. 1a, b). The vertebral artery exited the transverse foramen of the axis and bended laterally to pass through the transverse foramen of the atlas. From here, the artery turned posteriorly to pass around the posterior border of the superior facet and it went through the AF to become intradural (Fig. 1c, d).

On the contrary, none of the atlas of *L. africana* showed AF but only a groove for the passage of the vertebral artery from the transverse foramen to the foramen magnum (Fig. 2).

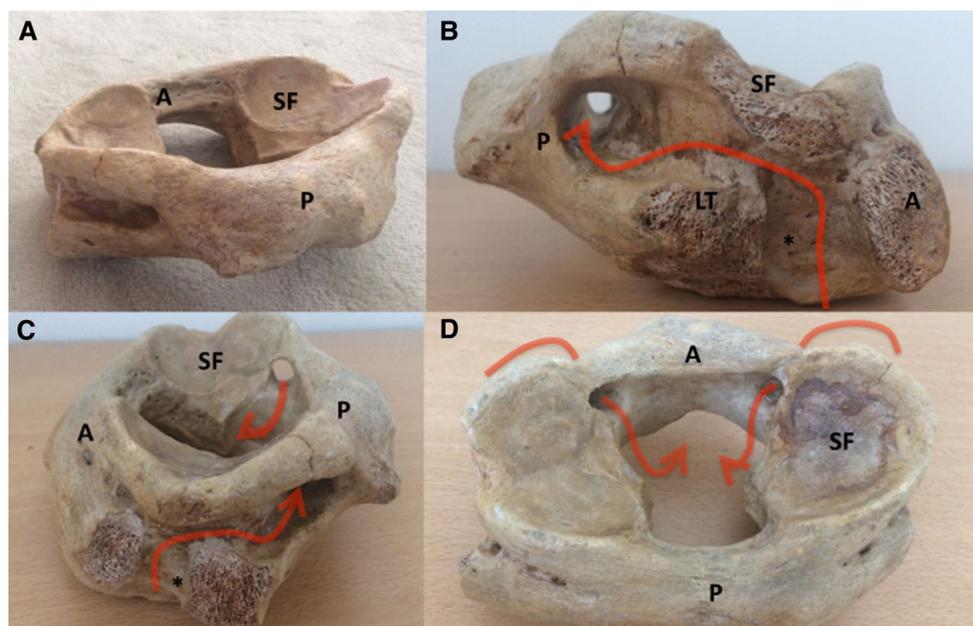
## Discussion

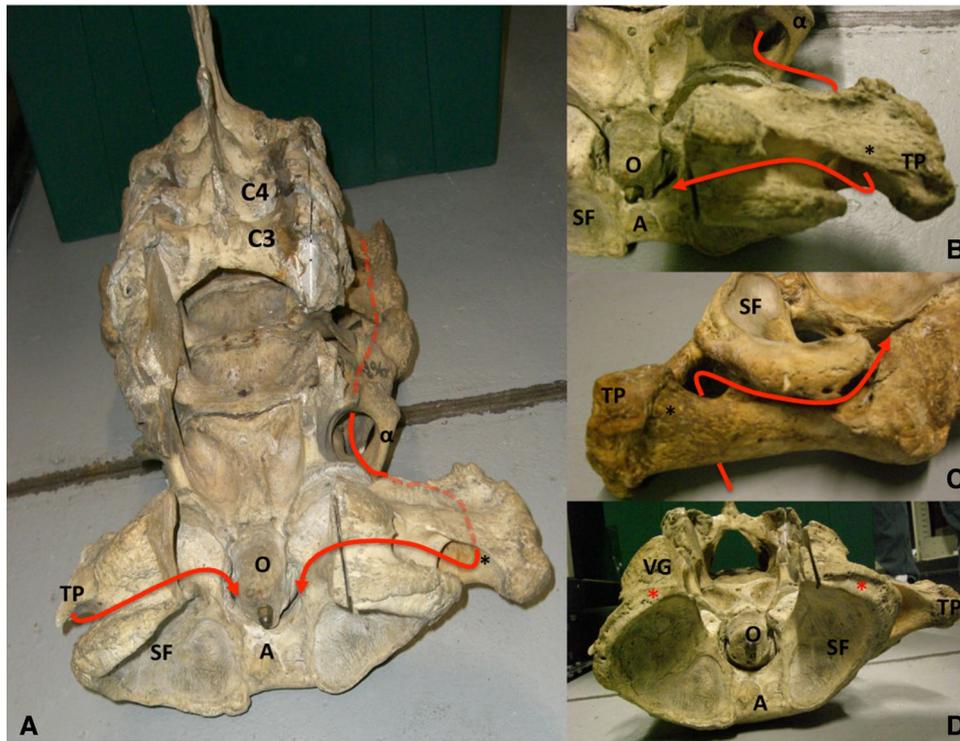
### Etiology of arcuate foramen

Embriology of the atlas is widely described in the literature [25], while the etiology of the arcuate foramen is still debated [2].

The ossification of the posterior arch and lateral masses of the atlas begins at the 7th week of intrauterine life with an ossification centre in each lateral mass and a progressive ossification dorsally [40]. Final fusion occurs at 4 years of life. The groove of the vertebral artery is situated behind the lateral masses of the atlas and different theories have been advances to explain the presence of a complete/incomplete

**Fig. 1** Atlas of Late Pleistocene Mammoths. **a** Oblique view, **b** lateral view, **c** superior oblique view, **d** superior view. A anterior tubercle, P posterior tubercle, SF superior articular facet, LT lateral tubercle, \*transverse foramen. All the samples analysed showed the presence of a bony bridge starting from the posterior surface of the superior articular process and thus delimitating the arcuate foramen (black star). The trajectory of the vertebral artery is marked by a red arrow. (Color figure online)





**Fig. 2** Atlas of *Loxodonta africana*. **a, b** Superior view of the cervical spine showing the course of the vertebral artery, **c** posterior view of the atlas of a young male, and **d** superior view of the cervical spine of an old male. *A* anterior tubercle, *P* posterior tubercle, *SF* superior articular facet, *LT* lateral tubercle, *O* odontoid,  $\alpha$  transverse foramina, *VG* vertebral groove, \*transverse foramen, red\*, vertebral canal of C1; red arrows, anatomical path of vertebral arteries. All the atlas presented only a groove for the vertebral artery on the superior surface of the posterior arch and no bony bridge or arcuate foramen

foramen. The ossification of the connective tissue surrounding the vertebral artery might be the cause, as well as the late ossification of the posterior atlanto-occipital membrane [34].

Other authors advance the hypothesis that the AF is consequent to an anomalous ossification of the posterior ponticulus, a delicate bony spiculum (remnant of the proatlas) arching backward from the posterior end of the superior articular process and forming an osseous bridge [7, 10, 18, 45]. A progressive ossification had been proposed by some authors, but in most of cases, a congenital alteration in grades of ossification has been supposed [9]. A greater external stress on the craniovertebral junction may also represent a favouring factor [19].

The ethnic predisposition is largely discussed in the literature [9]. A recent paper had been published claiming that the real frequency of the ponticulus posticus would be higher than expected in the general population, reaching 22.5%, being more frequent in men ( $p < 0.01$ ) and in black Americans ( $p < 0.01$ ) [31]. The lowest prevalence

was detected. In **a, b, d**, the posterior arches of the axis and the atlas have been removed. Large transverse foramina are evident and a large transverse foramen was also present in the atlas. Like in most mammals, the vertebral arteries ascend the cervical spine passing through the transverse foramina (red hatched curved), therefore, when crossing the transverse foramen of C1, arteries run along the posterior arch of the atlas in their groove (red continuous arrow). (Color figure online)

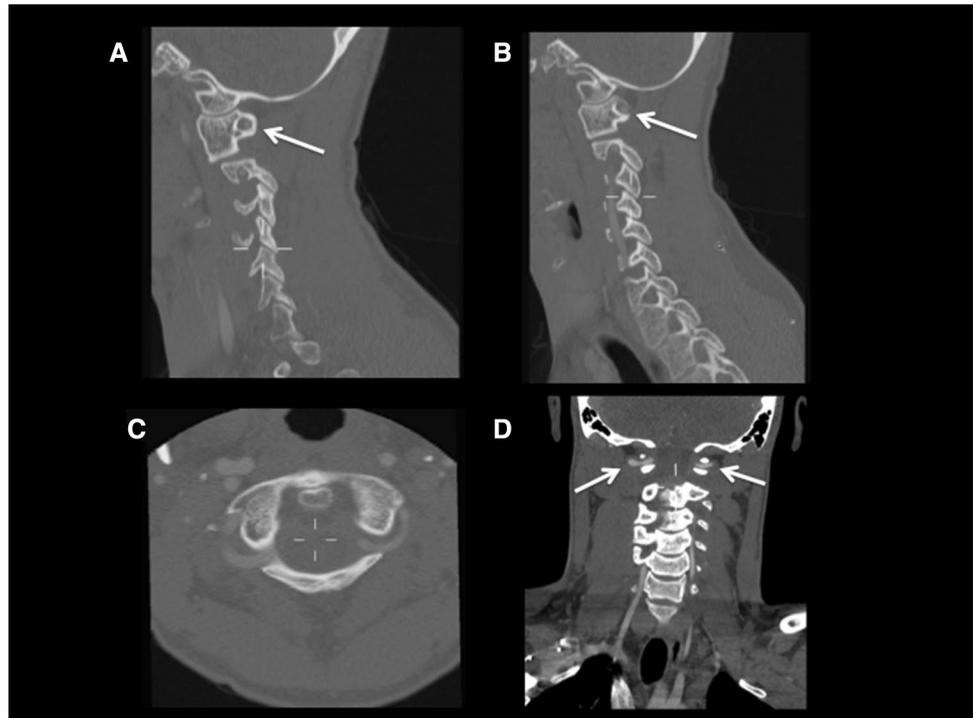
was, however, reported in South-East Asia and the highest in North America [9].

A bilateral and complete bilateral AF is the most commonly reported finding [4, 32] (Fig. 3).

### Pathological repercussion of AF

The fact that the atlas forms only a bony annular structure is important, as it allows the movement of rotation [28]. More than 50% of head rotation occurs at the atlantoaxial joint [15] and the most vulnerable tract of the vertebral artery is at the C1–C2 level and in particular in its passage in the transverse foramina and in the *sulcus arteriae vertebralis* [12, 29]. The vertebral artery is in fact compressed and stretched during extreme rotation movements. Animals showing a 360° rotation of the head, such as the owls, present very large transverse foramina, allowing head twist [11]. The presence of a supplementary bony canal for the vertebral artery, such as AF, may represent a supplementary constraint for head

**Fig. 3** A 29-year-old patient was diagnosed for an os odontoideum in the context of a transient tetraparesis after a cervical hyperflexion movement. The radiological workout showed a bilateral complete arcuate foramen (white arrows). The cervical CT shows the foramen in the sagittal plane (**a** left side and **b** right side) and in the axial place (**c**). The angio-CT in the coronal plane (**d**) shows the injected vertebral arteries passing through the foramen before turning anteriorly and becoming intradural (V3 segment)



movements, through a compression of the V3 segment, and it may predispose to vertebral artery injury [9, 41].

In the literature, variants of the upper cervical spine and craniocerebral junction anomalies were associated with anomalies of the vertebral arteries [35]. The presence of AF was associated with vertebral artery atherosclerosis [10, 26], musculoskeletal pain [7], chronic tension-type headaches, and sensori-neural hearing loss [18]. Movements of cervical stretching, rotation, and bending in the foramen may cause excessive external pressure on the V3 segment, with a dynamic stenosis and alterations in the normal blood flow [41]. This observation was associated with a higher incidence of Barre–Lieou syndrome [22], Bowhunter’s syndrome [38], or posterior circulation strokes in patients with AF [10, 26], as repetitive and even minimal injuries to the vertebral arteries are considered a risk factor. The presence of AF might also have a causative role in the genesis of vertebral dissection [10, 39] and it was described as predisposing factor for the sudden infant death syndrome [10].

One paper described also a high prevalence of ponticulus posticus in a small cohort of patients with Gorlin–Goltz syndrome (50% of patients) [14], thus confirming a previous study reporting an anomalous calcification of the atlanto-occipital ligament in this disease [21].

A higher incidence of AF was further recorded in patients with a class III malocclusion when compared to other classes ( $p < 0.05$ ) [1, 5] and in patients with cleft lip and palate [6].

The clinical significance of AF is unclear, but its presence should be carefully considered when a C1 instrumentation or

decompression is planned, because it may provide the false impression of a broader posterior arch [27] and it may be misleading in calculating the entry point for screws placement or in performing C1 laminectomy. A iatrogenic injury of the vertebral artery may easily occur in these cases [41].

### Consequences in the kingdom of evolution

We noted that the atlas of Late Pleistocene mammoths (*M. primigenius*) has a complete foramen for the vertebral artery, while the atlas of their closely related existent species, the African elephants (*L. africana*), has only a groove, as in humans. Through our observations and literature analysis, we would like to advance the hypothesis that the presence of AF might represent a disadvantage in the evolutionary process and its low prevalence in the human population was the result of a natural selection.

Mammoths had a precocious extinction and their high incidence of cervical ribs was associated with an increased incidence of congenital anomalies [30]. Hence, a combination of inbreeding and harsh conditions may be the most likely explanation for this phenomenon [23, 24]. As the number and morphology of cervical vertebrae are extremely conserved in mammals, we wonder if the presence of AF would have been an index of supplementary associated pernicious pleiotropic effect, disadvantageous for the species.

In the animal kingdom, almost all Japanese macaques (*M. fuscata*) have a bilaterally complete posterior bridge and the prevalence increases with age [44]. A founder effect may,

however, not be excluded. What we discovered, through a selective review of the literature existing on this species, is that the Japanese macaques have a significantly shorter life expectancy than the other species: the survival is estimated at 6 years for *M. fuscata* [37], and between 20 and 30 years for other macaques [8]. Similarly, the progressive disappearance of the atlantal ponticles constitutes an evolutionary tendency characteristic of primates, as studies of comparative anatomy reported a progressive trend of disappearance of the ponticles [14, 20, 33].

## Conclusion

Because the number and the morphology of cervical vertebrae are extremely preserved in embryogenesis, the presence of AF in the atlas of Late Pleistocene mammoths might have been a contributing factor to the extinction of this species.

AF might be associated to a negative selective pressure also in other species. This hypothesis has, however, to be confirmed by phylogenetic and epidemiological studies involving larger populations.

**Author contributions** GC, AA, and LMT design and conceptualization of the study, GC, AA, LMT, IZ, and PF analysis of the data, GC, AA, IZ, PF, SV, and CD interpretation of the data, GC, AA, LMT, IZ, PF, SV, and CD drafting of the manuscript, AA and GC writing of the manuscript, and GC, AA, LMT, IZ, PF, SV, and CD revision of the manuscript for intellectual content. AA and GC are responsible for the overall content as guarantor.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no personal conflicts of interest and no institutional financial interest in any drugs, materials, or devices described in this manuscript. The authors have no financial disclosures to report. In addition, all patients gave their informed consent for any medical and scientific investigations. This paper has not been published previously, is not under consideration for publication elsewhere. All authors are responsible for reported research.

## References

- Adisen MZ, Misirlioglu M (2017) Prevalence of ponticulus posticus among patients with different dental malocclusions by digital lateral cephalogram: a comparative study. *Surg Radiol Anat* 39:293–297. <https://doi.org/10.1007/s00276-016-1728-4>
- Ahn J, Duran M, Sylldort S, Rizvi A, D'Antoni AV, Johal J, Iwanaga J, Oskouian RJ, Tubbs RS (2018) Arcuate foramen: anatomy, embryology, nomenclature, pathology, and surgical considerations. *World Neurosurg* 118:197–202. <https://doi.org/10.1016/j.wneu.2018.07.038>
- Allen W (1879) The varieties of the atlas in the human subject, and the homologies of its transverse processes. *J Anat Physiol* 14:18–27
- Bayrakdar IS, Miloglu O, Altun O, Gumussoy I, Durna D, Yilmaz AB (2014) Cone beam computed tomography imaging of ponticulus posticus: prevalence, characteristics, and a review of the literature. *Oral Surg Oral Med Oral Pathol Oral Radiol* 118:e210–e219. <https://doi.org/10.1016/j.oooo.2014.09.014>
- Bayrakdar IS, Miloglu O, Yesiltepe S, Yilmaz AB (2017) Ponticulus posticus in a cohort of orthodontic children and adolescent patients with different sagittal skeletal anomalies: a comparative cone beam CT investigation. *Folia Morphol*. <https://doi.org/10.5603/FM.a2017.0075>
- Bayrakdar IS, Yasa Y, Duman SB, Karaturgut UE, Ocak A, Gunen Yilmaz S (2017) Cone beam computed tomography evaluation of ponticulus posticus in patients with cleft lip and palate: a retrospective radio-anatomic study. *Folia Morphol*. <https://doi.org/10.5603/FM.a2017.0076>
- Cakmak O, Gurdal E, Ekinci G, Yildiz E, Cavdar S (2005) Arcuate foramen and its clinical significance. *Saudi Med J* 26:1409–1413
- Cawthon Lang K (2005) Primate factsheets: rhesus macaque (*Macaca mulatta*) Taxonomy, Morphology, & Ecology. [http://pin.primate.wisc.edu/factsheets/entry/rhesus\\_macaque](http://pin.primate.wisc.edu/factsheets/entry/rhesus_macaque)
- Cirpan S, Yonguc GN, Edizer M, Mas NG, Magden AO (2017) Foramen arcuale: a rare morphological variation located in atlas vertebrae. *Surg Radiol Anat* 39:877–884. <https://doi.org/10.1007/s00276-016-1808-5>
- Cushing KE, Ramesh V, Gardner-Medwin D, Todd NV, Gholkar A, Baxter P, Griffiths PD (2001) Tethering of the vertebral artery in the congenital arcuate foramen of the atlas vertebra: a possible cause of vertebral artery dissection in children. *Dev Med Child Neurol* 43:491–496
- De Kok-Mercado F, Habib M, Phelps T, Gregg L, Gailloud P (2013) Adaptions of the owl's cervical & cephalic arteries in relation to extreme neck rotation. *Science* 339:514–515
- Elgafy H, Pompo F, Vela R, Elsamaloty HM (2014) Ipsilateral arcuate foramen and high-riding vertebral artery: implication on C1–C2 instrumentation. *Spine J* 14:1351–1355. <https://doi.org/10.1016/j.spinee.2014.01.054>
- Elliott RE, Tanweer O (2014) The prevalence of the ponticulus posticus (arcuate foramen) and its importance in the Goel-Harms procedure: meta-analysis and review of the literature. *World Neurosurg* 82:e335–e343. <https://doi.org/10.1016/j.wneu.2013.09.014>
- Friedrich RE (2014) Ponticulus posticus is a frequent radiographic finding on lateral cephalograms in nevroid basal cell carcinoma syndrome (Gorlin–Goltz syndrome). *Anticancer Res* 34:7395–7399
- Frisoni GB, Anzola GP (1991) Vertebrobasilar ischemia after neck motion. *Stroke* 22:1452–1460
- Gibelli D, Cappella A, Cerutti E, Spagnoli L, Dolci C, Sforza C (2016) Prevalence of ponticulus posticus in a Northern Italian orthodontic population: a lateral cephalometric study. *Surg Radiol Anat* 38:309–312. <https://doi.org/10.1007/s00276-015-1554-0>
- Gupta SC, Gupta CD, Arora AK, Maheshwari BB (1979) The retrotransverse groove (canal) in the Indian atlas vertebrae. *Anat Anz* 145:514–516
- Koutsouraki E, Avdelidi E, Michmizos D, Kapsali SE, Costa V, Baloyannis S (2010) Kimmerle's anomaly as a possible causative factor of chronic tension-type headaches and neurosensory hearing loss: case report and literature review. *Int J Neurosci* 120:236–239. <https://doi.org/10.3109/00207451003597193>
- Krishnamurthy A, Nayak SR, Khan S, Prabhu LV, Ramanathan LA, Ganesh Kumar C, Prasad Sinha A (2007) Arcuate foramen of atlas: incidence, phylogenetic and clinical significance. *Rom J Morphol Embryol* 48:263–266
- Le Minor JM, Trost O (2004) Bony ponticles of the atlas (C1) over the groove for the vertebral artery in humans and primates: polymorphism and evolutionary trends. *Am J Phys Anthropol* 125:16–29. <https://doi.org/10.1002/ajpa.10270>

21. Leonardi R, Santarelli A, Barbato E, Ciavarella D, Bolouri S, Harle F, Palazzo G, Lo Muzio L (2010) Atlanto-occipital ligament calcification: a novel sign in nevoid basal cell carcinoma syndrome. *Anticancer Res* 30:4265–4267
22. Limousin CA (1980) Foramen arcuale and syndrome of Barre-Lieou. Its surgical treatment. *Int Orthop* 4:19–23
23. Miller W, Drautz DI, Ratan A, Pusey B, Qi J, Lesk AM, Tomsho LP, Packard MD, Zhao F, Sher A, Tikhonov A, Raney B, Patterson N, Lindblad-Toh K, Lander ES, Knight JR, Irzyk GP, Fredrikson KM, Harkins TT, Sheridan S, Pringle T, Schuster SC (2008) Sequencing the nuclear genome of the extinct woolly mammoth. *Nature* 456:387–390. <https://doi.org/10.1038/nature07446>
24. Nystrom V, Humphrey J, Skoglund P, McKeown NJ, Vartanyan S, Shaw PW, Liden K, Jakobsson M, Barnes I, Angerbjorn A, Lister A, Dalen L (2012) Microsatellite genotyping reveals end-Pleistocene decline in mammoth autosomal genetic variation. *Mol Ecol* 21:3391–3402. <https://doi.org/10.1111/j.1365-294X.2012.05525.x>
25. Offiah CE, Day E (2017) The craniocervical junction: embryology, anatomy, biomechanics and imaging in blunt trauma. *Insights Imaging* 8:29–47. <https://doi.org/10.1007/s13244-016-0530-5>
26. Ouyang ZY, Qiu MJ, Zhao Z, Wu XB, Tong LS (2017) Congenital anomaly of the posterior arch of the atlas: a rare risk factor for posterior circulation stroke. *J Neurointerv Surg* 9:e27. <https://doi.org/10.1136/neurintsurg-2016-012731.rep>
27. Pekala PA, Henry BM, Pekala JR, Hsieh WC, Vikse J, Sanna B, Walocha JA, Tubbs RS, Tomaszewski KA (2017) Prevalence of foramen arcuale and its clinical significance: a meta-analysis of 55,985 subjects. *J Neurosurg Spine* 27(3):276–290
28. Prescher A (1997) The craniocervical junction in man, the osseous variations, their significance and differential diagnosis. *Anat Anz* 179:1–19. [https://doi.org/10.1016/S0940-9602\(97\)80126-4](https://doi.org/10.1016/S0940-9602(97)80126-4)
29. Provenzale JM, Morgenlander JC, Gress D (1996) Spontaneous vertebral dissection: clinical, conventional angiographic, CT, and MR findings. *J Comput Assist Tomogr* 20:185–193
30. Raikonen J, Vucetich JA, Vucetich LM, Peterson RO, Nelson MP (2013) What the inbred Scandinavian wolf population tells us about the nature of conservation. *PLoS One* 8:e67218. <https://doi.org/10.1371/journal.pone.0067218>
31. Saleh A, Gruber J, Bakhsh W, Rubery PT, Mesfin A (2017) How common is the Ponticulus Posticus? A CT based analysis of 2,917 patients. *Spine*. <https://doi.org/10.1097/BRS.0000000000002400>
32. Sanchis-Gimeno JA, Blanco-Perez E, Perez-Bermejo M, Llido S, Nalla S (2017) Retrotransverse foramen of the atlas: prevalence and bony variations. *Eur Spine J*. <https://doi.org/10.1007/s00586-017-5372-4>
33. Sanchis-Gimeno JA, Llido S, Miquel-Feutch M, Quiles-Guinou L, Rios L, Murillo-Llorente M, Perez-Bermejo M, Nalla S (2018) The decreasing prevalence of the arcuate foramen. *World Neurosurg* 110:521–525. <https://doi.org/10.1016/j.wneu.2017.10.037>
34. Simsek S, Yigitkanli K, Comert A, Acar HI, Seckin H, Er U, Belen D, Tekdemir I, Elhan A (2008) Posterior osseous bridging of C1. *J Clin Neurosci* 15:686–688. <https://doi.org/10.1016/j.jocn.2007.06.004>
35. Sivaraju L, Mani S, Prabhu K, Daniel RT, Chacko AG (2017) Three-dimensional computed tomography angiographic study of the vertebral artery in patients with congenital craniovertebral junction anomalies. *Eur Spine J* 26:1028–1038. <https://doi.org/10.1007/s00586-016-4580-7>
36. Stubbs DM (1992) The arcuate foramen. Variability in distribution related to race and sex. *Spine* 17:1502–1504
37. Takahata Y, Suzuki S, Agetsuma A, Okayasu N, Sugiura H, Takahashi H, Yamagiwa J, Izawa K, Furuichi T, Hill D, Maruhashi T, Saito C, Sato S, Sprague D (1998) Reproduction of wild Japanese macaque females of Yakushima and Kinkazan Islands: a preliminary report. *Primates* 39:339–349
38. Taylor WB III, Vandergriff CL, Opatowsky MJ, Layton KF (2012) Bowhunter's syndrome diagnosed with provocative digital subtraction cerebral angiography. *Proc (Bayl Univ Med Cent)* 25:26–27
39. Travan L, Saccheri P, Gregoraci G, Mardegan C, Crivellato E (2015) Normal anatomy and anatomic variants of vascular foramina in the cervical vertebrae: a paleo-osteological study and review of the literature. *Anat Sci Int* 90:308–323. <https://doi.org/10.1007/s12565-014-0270-x>
40. Travan L, Saccheri P, Sabbadini G, Crivellato E (2011) Bilateral arcuate foramen associated with partial defect of the posterior arch of the atlas in a medieval skeleton: case report and review of the literature. Looking backward to go forward. *Surg Radiol Anat* 33:495–500. <https://doi.org/10.1007/s00276-010-0760-z>
41. Tubbs RS, Johnson PC, Shoja MM, Loukas M, Oakes WJ (2007) Foramen arcuale: anatomical study and review of the literature. *J Neurosurg Spine* 6:31–34. <https://doi.org/10.3171/spi.2007.6.1.6>
42. Varela-Lasheras I, Bakker AJ, van der Mije SD, Metz JA, van Alphen J, Galis F (2011) Breaking evolutionary and pleiotropic constraints in mammals: on sloths, manatees and homeotic mutations. *EvoDevo* 2:11. <https://doi.org/10.1186/2041-9139-2-11>
43. Wysocki J, Bubrowski M, Reymond J, Kwiatkowski J (2003) Anatomical variants of the cervical vertebrae and the first thoracic vertebra in man. *Folia Morphol* 62:357–363
44. Yamamoto A, Kunimatsu Y (2006) Ontogenetic change and geographical variation of atlas bridging in Japanese macaques (*Macaca fuscata*). *Anthropol Sci* 114:153–160
45. Young JP, Young PH, Ackermann MJ, Anderson PA, Riew KD (2005) The ponticulus posticus: implications for screw insertion into the first cervical lateral mass. *J Bone Joint Surg Am* 87:2495–2498. <https://doi.org/10.2106/JBJS.E.00184>