



Evidence on relation of brain to endocranial cavity in oviraptorid dinosaurs

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Brains in living tetrapods other than birds and mammals do not entirely fill the brain cavities. Examination of dinosaur braincases does not usually allow determination relating to how close walls of endocranial cavity lay to the surface of brain. The here described fragment of a skull roof of an oviraptorid dinosaur, *Ingenia yanshini*, shows perfectly preserved, numerous vascular imprints that cover the internal surfaces of frontals and parietals in the region roofing the cerebral hemispheres and cerebellum. This specimen shows that in oviraptorids the brain closely fitted the brain cavity, to the extent found in birds and mammals. Among dinosaurs, only one similar case has been previously reported in an ornithomimid, *Dromiceiomimus brevitertius*, but the preserved vascular imprints are less numerous and regular in this dinosaur than in *Ingenia yanshini*.

Introduction

It has been assumed (Jerison 1973) that the cranial cavity in fossil reptiles may have had a volume about twice that of the brain size that it contained in life. Hopson (1979) considered that the relationship might be variable in fossil forms, as it is in the living reptiles. He pointed to endocasts of pterosaurs and some theropods, which display a rather elaborate form, and are very brain-like in appearance, suggesting that disparity in size between the brain and the cranial cavity was not so great. (According to Dr. Philip J. Currie's personal communication, January 2004: "this is also true for troodontids and dromaeosaurids, which are well enough preserved to show ventrolateral displacement of the optic lobes, and often have shallow canals on the ventral surfaces of frontoparietals"). Brains of living reptiles, unlike those of birds and mammals, usually do not entirely fill the cranial cavities. In birds and mammals, the brain surface is closely appressed to the bones of the cranial roof, and leaves distinct impressions of the intracranial vascular channels on the undersurfaces of bones in this region. Among dinosaurs, the so far published evidences of direct contact between brain and the roofing bones have only been clearly preserved in an ornithomimid *Dromiceiomimus brevitertius* (Russell 1972), and also suggested for a troodontid, *Troodon inequalis* (Russell 1969). The latter case is, however, not conspicuous,

only one paired groove being preserved beneath the fused parietals that, according to Hopson (1979: fig. 13b), may mark the course of a blood vessel. In *Troodon inequalis*, some vascular imprints have also been found on the laterosphenoid by Currie (1985).

The present paper reports another case of preserved impressions of brain vessels in an oviraptorid theropod, *Ingenia yanshini*. In the referred specimen, the undersurfaces of the skull roof bones are perfectly preserved, and do not bear any trace of etching (e.g., by plant rootlets), allowing observation of the most delicate details.

Description

The specimen on which observations have been made is a 42 mm long fragment of the skull roof of *Ingenia yanshini* from the collection of the Paleontological Center, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia (abbreviated GIN). It comes from the Late Cretaceous White Beds of Hermin Tsav (Gradziński et al. 1977; the age equivalent of the Nemegt Formation) at Hermin Tsav locality, Ömnögov' aimag, Mongolia.

This specimen (GIN 100/31) was previously briefly described by Barsbold (1983) and Osmólska (2003). Its drawing has also formed a part of the illustration of the braincase of "oviraptor from Hermin Tsav" in Barsbold's 1977 (fig. 4) paper. Based on comparisons with some completely preserved skulls of other oviraptorids, an estimated basal length of the skull would be 110–130 mm, which is an average skull length for adult oviraptorids. The major part of the fragment is formed from the parietals (sagittal length 30 mm), which constitute the largest part of the skull roof in the oviraptorids. The parietals are complete rostromedially, where they wedge between the frontals, but lack their most caudal portions. The contacting surfaces of parietals and frontals are oblique, so that the parietals overlap the frontals dorsally for a short distance. Only a medial portion of the right frontal is preserved, the left one being broken off along the frontoparietal and interfrontal sutures. The interdigitating frontoparietal sutures are well exposed on the undersurface of the roof. More than half of the posterodorsal surfaces of the parietals are damaged, thereby revealing that the parietals (as well as the frontals) are pneumatic

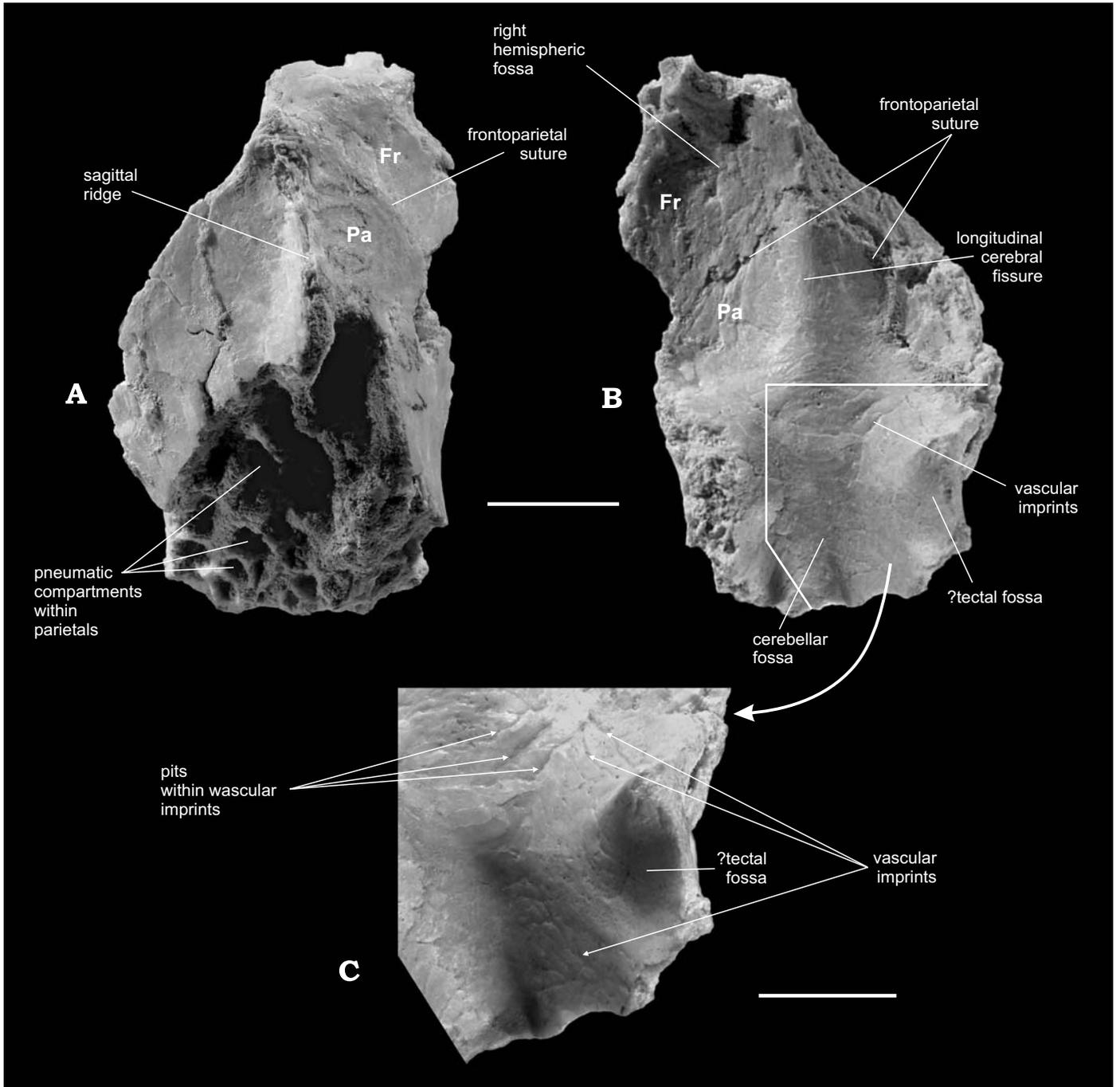


Fig 1. *Ingenia yanshini* Barsbold, 1983. GIN 100/31. **A.** Frontoparietal fragment of skull roof, dorsal view. **B.** Same specimen, ventral view. **C.** Enlarged fragment of B, the arrows showing distribution of pits and details of branching of vascular imprints. Fr, frontal; Pa, parietal. Scale bars 10 mm.

(Fig. 1A). Pneumatization of most of the skull bones is characteristic of the oviraptorids. Due to the extensive pneumatization along the medial portion of the skull roof in *Ingenia yanshini*, the thickness of the parietals (and the frontals) is greatest medially, and the bones become thinner laterally. In this species, the parietal pneumatic system consists of small chambers that are roughly pentagonal or quadrangular in cross-section. On the external surface, the sagittal ridge surmounts the interparietal suture, but fusion

between the parietals is complete on the undersurface, and there is not the slightest trace of the suture visible.

On the undersurface of the skull roof, a pair of shallow depressions is visible that is followed caudally by a deeper and narrower concavity. They covered respectively the cerebral hemispheres and the cerebellum (Fig. 1B). The right hemispheric fossa is more completely preserved, and is about 20 mm long. As preserved, it is about 9 mm wide, but judging from the partially exposed cerebral hemispheres of other

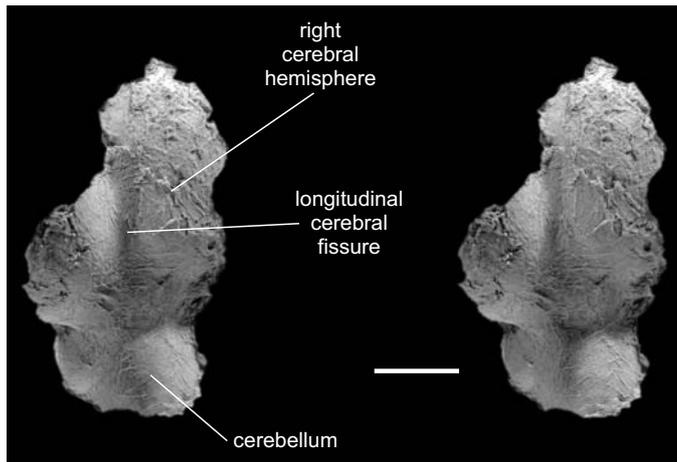


Fig. 2. *Ingenia yanshini* Barsbold, 1983. GIN 100/31. Stereophotograph of latex cast of the frontoparietal fragment; transverse ridges across central region of the cast mark edges of bone lamellae; ridges on right hemisphere are due to abrasion of bone. Scale bar 10 mm.

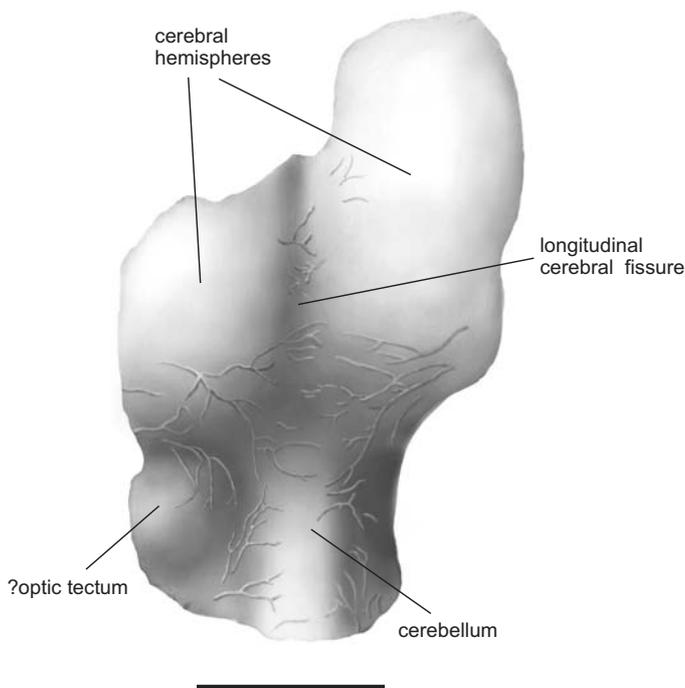


Fig. 3. *Ingenia yanshini* Barsbold, 1983. GIN 100/31. Schematized drawing of endocast; pitting omitted. Based on latex cast of undersurface of frontoparietal fragment of skull roof. Scale bar 10 mm.

oviraptorid skulls, it was evidently wider. The right hemispheric fossa extends along the frontal, and continues caudally over about the rostral half of the right parietal.

As seen on the latex endocast of the skull roof fragment (Figs. 2, 3), the hemispheres are separated rostrally by a narrow, deep longitudinal cerebral fissure. This becomes shallower and wider caudally where it merges with an almost flat central region between the cerebrum and cerebellum. The transverse fissure of the brain is deeply incised laterally, but

is rather indistinct across the medial portion of the brain. The preserved cerebellar part is entirely roofed by the parietals. It is somewhat more than half as wide, but deeper than, the preserved part of the cerebrum. Its axial profile is inclined dorsocaudally. A cross-section through the caudal section of the cerebellar region has the shape of a wide, inverted V. Ventrolaterally, just behind the transverse fissure there is a small lobe at the base of the cerebellum. It seems to be a fragment of a larger lobe, possibly representing the tectum opticum (Fig. 1B).

Clear imprints of vessels are preserved on undersurfaces of the bones of the hemispheric fossae, and the post-cerebellar region (Fig. 1B, C). They are most numerous and most distinct on the parietals, and are less well preserved on the frontals. The arrangement of the imprints is relatively regular, the major branches on the left and right sides approximately correspond with each other. This arrangement is especially evident on the cerebellar fossa, as well as over the central platform between the hemispheric and cerebellar fossae. The major vascular branches on both sides of the cerebellar fossa ramify dorsad, and the end rami approach the midline of the brain. The dense vascularization on the cerebellar fossa is striking.

Numerous, sparsely distributed tiny punctures cover the undersurface of the skull roof fragment, and are most dense on the preserved fragment of the tectal fossa; some punctures are found within the vascular branches (Fig. 1C). The punctures penetrate the bone, but it is not clear whether they reached the pneumatic system within the bone.

Discussion

The dense and relatively regular imprints of the brain vascularization preserved on the undersurface of the skull roof in the oviraptorid theropod evidence that the brain tightly filled the endocranial cavity, similarly as it does in birds and mammals. Another case of such exceptional preservation has been previously reported in the ornithomimid dinosaur (Russell 1972), and is known also in the troodontids and dromaeosaurids (Philip J. Currie personal communication). According to some recently accepted theropod phylogenies (e.g., Holtz 1996; Maryńska et al. 2002) ornithomimosaur, troodontids, dromaeosaurids, and oviraptorosaurs represent the clade Maniraptoriformes, the first of these subclades being more basal than the remaining ones (compare the cladogram in Maryńska et al. 2002). Therefore, it seems probable that the advanced state of the brain tightly filling the endocranial cavity is a maniraptoriform synapomorphy.

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