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The Neanderthal endocast from Gánovce (Poprad, Slovak Republic)

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Summary - *A Neanderthal endocast, naturally formed by travertine within the crater of a thermal spring, was found at Gánovce, near Poprad (Slovakia), in 1926, and dated to 105 ka. The endocast is partially covered by fragments of the braincase. The volume of the endocast was estimated to be 1320 cc. The endocast was first studied by the Czech paleoanthropologist Emanuel Vlček, who performed metric and morphological analyses which suggested its Neanderthal origin. Vlček published his works more than fifty years ago, but the fossil is scarcely known to the general paleoanthropological community, probably because of language barriers. Here, we review the historical and anatomical information available on the endocasts, providing additional paleoneurological assessments on its features. The endocast displays typical Neanderthal traits, and its overall appearance is similar to Guattari 1, mostly because of the pronounced frontal width and occipital bulging. The morphology of the Gánovce specimen suggests once more that the Neanderthal endocranial phenotype had already evolved at 100 ka.*

Keywords - *Paleoneurology, Neanderthals, Natural endocast, Central Europe.*

The Gánovce endocast

A natural endocast (Fig. 1) was found in 1926 during the quarrying of a travertine knoll at Gánovce, near Poprad, Slovakia. A Czech amateur naturalist, Jaroslav Petrbok, officially acquired the cast and other mammal fossil samples from the same site. The endocast was then stored in the National museum's depositories in Prague until 1948, when a young paleoanthropologist named Emanuel Vlček (Fig. 2) performed a comprehensive study of the specimen. Vlček was the first to recognise that the endocast did not belong to a modern human, but rather to a Neanderthal (Vlček, 1949). In his early study, he describes the general form of the cast as low, flat and long, and determines that traits including a wide frontal region with posterior inclination, narrow postorbital area, concave orbital parts of frontal lobes, and a kyphotic angle of 131°, were characteristic of Neanderthal morphology (Vlček, 1949). Later, Vlček provided detailed metrics of the cast, comparing its morphology to diverse fossils and modern human specimens (Vlček, 1953, 1955, 1969). He also considered pathological conditions, such as plagiocephaly and microcephaly (Vlček, 1953, 1969). Notably, Vlček's morphological study included geometric (shape) comparisons of the endocast, employing outlines and superimposition criteria (Fig. 3). He used a reconstruction of the endocast without the bone fragments attached to the endocranial mould, and measured the cast after the method of Kappers (1929), using photographs of the lateral profile. He analysed the whole endocast, as well as the frontal, occipital, and temporal regions separately. Vlček's results supported the affinity between the Gánovce endocast and Neanderthals, when taking into account the size and shape of its frontal regions, the overall form of the endocranium, and its overall size. According to his morphological survey, Gánovce was similar

Fig. 1 - The original fossil endocast from Gánovce (from top to bottom and left to right: right lateral, left lateral, anterior, posterior, superior, and inferior views). Photographs by Martin Frouz. The colour version of this figure is available at the JASs website.

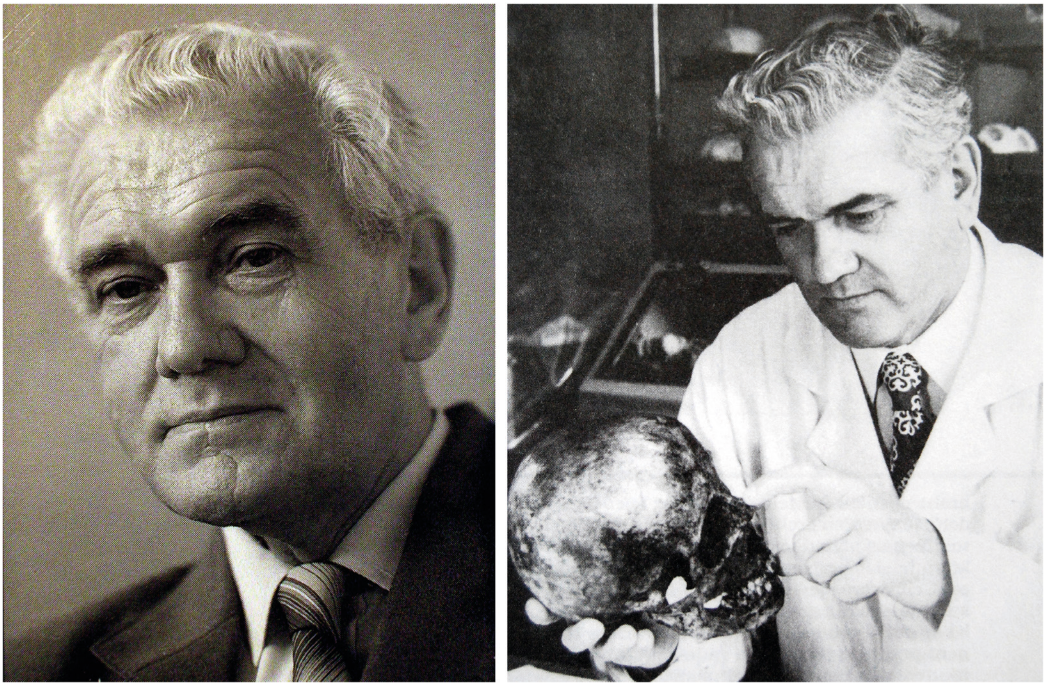

Fig. 2 - Prof. Emanuel Vlček (1925 – 2006) was a Czech anthropologist and medical doctor. His principal research concerned human evolution in Central Europe. Vlček is also known for anthropological studies of the remains of historical personalities, including Czech kings, saints, and other public figures. (Photographs from the archive of the National Museum in Prague). The colour version of this figure is available at the JASs website.

to fossil specimens like Krapina 3, Saccopastore 1, Kabwe 1, and particularly Gibraltar 1 (Vlček, 1969). Vlček published more analyses on the morphological affinity of the Gánovce endocast (e.g. Vlček, 1950, 1953, 1955, 1969, 1988, 1995), but he also considered histological (Vlček, 1961), chemical (Vlček, 1956), and radiological (Vlček, 1988) aspects of the cast. Nevertheless, at present the Gánovce Neanderthal remains relatively unknown in current paleoanthropological debates. This is probably due to the fact that Vlček published mainly in Czech and Slovak. In 1957, Petrbok donated the Gánovce fossil to the National Museum in Prague, where it has been housed ever since. In this paper, we review the information available on the Gánovce endocranial cast, and provide some additional paleoneurological considerations on its features and proportions.

Geology and chronology

The travertine mound of Hrádok in the village of Gánovce was deposited by a strong thermal spring. The middle part of the hill still contains part of the principal crater of the former spring. The main layers of the stratigraphic profile in the crater can be correlated with the layers of the crater margin (see Kukla, 1958; Prošek, 1958). Gánovce-Hrádok is a Late Pleistocene site with several fossil remains, mostly molluscs and mammals (see Fejfar, 1958, Sabol *et al.*, 2017), fossil plants, and archaeological artefacts from the Middle and Upper Palaeolithic (Vlček, 1953, 1995; Ďurišová *et al.*, 2016). The assemblage also contains several pieces of charcoal and burnt animal bones (Vlček, 1995; Ďurišová *et al.*, 2016). The Neanderthal endocast comes from a cultural layer containing microlithic industry determined as Taubachian (Vlček, 1995; Ďurišová

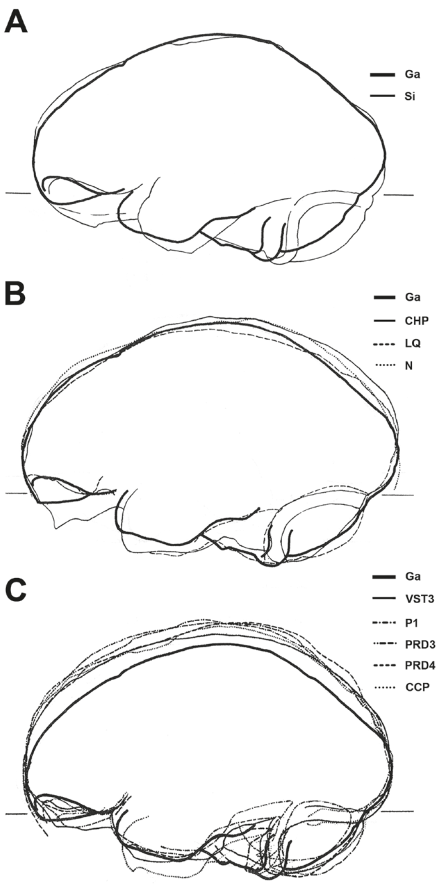

Fig. 3 - Half a century ago, Vlček used outline superimposition to compare the profile of Gánovce with other fossil hominids. Here, the endocast outline of Gánovce (Ga) is compared with (a)* Homo erectus *(Sinanthropus - Si), (b) Neanderthals (La Chapelle aux Saints 1 – CHP, La Quina – LQ, Neanderthal - N), and (c) anatomically modern humans (Dolní Věstonice 3 – VST3, Předmostí 3 – PRD3, Předmostí 4 – PRD4, Pavlov 1 – P1, Combe Capelle - CCP). (Modified after Vlček, 1969)

et al., 2016), which was a technology spread across Central Europe and Germany, characterised by a non-Levallois discoid method relying on small pebbles (Valoch, 1984). In addition to the Neanderthal endocranial cast, two more human remains were found in 1955. These are two long bone imprints in the travertine wall on the edge of the central crater, which include partial casts of the medullary cavities of the left tibia and fibula. These traces fit stratigraphically into the third cultural complex (Fig. 4), and it was hypothesized that the bones belonged to a gracile – possibly juvenile – individual (Vlček, 1956, 1969, 1995). The endocast was dated to 105 ka (+10.2 ka, -9.4 ka) according to the absolute radiometric dating of the travertine (^{230}Th dating; Jäger, 1989). Fluorine absorption dating also places the cast in the second half of the interglacial, about 100 ka (Vlček & Pelikán, 1956). Vlček & Pelikán (1956) determined the proportion of fluorine to phosphoric acid in the bone ash of several samples from the Gánovce site, including the petrous part of the temporal bone fragment of the cast, and then estimated the relative age of the samples (see Vlček & Pelikán, 1956). The petrographic and stratigraphic analyses converge on the same time period (Vlček, 1955, 1995).

Endocranial form and vascular morphology

The cast of the endocranium was naturally formed by travertine. The volume of the endocast was estimated to be 1320 cc (Vlček, 1969). Vlček studied the taphonomic process associated with the cast and estimated the probable position of the skull from the sedimentation of the travertine. He observed that the top layer of the sediment reaches the region of the left frontal lobe, and concluded that the skull was trapped in the crater of the central spring on its occipital parts (Vlček, 1988). The endocast is partially covered by attached mineralized bone fragments of the cranial vault, mostly in the left dorsal region. The rest of the cranial bones were probably lost during the quarrying process. The surface of the bone fragments is uneven and multi-coloured because of the corroded travertine layer, which is stained by iron salts (Vlček, 1953, 1955). Vlček determined that the specimen was an adult individual, according to the obliteration of the squamosal suture (Vlček, 1953, 1969). The endocast also displays well preserved inferior and occipital regions, with visible juga cerebralia, foramen magnum, and dural venous sinuses. The dural venous sinuses show an infrequent vascular pattern, with

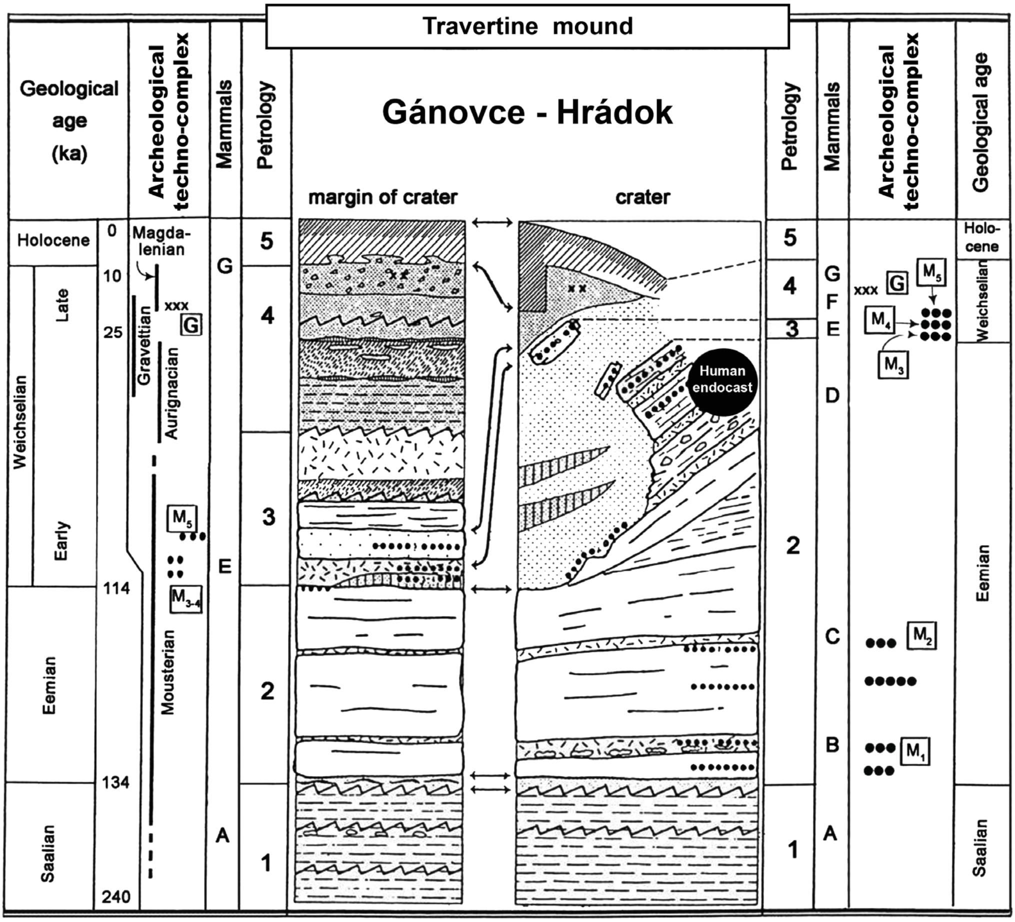

Fig. 4 - The stratigraphy of the Gánovce site with archaeological finds and finds of mammals. Archaeological techno-complexes: G (xxx) – Gravettian; M (•••) – Mousterian. Mammalian fauna: A, B – Late Saalian glacial fauna with woolly mammoth and rhinoceros; C – warm forest fauna with forest elephant and rhinoceros; D, E – the most numerous fauna, with both forest and steppe elements; F – Weichselian glacial fauna with woolly rhinoceros, reindeer, horse, arctic fox and lemming (Fejfar, 1958). Petrological stages according to Kukla (1958). (Modified after Ďurišová et al.***, 2016; Vlček, 1995)***

the superior sagittal sinus splitting into both transverse-sigmoid and occipito-marginal vascular systems (Fig. 5). The former represents the most frequent drainage system in humans, running between the cerebral and cerebellar hemispheres. The latter is a complementary system which usually disappears early in ontogeny, running between the cerebellar hemispheres and retained in some few adult individuals (see e.g. Píšová *et al.*, 2017; Eisová *et al.*, 2019). The vascular imprints suggest that in Neanderthals the superior sagittal sinus frequently runs only into the right transverse sinus, with a strong deviation from the midsagittal line (Rosas *et al.*, 2008; Peña-Melian *et al.*, 2011). Apparently, this is not the case of Gánovce, that displays a distinct scheme, without a pronounced asymmetrical pattern and without a marked blood flow separation between the right and left side. Modern humans also have a general dominance of the right transverse sinuses but,

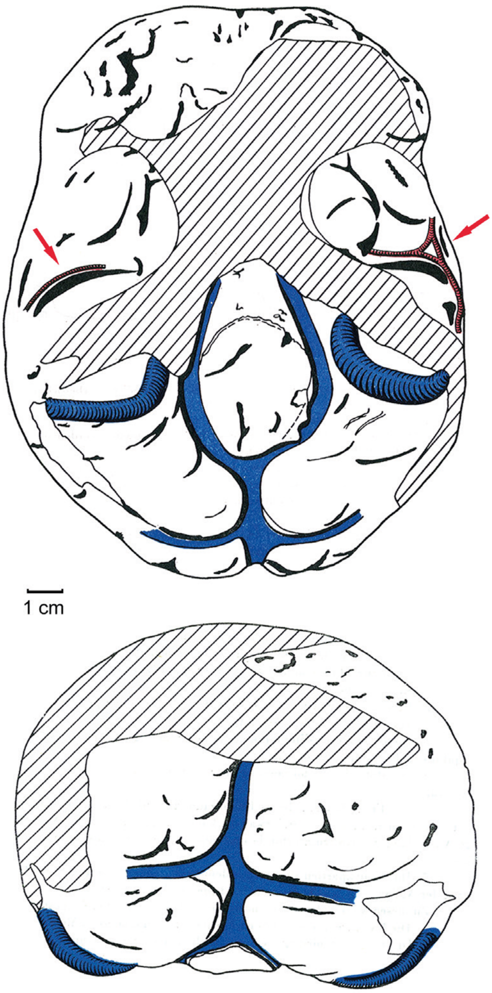

Fig. 5 - Drawings of the Gánovce endocast with dural venous sinuses (in blue) and middle meningeal vessels (in red; arrows) from the inferior (top) and posterior (bottom) view (modified from Vlček, 1969). The colour version of this figure is available at the JASs website.

nonetheless, these features are very variable, with many individual variants and a noticeable intraspecific diversity (Eisová *et al.*, 2019).

Because of the bad preservation of the endocranial surface, the traces of the middle meningeal arteries are not visible, except for very minor portions of the two (right and left) basal branches, which are anyway not sufficient to make any inference on their gross morphology.

Vlček used radiographic methods and later computed tomography (CT) to measure the thickness of the bone fragments, at the squama occipitalis (10 mm), left parietal bone (6-7 mm), right parietal bone (5-6 mm), and frontal bone (6-7 mm) (Vlček, 1988). Recently, a new CT scan of the fossil was performed at the Department of Radiology of the Na Homolce Hospital in Prague with a Siemens Somatom 16, yielding similar results. The average bone thickness is 7.4 mm at the occipital squama, 7.8 mm at the left parietal bone, 4.3 mm at the right parietal bone, and 4.8 mm at the frontal bone. These figures are compatible with adult Neanderthals (see Bruner *et al.*, 2017). The new CT scan (voxel size: 0.39 x 0.39 x 0.30 mm^3) was further processed with Fiji (Schindelin *et al.*, 2012; Rueden *et al.*, 2017) and with Mimics 17.0 (Materialise, Leuven, Belgium). We used advanced segmentation tools to distinguish the bone fragments from the rest of the travertine cast. Figure 6 shows the new digital reconstruction of the endocast and of the remnant bones. The fragments of calvaria are mostly damaged on the extracranial surface and in some regions are also impaired by the travertine. The original bone mass is preserved in the upper region of the occipital squama and in the left parietal bone.

Table 1 shows the main endocranial diameters of the original endocast, following chords and arcs as in Holloway *et al.* (2004). Nonetheless, the surface of the cast is particularly damaged and irregular, and these values must be therefore interpreted as indicative. Because of the bad preservation of the surface, the uncertainty associated with landmarks identification for this specimen is larger than in more standard paleoneurological situations (Pereira-Pedro & Bruner, 2018), especially when considering those measurements based on bregma and lambda (E, F, G, H). Averaging the original measurements by Vlček, our own measurements of the cast, and the metrics from the new CT scans, Gánovce displays a maximum hemispheric length of 175 mm, maximum endocranial width of 136 mm, and frontal width of 118 mm. Compared with modern human morphology, the Gánovce

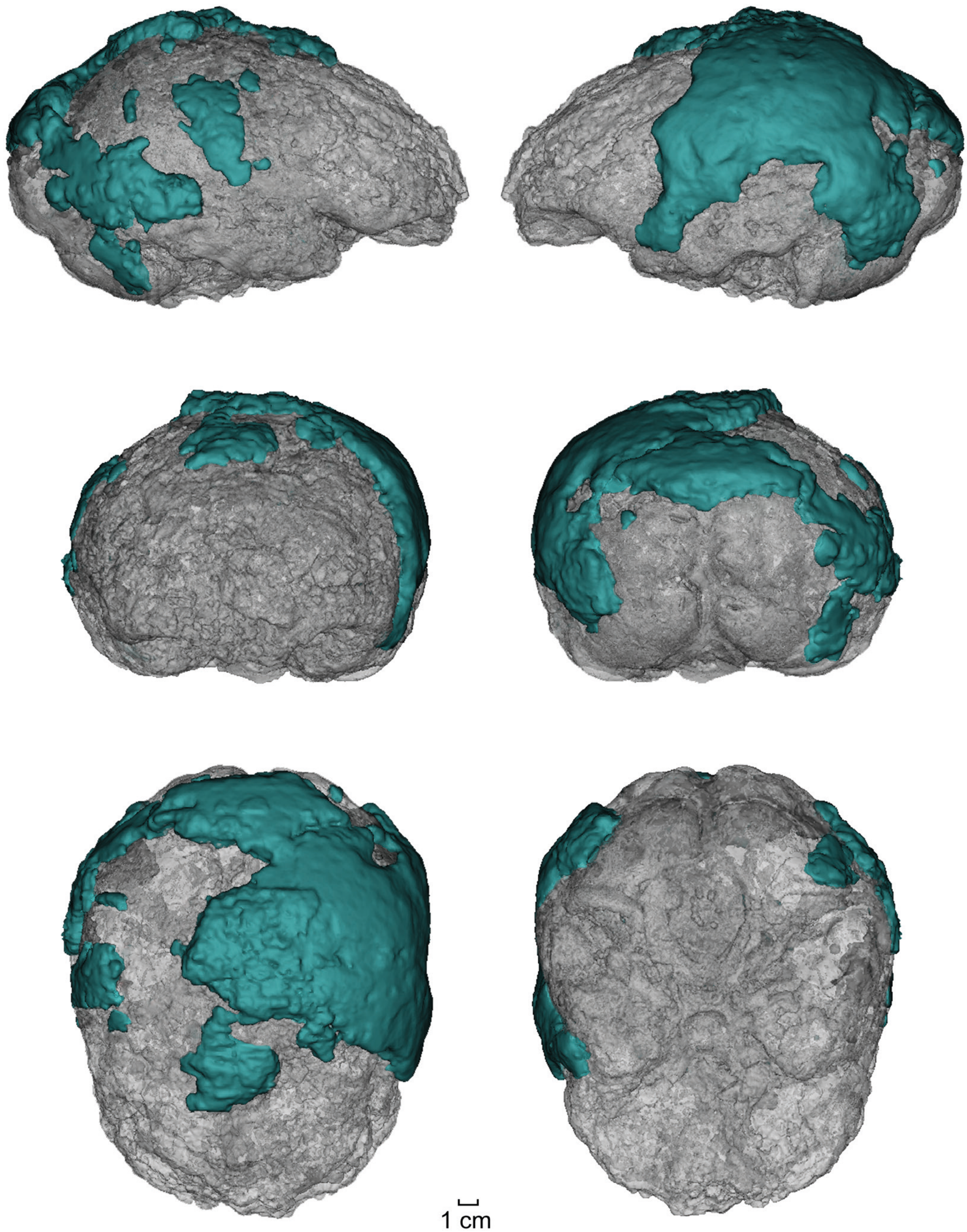

Fig. 6 - Digital reconstruction of the Gánovce fossil with highlighted (coloured) bone fragments (from top to bottom and left to right: right lateral, left lateral, anterior, posterior, superior, and inferior views). Segmentation and reconstruction was computed with Mimics 17.0 (Materialise, Leuven, Belgium). The colour version of this figure is available at the JASs website.

Tab. 1 - Endocranial metrics (A-N following to Holloway et al., 2004)

		R	L
Maximum AP chord (A)		174	176
Maximum AP dorsal arc (B1)		253	252
Maximum AP lateral arc (B2)		236	231
Maximum breadth chord (C)	138		
Maximum breadth arc (D)	197		
Bregma-Lambda chord (E)	82		
Bregma-Lambda arc (F)	91		
Bregma-Basion chord (G)	109		
Bregma-Cerebellum chord (H)		128	122
Maximum cerebellar width (L)	112		
Maximum cerebellar width (M)	105		
Vertex-Temporal depth (N)		111	109
Cerebellar length		62	65
Chord diameter of Broca's caps	115		
Prefrontal arc	148		
Maximum frontal width	117		
Foramen magnum length	43		
Foramen magnum breadth	29		

endocast is wide and flat, with a remarkable frontal width and flat superior parietal regions. Both features are generally typical of Neanderthals (Bruner *et al.*, 2003; Bruner, 2004). Wide frontal lobes are a derived trait shared with modern humans, possibly associated with a lateral redistribution of the cortical tissues due to vertical constraints associated with the eyes and orbits (Bruner & Holloway, 2010; Pereira-Pedro *et al.*, 2017). Short parietal lobes are instead a human plesiomorphic trait (see Bruner, 2018). Taking into account the major endocranial diameters (maximum hemispheric length, maximum endocranial width, frontal width, and vault height), the overall endocranial proportions are compatible with the Neanderthal morphotype, similar to the La Chapelle aux Saints 1, Feldhofer and Guattari 1 (Fig. 7). Both Gánovce and Guattari 1 display wide endocasts, with a notable frontal width and bulging occipital lobe. Because of the irregular and damaged surface, a detailed paleoneurological analysis considering sulcal patterns and cortical proportions is unreliable.

Conclusions

Although the natural endocast from Gánovce is poor in detail, it is fairly complete in its overall form. Nonetheless, the fossil is scarcely known to the paleoanthropological community. This review is aimed at increasing the visibility of this specimen. Its Neanderthal appearance was recognised by Emanuel Vlček fifty years ago, in agreement with the paleoneurological features associated with this endocast. Similarly to Saccopastore 1 (Bruner & Manzi, 2008), Gánovce suggests that a Neanderthal endocranial morphology was established earlier than 100 ka. It is thus likely that Neanderthal brain proportions evolved long before the increase in brain size described in later ("classic") Neanderthal populations (Hublin, 2009). The fossil from Gánovce represents one of the very few early Neanderthal endocasts, and further supports this hypothesis.

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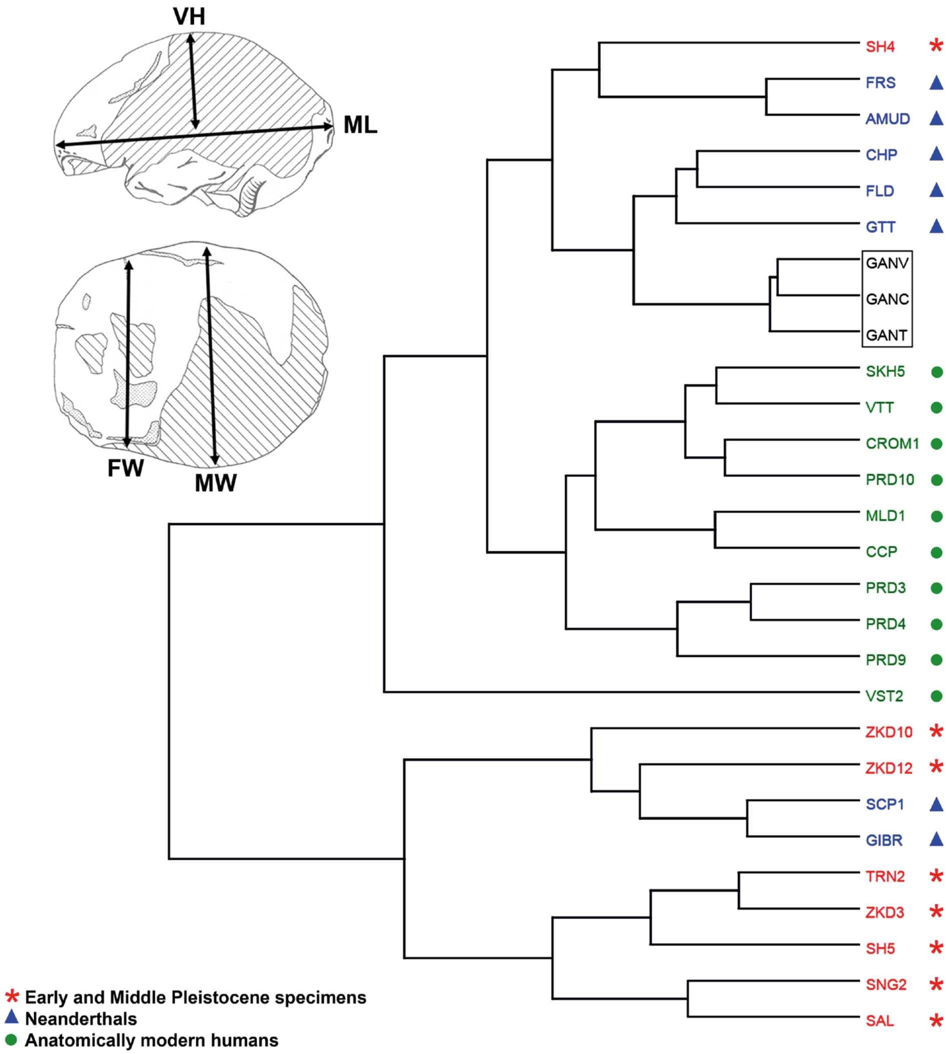

***Fig. 7** - Maximum hemispheric length (ML), maximum endocranial width (MW), frontal width (FW), and vault height (VH) are used to compare the overall endocranial dimensions in Gánovce and other human fossil specimens, after the Unweighted Pair Group Method with Arithmetic mean (UPGMA). We used the original measures by Vlček (GANV), our own measurements of the cast (GANC), and the metrics from the new CT scans (GANT). The three estimates for Gánovce cluster together, suggesting good agreement between the three measurements. Specimens: Salé (SAL), Sima de los Huesos 4 (SH4), Sima de los Huesos 5 (SH5), Trinil 2 (TRN2), Sangiran 2 (SNG2), Zhoukoudian 3 (ZKD3), Zhoukoudian 10 (ZKD10), Zhoukoudian 12 (ZKD12), Amud 1 (AMUD), Feldhofer 1 (FLD), Gibraltar 1 (GIBR), Guattari 1 (GTT), La Chapelle aux Saints 1 (CHP), La Ferrassie 1 (FRS), Saccopastore 1 (SCP1), Combe Capelle 1 (CCP), Cro-Magnon 1 (CROM1), Mladeč 1 (MLD1), Předmostí 3 (PRD3), Předmostí 4 (PRD4), Předmostí 9 (PRD9), Předmostí 10 (PRD10), Skhul 5 (SKH5), Dolní Věstonice 2 (VST2) and Vatte di Zambana (VTT). A cluster analysis based on the unweighted pair group method with arithmetic mean (UPGMA) was computed with PAST 3.18 (Hammer* et al., *2001). The colour version of this figure is available at the JASs website.*

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