

External brain morphology of juvenile cave hyena (*Crocota crocuta spelaea*) from the Jasovská jaskyňa Cave (Slovakia) revealed by X-ray computed tomography

Vlasta Petrovič¹, Martin Sabol², Juraj Šurka³, Martin Pyszek⁴ & Ladislav Stehlík⁴

¹ Department of Zoology, Faculty of Natural Sciences, Charles University, Viničná 7, CZ–12844 Praha 2, Czech Republic; petrovicv@natur.cuni.cz

² Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University in Bratislava, Ilkovičova 6, SK–84215 Bratislava, Slovak Republic; martin.sabol@uniba.sk;

³ Earth Science Institute, Slovak Academy of Sciences, branch Banská Bystrica, Ďumbierska 1, SK–974 01 Banská Bystrica, Slovak Republic; surka@savbb.sk.

⁴ University of Veterinary and Pharmaceutical Sciences Brno, Palackého tř. 1946/1, CZ–612 42 Brno, Czech Republic; pyszek@vfu.cz, lstehlik@vfu.cz

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Abstract: The external brain morphology of a juvenile cave hyena (*Crocota crocuta spelaea*) from the Jasovská jaskyňa Cave is described and compared with virtual endocasts of adult specimens of cave and modern spotted hyenas. Apart from differences in the development of olfactory tubercles and posterior endocast portion, the virtual endocast of the adult cave hyena has predominantly more developed sulcal and gyral impression patterns than the juvenile specimen. The smaller change in brain size during ontogeny compared with the increasing of the skull size is also observed. Additionally, the adult *C. c. spelaea* has a smaller anterior cerebrum volume in comparison with modern *C. crocuta*. Data obtained by these comparisons are discussed from the viewpoint of differences in social behaviour development and foraging strategies in extinct cave hyenas and extant spotted hyenas.

Key words: *Crocota crocuta spelaea*, virtual endocast, external brain morphology, social behaviour, Late Pleistocene, Jasovská jaskyňa Cave, Slovakia

1. INTRODUCTION

The computed tomography scan (CT), which until recently has been mainly applied in medical science, is now widely used in various palaeobiological studies. This “industrial CT scanning” is especially beneficial in the examination of internal structures of fossil objects, and very good results have been achieved in vertebrate palaeontology (Iurino et al., 2013). The utility of CT scanning for other areas of palaeobiological research is also considerable, and CT imaging techniques have now fully superseded the original external brain morphology studies based on the latex moulding of endocranial surface.

Computed tomography study in hyenids initially focused on the interspecific variability (e.g., Dockner, 2006), and later on sexual dimorphism (e.g., Arsznov et al., 2010) or brain volume and social behaviour (e.g., Sakai et al., 2011; Vinuesa et al., 2016). The brain volume varies generally from species to species and also within the species, thus reflecting inter-individual differences such as gender (e.g., Nopoulos et al., 2000) and ontogenetic stages (e.g., Macrini et al., 2007). Intraspecific variation with respect to regional or total brain volumes affects both the functional characterisation of brain areas and the results of interspecific comparisons of brain size (Arsznov et al., 2010).

Recent advances in radiographic imaging have enabled creation of virtual 3-dimensional endocasts based on computed tomography, but these still do not permit analysis of subcortical brain structures. This technique is now also utilised in the study of the external brain morphology of the cave hyena juvenile [*Crocota crocuta spelaea* (Goldfuss, 1823)] from the Jasovská jaskyňa Cave. Herein, the virtual endocasts of this juvenile and another adult

cave hyena from Prepoštská jaskyňa Cave were created, and the brain cavities and areas were compared with those of modern spotted hyenas [*C. crocuta* (Erxleben, 1777)] from Africa.

2. LOCALITY

The Jasovská jaskyňa Cave is situated near Jasov village in the Medzevská pahorkatina (Medzev Hills) of the Košická kotlina (Košice Basin), approximately 20 km W-SW from Košice town (48° 40′ 36″ N, 20° 58′ 35″ E) in the Slovenský kras National park (Fig. 1) (Bella, 2003; Bella et al., 2007^b). The entrance to this 2,811 m long and 55 m deep fluvio-karst cave is situated at 257 m elevation (Bella et al., 2007^b). The cave is formed in Middle Triassic grey Guttenstein Dolomite and light Steinalm Limestone and Dolomite of the Silica Nappe; it is connected with the Okno (Window) Cave and genetically related to the Oblúková jaskyňa Cave (Arc Cave), the Fajka (Pipe) Cave, and the Kamenná pivnica (Stone Cellar) Cave (Bella, 2003). The original cave entrance (now cave exit) forms probably an evolutionary phase of the ponor portion of the cave system (Bella et al., 2007^a). A short history of the cave exploration and palaeontological excavations at the site can be found in Sabol et al. (2018).

3. MATERIAL AND METHODS

The studied skull of juvenile cave hyena (an individual younger than one year) from Late Pleistocene deposits of the Jasovská jaskyňa Cave is housed and exhibited in the Slovak National



Fig. 1. Location of the Jasovská jaskyňa Cave in south-eastern Slovakia and the cave ground plan (<http://www.ss.sk/sk/jaskyňa/11-jasovska-jaskyňa>, 2018; modified).

Museum – Natural History Museum in Bratislava with collection number Z 215 (P 1494/1961). It is the best preserved fossil record of this hyenid taxon in Slovakia, found in Upper Pleistocene sediments (Sabol et al., 2018). Its neurocranial portion was CT scanned especially for detailed description of the external brain surface morphology. This was subsequently compared to the external brain surface morphology of the virtual endocast created by the CT scanning of the neurocranial fragment of the cave hyena adult individual (A-IX/839.4) from the Last Glacial deposits (> 49 – 24.5 ka uncal BP) of the Neanderthal site Prepoštská jaskyňa Cave (Čeklovský et al., 2016), housed in the Horná Nitra Museum in Prievidza. For comparison of cranial cavities, regardless of gender, a further three skulls of adult hyenas (older than 30 months of age) were used. One of these skulls is from the Last Glacial cave hyena from the Sloupské jeskyňe Caves (An 244) and it is housed in the Anthropos Museum in Brno (Moravia, Czech Republic). The other two skulls are from individuals of the modern African spotted hyena and come from the depositary of the Anthropos Museum (Reg. No. 1133) and a private collection (un-numbered). The morphological features of the virtual brain endocasts were also compared with those described and figured in Dockner (2006), Arsznov et al. (2010), Sakai et al. (2011), and Vinuesa et al. (2015, 2016).

The juvenile skull and the adult neurocranial fragment were scanned by Phoenix v|tome|xL 240 tomographic device (industrial CT scanning) at the Earth Science Institute of the Slovak

Academy of Sciences in Banská Bystrica (Slovakia). The remaining hyena skulls were scanned using the GE LightSpeed 16 Slice tomographic device (medical CT scanning) at the University of Veterinary and Pharmaceutical Sciences Brno. In both cases, X-ray computed tomography used irradiation to produce two-dimensional images of the scanned objects in the transverse plane. These can also be examined in other planes (multiplanar reconstructions) or viewed as volume data (3D view).

The juvenile and adult cave hyena specimens were scanned in Banská Bystrica and analysed by using 240kV/320W microfocus tube. Scanning parameters for the hyena skull from the Jasovská jaskyňa Cave were set as follows: voltage 130 kV, current 300 μ A, projections 2,400, average 3, skip 1, timing 750 ms, and voxel size 113 μ m. The hyena specimen from the Prepoštská jaskyňa Cave was scanned with these parameters: voltage 150 kV, current 350 μ A, projections 2,400, average 3, skip 1, timing 500 ms, and voxel size 80 μ m. A 0.1 mm Cu filter was used for filtration.

Tomographic images from the CT scanner in Brno were taken at 100 kV with automatic mA (13 to 25 mAs), in a high-frequency algorithm (bone) with helical mode, slice thickness 1.25 mm, spiral pitch 1.375, image matrix 512 x 512 pixels per slice with 360 μ m pixel size. The CT images were stored in DICOM (Digital Imaging and Communications in Medicine) format and generated by TomoCon Lite 20 software.

The modern development in CT techniques has also enabled creation of virtual endocasts of cave hyena skulls (juvenile and

adult specimens). These 3D virtual models, which are digital casts of the intracranial space enclosed by cranial bones, were generated from the CT-scans using myVGL 2.2 software. The external brain morphology, including gyral and sulcal patterns, was inferred from both virtual endocasts and CT-slices.

The identical nomenclature of the external brain morphology is applied for sulci and gyri found in similar locations and with similar topography in correlated 3D virtual models. The cortical nomenclature follows that of Brauer and Schober (1970, 1976), Radinsky (1973), and Lyras & Van der Geer (2003). Five measurements of the 3D virtual endocasts were taken (Fig. 2). The measured data are in millimetres (Tab. 1).

posterior to the cruciate sulcus, but anterior to the tentorium cerebelli. The cerebellum is housed within the intracranial cavity in the posterior cranial fossa (Arsznov et al., 2010).

The olfactory bulbs are relatively large, moderately higher than wide, and protruding in the rostral direction. The external surface of the endocast cerebrum has deep and well-defined sulcal impression patterns. These include the following: the occipital sulcus in the caudal to caudoventral surface, short endolateral sulcus, longitudinal marginal (lateral) sulcus located laterally to endocast midline, inverted U-shaped suprasylvian sulcus (medial, rostral, caudal) located dorsally to the sylvian and ectosylvian sulci, posteriorly situated ectosylvian sulcus

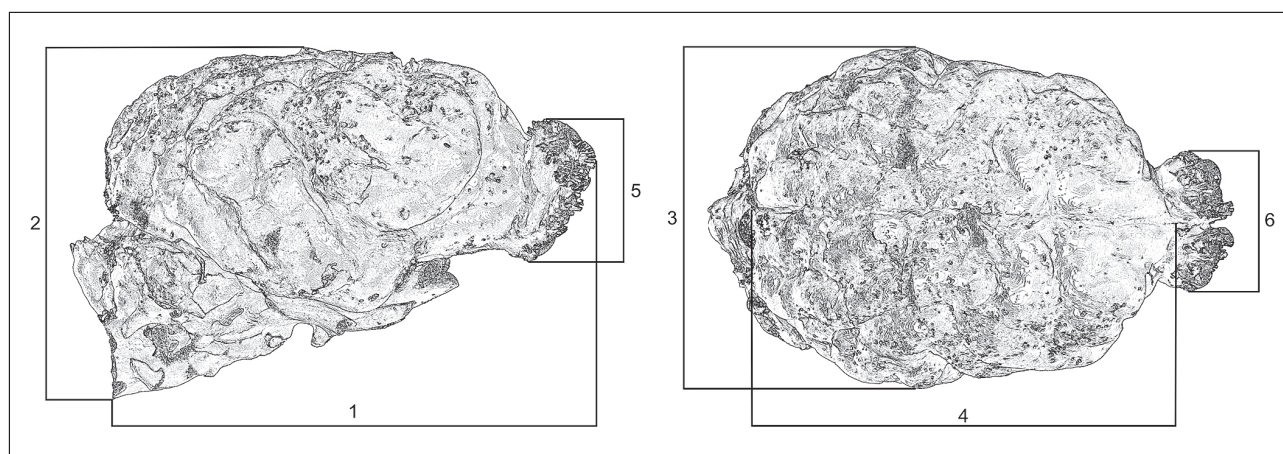


Fig. 2. Measurement method of hyenas' virtual endocasts. (1) endocast length measured from olfactory bulbs to medulla oblongata posteriorly bordered by the foramen magnum, (2) maximum endocast height, (3) maximum endocast (cerebrum) width, (4) cerebrum length, (5) height of the olfactory bulb region, (6) maximum width of the olfactory bulb region.

Table 1. Measurements (in mm) of virtual endocasts of cave and spotted hyenas under study. Measurement number key as in the legend for figure 2.

Measurements	Z 215	A-IX/839.4	An 244	1133	private coll.
(1)	105.0	–	120.4	103.2	120.1
(2)	64.1	64.1	63.0	55.5	53.5
(3)	66.9	69.5	70.0	61.1	63.0
(4)	83.1	–	86.8	77.7	83.2
(5)	28.0	–	25.2	16.7	17.8
(6)	27.6	–	28.0	23.3	23.8

4. RESULTS

4.1. Description of external brain morphology of juvenile cave hyena

The morphology of the studied juvenile cave hyena skull from the Jasovská jaskyňa Cave was described in detail in Sabol et al. (2018). The main morphological characters of the virtual endocast from lateral and dorsal view include olfactory bulbs, anterior and posterior cerebrum, cerebellum, sulci and gyri (Fig. 3). The anterior cerebrum is the region rostral to the junction of the cruciate sulcus and midline, and caudal to the olfactory bulbs. The posterior cerebrum includes the endocranial volume

(caudal), presylvian sulcus as the rostral continuation of the sylvian sulcus, short coronal sulcus, ventrally located rhinal sulcus divided to rostral and caudal parts, ansate sulcus as the mediolateral continuation of the marginal sulcus, short prore-al sulcus, transversal cruciate sulcus, and intraorbital sulcus located just rostral to the presylvian sulcus. The sylvian sulcus (fissure) forms a distinct lateral structure dividing the endocast into anterior and posterior portions. The upper sagittal sinus (longitudinal fissure) is also clearly visible in dorsal view, and this divides the brain into left and right hemispheres. The cruciate sulcus is a prominent landmark on the virtual endocast, running transversely across the rostradorsal surface of the cerebrum and dividing it into the anterior and posterior cerebrum. The most

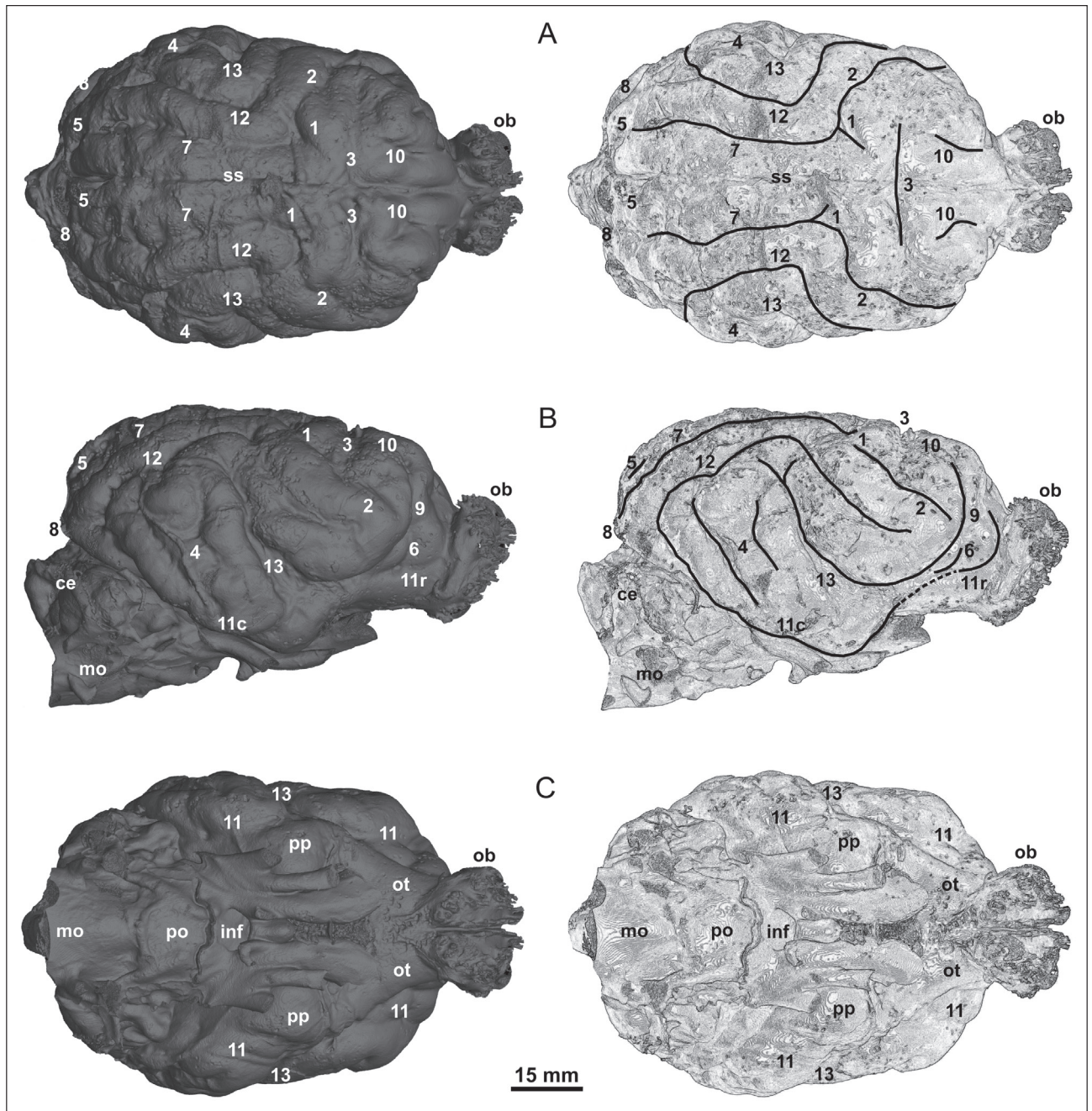


Fig. 3. Virtual endocast of juvenile cave hyena (Z 215) from the Jasovská jaskyňa Cave. A – dorsal view, B – lateral (right) view, C – ventral view; (1) ansate sulcus, (2) coronal sulcus, (3) cruciate sulcus, (4) ectosylvian sulcus, (5) endolateral sulcus, (6) intraorbital sulcus, (7) marginal (lateral) sulcus, (8) occipital sulcus, (9) presylvian sulcus, (10) proreal sulcus, (11) rhinal sulcus (c – caudal, r – rostral), (12) suprasylvian sulcus, (13) sylvian sulcus (fissure), (ce) cerebellum, (inf) infundibulum, (mo) medulla oblongata, (ob) olfactory bulbs, (ot) olfactory tubercles, (po) pons, (pp) palaeopallium, (ss) sagittal sinus (longitudinal fissure).

obvious gyral impressions of the virtual endocast are: the occipital gyrus, marginal gyrus, suprasylvian gyrus (medial, rostral, caudal), ectosylvian gyrus (medial, rostral, caudal), sylvian gyrus (rostral and caudal), proreal gyrus, and the praecruciate gyrus. The cerebellum is a relatively distinct element in the posterior part of the studied endocast and the anterior part of the medulla oblongata is visible below it.

Other “brain” elements can be distinguished in ventral view. The most visible is the pons, topographically situated in front of the cerebellum. The funnel-shaped infundibulum is anterior to

the pons and this connects the hypothalamus and hypophysis. Some cranial nerves are distinguished here, and the optic chiasm, connecting the optic nerves, is located in front of this structure. The palaeopallium is developed laterally from the abovementioned cranial nerves, and the caudal composite gyrus winds dorsally from this evolutionary oldest part of the telencephalon. The olfactory tubercles are only weakly distinguishable.

It is not possible to detect the studied individual’s gender at the presumed age (between 6 months and 1 year old) based solely on endocast surface morphology (see also Arsznov et al., 2010).

4.2. Comparison

In comparison with the virtual endocast of the partially preserved skull of the adult cave hyena from the Prepoštská jaskyňa Cave, the external brain structures of both specimens are morphologically quite similar. The main differences are in the posterior portion and in the more developed sulcal and gyral impression patterns with their complete and simplified course in the adult specimen. The shape and size of individual gyri changed during the brain ontogeny – these began to grow and expand gradually,

with the number and size of sulci beginning to shorten. Part of the sulci most likely disappeared and were covered by expanding gyri by the time the adult stage was reached. For example, a short sulcus, dividing the posterior limb of the suprasylvian gyrus in the juvenile cave hyena, is reduced or missing in the adult animal. In addition, the crucial sulcus is more visible in dorsal view in the juvenile virtual endocast and the adult specimen had most likely more developed olfactory tubercles (Fig. 4).

The studied skull CT cross-sections clearly shows the different ratio between the increasing skull basal length and the

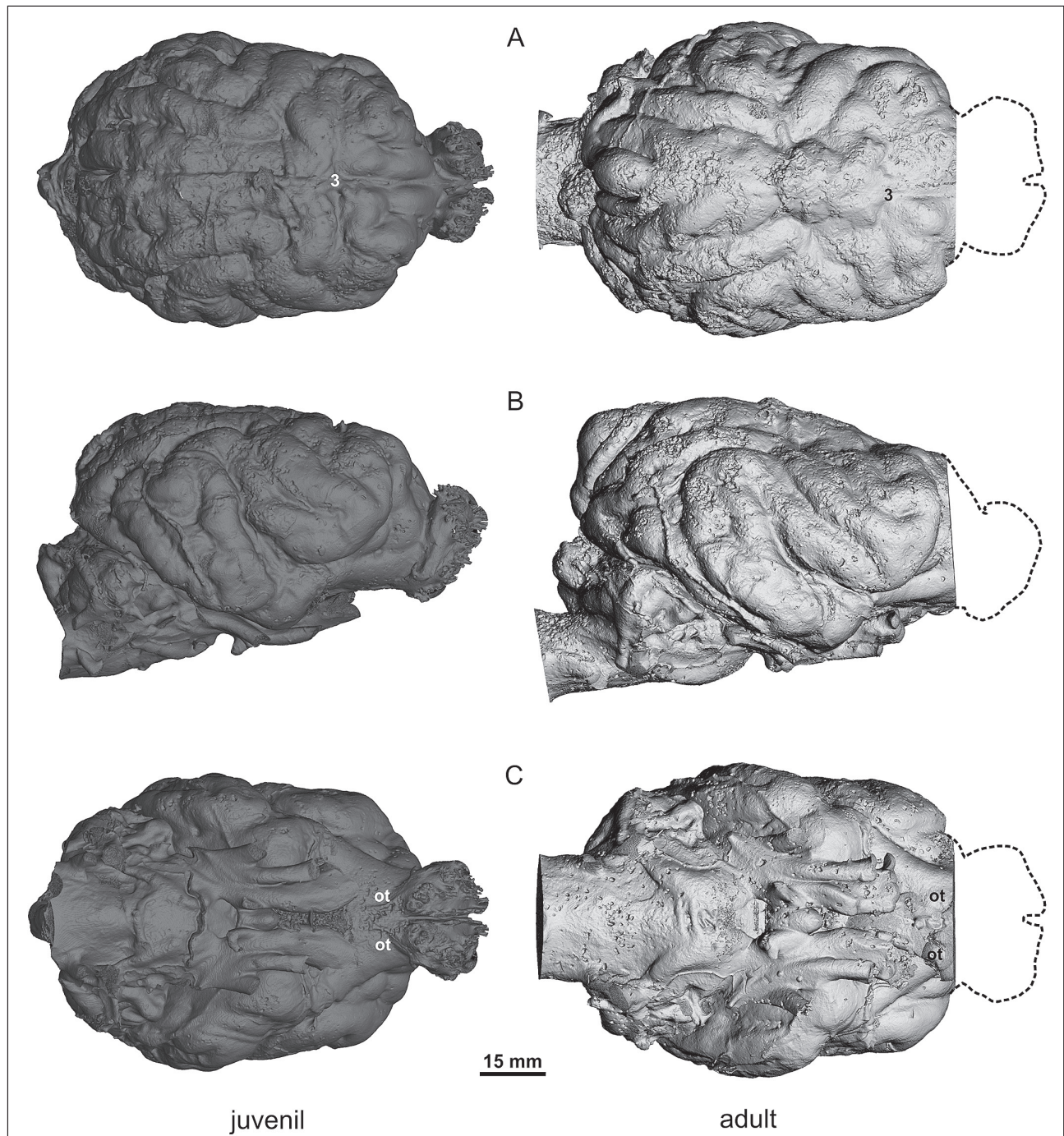


Fig. 4. Comparison of virtual endocasts of the juvenile cave hyena (Z 215, left) from the Jasovská jaskyňa Cave and the adult cave hyena (A-IX/839.4, right) from the Prepoštská jaskyňa Cave. Abbreviations as in the legend for figure 3. A – dorsal view, B – lateral (right) view, C – ventral view.

brain volume during the ontogeny. The skull basal length distinctly increases towards the adult stage. This is especially observed in prolongation of the splanchnocranial portion (including also the increasing of frontal sinuses volume), but the brain volume increases much less markedly from the juvenile to adult stage in proportion to skull size (Fig. 5, Tab. 1). This increases to approximately 85% of the adult volume by the first 14 months of age (Arsznov et al., 2010). Differences in the brain (endocranial) volume have already been described in adults of extant hyenid species (Sakai et al., 2011) and extinct ones (Vinuesa et al., 2015, 2016), and also in adult males and females

of modern African *C. crocuta*, where overall brain volume does not differ between the sexes (Arsznov et al., 2010). There is only small brain volume increase towards the adult stage; and this is mainly observed in enlargements of the male anterior cerebrum and the female posterior cerebrum (Arsznov et al., 2010: Fig. 4A).

The main difference in the adult virtual endocasts is the distinctly smaller ratio between relative lengths of the anterior and posterior cerebrum in modern *C. crocuta* compared to *C. c. spelaea* (Fig. 6). This indicates a shorter anterior cerebral length when the total cerebrum length in cave hyena is considered.

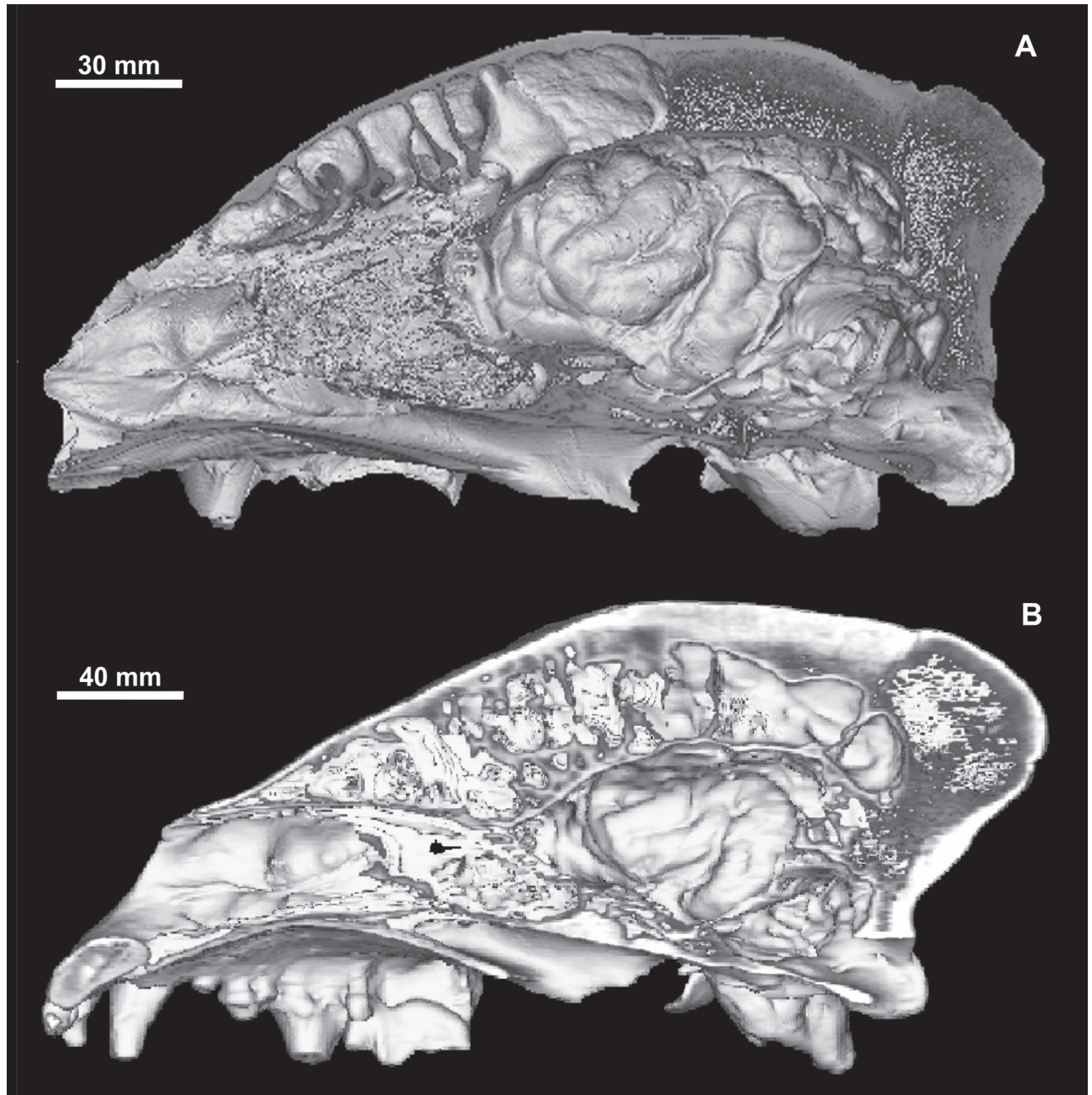


Fig. 5. Comparison of CT cross-sections of (A) juvenile cave hyena skull from the Jasovská jaskyňa Cave (Z 215) and (B) adult cave hyena skull from the Sloupské jeskyňe Caves (An 244). The prolongation of the splanchnocranial portion and the increasing of frontal sinuses volume is observed towards the adult stage, while the brain volume increases much less markedly.

This may be associated with less enhanced ability to process social information in *C. c. spelaeae* (see also Sakai et al., 2011 or Vinuesa et al., 2016) or it may also be connected with a more impulsive aggressive behaviour of cave hyenas. However, further analyses are required to validate or rebut this assumption.

5. DISCUSSION

Despite the smaller anterior brain, which is more comparable to that of extant bone-cracking *Hyaena* and *Parahyaena* (Vinuesa et al., 2016), the cave hyena virtual endocast is generally more similar

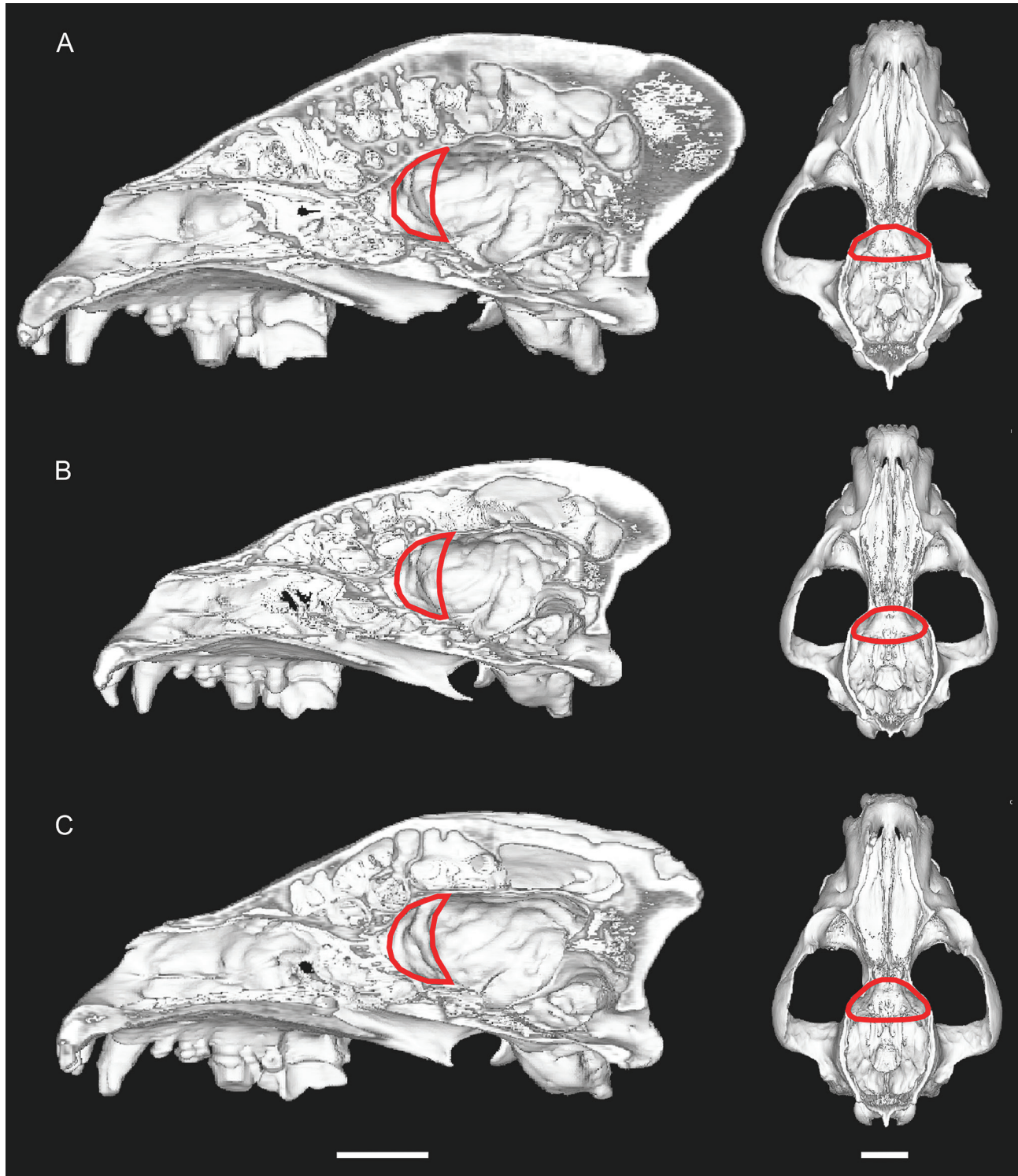


Fig. 6. Vertical and horizontal CT cross-sections of adult hyena skulls under study with the highlighted portion of the anterior cerebrum (red line). Scale bars are 40 mm. A – cave hyena from the Sloupské jeskyňe Caves (An 244), B – modern spotted hyena from Africa (1133), C – modern African spotted hyena from private collection (unnumbered).

to that of the spotted hyena than to endocasts of other extinct and extant hyenid species (see also Sakai et al., 2011; Vinuesa et al., 2015), what confirms the close relationship between these both taxa (Fig. 7). The endocast similarity between extinct *C. c. spelaea* and modern *C. crocuta* is also documented by Vinuesa et al. (2016). These authors especially support the presence of the proreal sulcus close to the presylvian sulcus and the length and curvature of the major sulci, including the development and length of the suprasylvian sulcus. In contrast, the cave hyena's endocast differs from that of extant *Crocuta* in several features; particularly in the position of the cruciate sulcus and in the relative size of the anterior cerebrum previously mentioned herein (Vinuesa et al., 2016). The relatively shorter anterior cerebral portion in the extinct Eurasian *Crocuta* species can be assumed a "plesiomorphic

condition" in comparison with the modern species, retained after separation from the ancestral African populations. Moreover, the greater development of the frontal portion of the brain in extant *C. crocuta* is a recent evolutionary acquisition, most likely post-dating the last inferred dispersal event from Eurasia into Africa at approximately 63 ka (Sheng et al., 2014).

The modern spotted hyenas are the most advanced modern hyenid species (Koepfli et al., 2006). They have highly-developed sociability (Mills, 1990; Cooper et al., 1999) and live in smaller or larger clans (Kruuk, 1972) similar in size and structure to troops of some species of cercopithecine primates (Drea & Frank, 2003; Holekamp et al., 2007^a). These clans are hierarchical, with the dominance of adult females (Tilson & Hamilton, 1984; Frank, 1986) and immigration of males from other clans. This

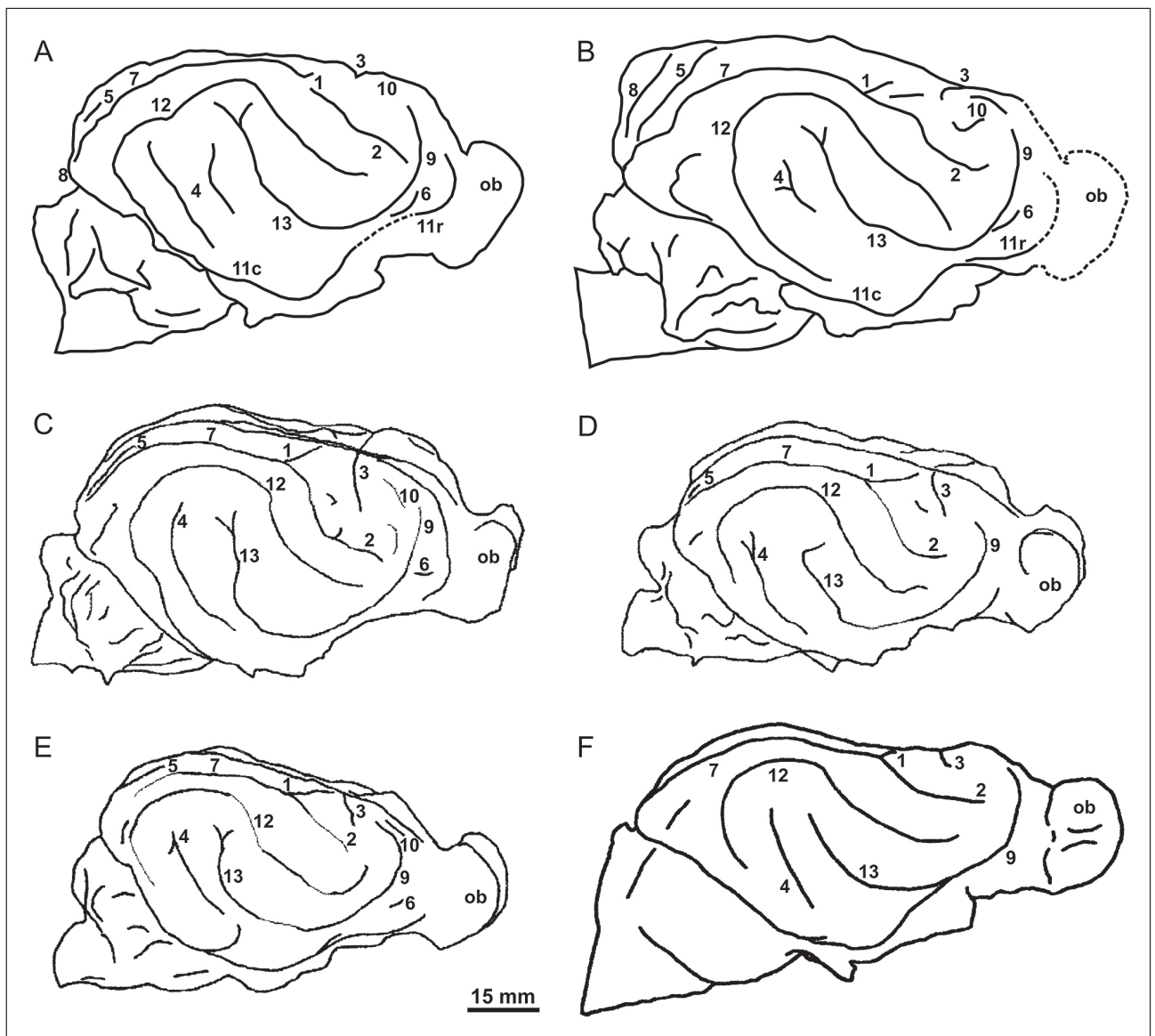


Fig. 7. Line drawing of a lateral – dorsolateral view of the virtual endocasts of samples under study and other hyenid species, showing the location and relative position of prominent sulci. Number key as in the legend for figure 3 (ob – olfactory bulb). A – juvenile cave hyena from the Jasovská jaskyňa Cave (Z 215), B – adult cave hyena from the Prepoštská jaskyňa Cave (A-IX/839.4), C – modern adult spotted hyena (*Crocuta crocuta*), D – modern adult striped hyena (*Hyaena hyaena*), E – modern adult brown hyena (*Parahyaena brunnea*), F – adult *Pliocrocuta perrieri* from European Plio-Pleistocene (C-E – modified according to Sakai et al., 2011: Fig. 4a-c; F – modified according to Vinuesa et al., 2015: Fig. 2k).

most likely accounts for the noted differences in brain volume or organisation between the sexes (Arsznov et al., 2010). There is a significant relationship between relative brain size and social complexity in mammals (Pérez-Barbería et al., 2007; Schultz & Dunbar, 2007; Swanson et al., 2012), and this was also confirmed by Sakai et al. (2011) in *Croculta*. These authors reported positive correlation between the relative size of the anterior brain and group-size in this hyenid. The frontal cortex is known to mediate complex social behaviour in mammals (Adolphs, 2001) and spotted hyena females are not only socially dominant to males, but they are also much more aggressive (Arsznov et al., 2010). In comparison with the *C. c. spelaea*, a more developed anterior brain region may therefore indicate greater hunting ability, more flexible foraging behaviour (Vinuesa et al., 2016) and more complex social behaviours, especially in specimens living in open habitats (Smith et al., 2012).

The extinct cave hyena as a bone accumulator was also a gregarious carnivore that most likely lived in clans similar to spotted hyenas from today's African savannahs (Turner & Antón, 1996; Boaz et al., 2000; Holekamp et al., 2007^a, 2007^b, 2015). However, this assumption contrasts with more recent palaeoneurological studies (Arsznov et al., 2010; Sakai et al., 2011; Vinuesa et al., 2015, 2016) that rather support a limited sociability in this extinct taxon. Several aspects of social behaviour, including gregariousness, hunting abilities, territoriality and foraging strategies are closely linked to relative frontal brain size. Therefore *C. c. spelaea*, with the less anterior brain volume in comparison with the *C. crocuta*, could be interpreted as an extinct hyenid with reduced social abilities, dietary differences and/or less behavioural flexibility. These disadvantages presumably resulted in less adaptability to new and unpredictable environments than that reported for extant spotted hyenas (Vinuesa et al., 2015). Moreover, the inverse correlation between the anterior cerebrum volume and both home range and forelimb usage, previously recorded by Swanson et al. (2012) for terrestrial carnivores in general, most likely indicates, in cave hyenas in connection with their assumed smaller anterior cerebrum volume, a more restricted home range and less pronounced forelimb usage when searching for prey.

However, it cannot be excluded that cave hyenas, similarly to extant spotted hyenas, were also hunters rather than scavengers (Baryshnikov, 1999). The assumed different relative size of the anterior cerebrum could rather indicate a different foraging strategies in both *Croculta* taxa than the differences in their social behaviour. This can be also supported by the relative similarity of encephalisation in their early stages of ontogeny. From the viewpoint of competition, the recent isotopic analysis showed a competitive exclusion between cave hyenas and cave lions (Bocherens et al., 2011). Thus, the only potential competitor for cave hyenas could be (except man) large brown bears from the Last Glacial, which are considered more carnivorous than their close modern relatives (Bocherens, 2015; Marciszak et al., 2017).

6. CONCLUSIONS

Based on analysis of the virtual endocasts, the external brain morphology of the cave hyena juvenile from the Jasovská jaskyňa

Cave is described and compared with adult endocasts of the same taxon and modern African spotted hyenas. There are only relatively small differences between the juvenile and adult cave hyena endocasts in the development of olfactory tubercles, in the posterior endocast portion, and in the more developed sulcal and gyral impression patterns in the adult specimen, which has smaller anterior cerebral volume than the modern *C. crocuta*. The relative encephalisation in early ontogeny stages suggests rapid development of pack social behaviour, and the differences in anterior cerebral size in the adult cave hyenas and spotted hyenas most likely indicates different foraging behaviour. The analysis in this study also highlighted the lesser change in brain size during ontogeny compared to the increasing skull size.

Finally, although further analysis of external brain morphology of variously-aged cave hyena specimens is required to validate the presented palaeobiological inferences, the obtained data can stimulate future investigation into the social behaviour and foraging strategies of extinct hyenid taxa (but not just these).

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