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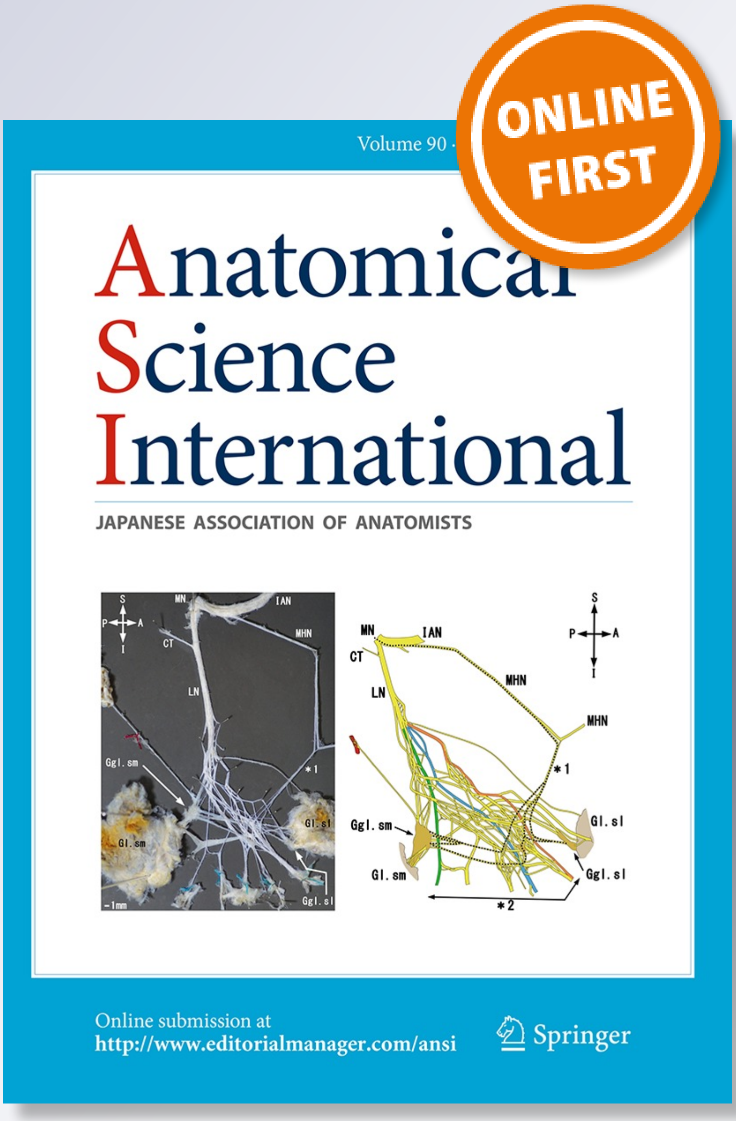

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ORIGINAL ARTICLE

Brain ventricle development in *H. huso* (*Beluga sturgeon*) larvae

S. H. Tavighi[1] · Z. Saadatfar[1] · B. Shojaei[2] · M. Behnam Rassouli[3]

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Abstract The development of ventricles in the brain of *H. huso* (Beluga sturgeon) from 1 to 54 days old is presented in this study. The components observed in the 1-day-old ventricular system were the telencephalic, tectal, and cerebellar ventricles. These ventricles were not observed to have any recess or sulcus. They were surrounded by copious ependymal and embryonic cells. Two different parts were detected in the 6-day-old telencephalic ventricle: the olfactory and lateral ventricle. The olfactory ventricle was observed as a cranial extension of the telencephalic ventricle from 6 days old, as was the inner cell layer of the olfactory bulb (ic) adjacent to this extension. In the preoptic region, the lateral ventricle was connected to the preoptic recess from 15 days old, and this recess was connected by the interventricular foramen to the third ventricle in the diencephalon. At 6 days old, the third ventricle in the diencephalon was visible at the caudal part of the lateral ventricle, and the third ventricle had a recess near to the inferior lobe of the hypothalamus. At 6 days old, the tectal ventricle was observed to have bilateral extensions which proceeded to grow with age. The cerebellar ventricle, situated between the two lobes of the cerebellum, was observed from 1 day old. The cerebellar ventricle grew with age, extending laterally from 6 days old. The connection of the cerebellar ventricle to the fourth ventricle in the medulla oblongata was visible from 6 days old. Upon dividing the ventricular system into three regions (forebrain, midbrain, and hindbrain), stereological studies performed utiizing Cavalieri's principle indicated that the forebrain ventricular region had the smallest volume while the hindbrain ventricular region had the largest.

Keywords *H. huso* · Brain · Ventricle · Development · Stereological

Abbreviations

Caq	Cerebral aqueduct
cc	Central canal
co	Commissural organ
cp	Choroid plexus
Crc	Crown cell
Crv	Cerebellar ventricle
D	Diencephalon
ECrv	Extension of cerebellar ventricle
EM	Embryonic cell
EOTV	Extension of tectal ventricle
ep	Ependymal cell
Etv	Extension of telencephalic ventricle
FV	Fourth ventricle
h	Habenula
Hypr	Hypothalamic recess
Hypv	Hypothalamic ventricle
ic	Inner cell layer of olfactory bulb
ivf	Interventricular foramen
lr	Lateral recess of ventricle
Lav	Lateral ventricle
Ma	Mauthner cell
MO	Medulla oblongata

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NAT	Anterior tuberal nucleus
NLT	Lateral tuberal nucleus
NRP	Nucleus of posterior recess
Olb	Olfactory bulb
Olv	Olfactory ventricle
OT	Optic tectum
OTV	Tectal ventricle
Phr	Posthabenular recess
POR	Posterior recess
PR	Preoptic region
PRr	Preoptic recess
pvopa	Anterior part of the paraventricular organ
Septa	Subependymal arteries
SHypv	Sulcus hypothalamicus
Sih	Sulcus intrahabenularis
SlH	Sulcus limitans of HIS
Slt	Sulcus limitans telencephali
SPR	Sulcus preopticus
Ssh	Sulcus subhabenularis
SV	Saccus vasculosus
T	Telencephalon
TH	Telencephalic hemisphere
thv	Third ventricle
Tpp	Periventricular nucleus of the posterior tuberculum
tv	Telencephalic ventricle
VC	Valvula cerebelli
VIIv	Facial viscerosensory lobe
Vnl	Vagal viscerosensory lobe

Introduction

H. huso (Beluga sturgeon) is an especially long-lived sea-dwelling fish species that is well-known commercially due to the high value of *H. huso* caviar (Birstein et al. 1998), although it is also an important source of valuable fish meat. Adult *H. huso* are not deep-sea fish (they usually live in the middle depths), these pelagic fishes require a relatively low-light environment and make use of special senses; for instance, they can perceive the Earth's magnetic field and without using other environmental factors to navigate while migrating (Kimley et al. 2002). Other sturgeon species are normally benthic—they swim along the sea bottom (Bergquist 1932). Obviously, this difference between the behavior of *H. huso* and that of other sturgeon species is reflected in differences in brain development between these species (Bemis et al. 1997).

The brain structure of a ray-finned fish changes during the development of the fish (Northcutt 1978 and 1996), and these changes correlate with key points in the development of its brain ventricles. However, despite all of the research that has been performed on brain ventricles, there have been few studies on the morphology and evolution of the brain ventricles in *H. huso* larvae.

The central nervous system grows from a hollow tube during the embryonic period. The walls of this tube thicken and form the brain and the spinal cord. The hollow tube fills with the CSF of the ventricular system. This system develops laterally and forms different parts of the brain in all vertebrates, including the olfactory bulb, telencephalic hemispheres, midbrain, and hindbrain or cerebellum (Butler and Hodos 2005).

In most vertebrates, the ventricular system of the brain extends laterally within the telencephalic hemispheres, forming a region known as the lateral ventricle. This ventricle connects to the interventricular foramen (Butler and Hodos 2005), which in turn links to the third ventricle, which is a median ventricular space in the diencephalon. In the dorsal region of this ventricle, the tectal ventricle occupies the midbrain space. In the caudal part of the third ventricle is a thin canal called the cerebral aqueduct, which connects to the fourth ventricle in the hindbrain (Butler and Hodos 2005). The fourth ventricle extends caudally to the central canal of the spinal cord.

The walls of the ventricles are completely covered with a thin ependymal layer and meninx, which form the tela chorioidea or choroid plexus. This structure consists of blood vessels and produces cerebrospinal fluid (CSF) in the ventricular system (Broglio et al. 2003). CSF circulates in the ventricular system, protecting the brain against physical trauma and other damage (Butler and Hodos 2005).

While there have been studies of ventricular development in the teleost brain (Ekstrom et al. 2001), the evolution of the CNS in sturgeons (Von Kupffer 1906), the ontogenesis of the brain in *A. ruthenus* (Nieuwenhuys 1962 and 1963), and brain development in *A. naccari* (Vazquez et al. 2002), there has been no research into the evolution of the brain ventricles in *H. huso* larvae. Therefore, in the research reported in the present paper, we studied ventricular morphogenesis and volume in 1- to 54-day-old *H. huso* larvae. Ventricular volumes were estimated by Cavalieri's principle, which is often used in stereological research to estimate organ volumes (Gundersen and Jensen 1987). In this approach, sections of the organ are prepared and then sampled at regular intervals. A point grid is then applied to each sampled section, and the number of grid points that occur within the section is noted. Knowledge of the number of grid points within each section as well as the interval between sections allows the volume of the organ of interest to be estimated (Howard and Reed 1998).

Materials and methods

For this research, we obtained 40 samples of *H. huso* larvae aged 1, 3, 6, 15, 21, and 54 days post-hatch (dph) from the Shahid Marjani Aghghela propagation station in Gorgan. Six larvae of each age were fixed in 10 % neutral buffered formalin, dehydrated with an ethanol series to 100 %, cleared in xylene, and embedded in paraffin. Because the larval brains were very small, each head was fixed and sited in paraffin blocks. Blocks were cut frontally into serial sections six microns thick from the start to the end of the specimen using a microtome. Tissue sections were deparaffinized and stained with hematoxylin and eosin for general histological studies. They were then studied using a light microscope. Stereological studies were performed utilizing Cavalieri's principle to estimate ventricular volumes. About ten sections were selected from each specimen and figures were prepared using a camera attached to the light microscope. A point grid with a spacing of 0.5 cm was used for point counting. After counting the number of grid points in each section from the ventricle of interest, an unbiased estimate of the ventricular volume was obtained using the following formula:

$$V\ (\mathrm{mm}^3) = d \times \sum p \times \mathrm{a}\ (p),$$

where d is the interval between sections (or the section thickness), $\sum p$ is the total number of points found within the sections, and $a(p)$ is the area represented by each point in the grid.

Results

The following components were observed in the ventricular systems of 1- and 3-day-old *H. huso* larvae (Fig. 1):

1. Telencephalic (forebrain) ventricle
2. Tectal (midbrain) ventricle
3. Cerebellar (hindbrain) ventricle

These ventricles were not observed to have any recess or sulcus. They were surrounded by copious ependymal and embryonic cells. Significant changes in these three ventricular components were seen in the 6-day-old larvae and upon further aging.

Telencephalic ventricle

Two different parts were detected in this ventricle from 6 days old (Fig. 2):

1. Olfactory ventricle
2. Lateral ventricle

The olfactory ventricle was seen as a cranial extension of the telencephalic ventricle that was covered with a thin layer of ependymal cells (Fig. 2). Its expansion to the olfactory bulb developed with age. Adjacent to this extension, the inner cell layer of the olfactory bulb (ic) (Fig. 2) was observed from 6 days old. The olfactory ventricle was followed by the lateral ventricle at the caudal part of the telencephalon; these were situated inside the telencephalic hemispheres.

From 15 days old, the sulcus limitans telencephali appeared in the caudomedial part of the lateral ventricle and the caudal part of the pallium (Fig. 5). It was surrounded by subependymal arteries and eventually ended at the preoptic region (Fig. 5).

The connection of the lateral ventricle duct in the preoptic region to the preoptic recess was first seen in 15-day-old larvae (Fig. 5). The sulcus preopticus was observed caudal to the preoptic recess (Fig. 5). The preoptic recess was connected by the interventricular foramen to the third ventricle in the diencephalon. From 6 days old, the third ventricle in the diencephalon was visible at the caudal part of the lateral ventricle (Fig. 2).

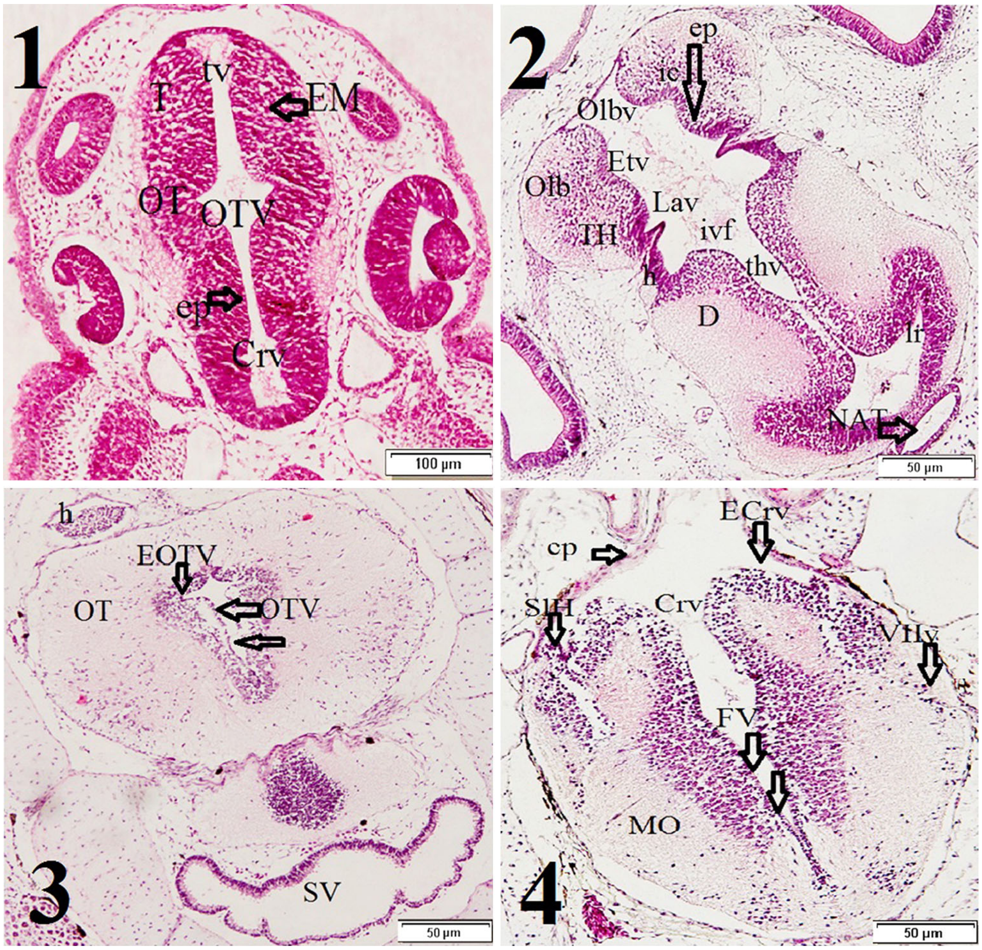
The habenula ganglion was located in the cranial part of the third ventricle (Fig. 2); the following two ventricular sulci were observed in this area in 15-day-old larvae (Fig. 6):

- The sulcus intrahabenularis penetrated the diencephalic wall and bordered the habenula caudally
- The sulcus subhabenularis was located on the lateral part of the third ventricle, rostral to the commissural organ, and extended into the posthabenular recess (Fig. 6)

From 15 days old, the anterior part of the paraventricular organ (pvopa) was visible in the medial part of the third ventricle, adjacent to the thalamus (Fig. 6). On its rostral portion, the periventricular nucleus of the posterior tuberculum (Tpp) was also first noted at this age (Fig. 6).

In the caudal part of the third ventricle, adjacent to the inferior lobe of the hypothalamus, paired lateral recesses were observed at 6 days old (Fig. 2). Caudally at the junction of these two recesses, the anterior tubular nucleus (NAT) was also detected at this age (Fig. 2). Much later, at 54 days old, due to the development of the hypothalamus, the lateral recesses had changed into the hypothalamic ventricle, which was bordered by the sulcus hypothalamicus (Fig. 9).

The tectal ventricle was observed from the first day of the larval period (Fig. 1); at 6 days old, the third ventricle of the diencephalon was seen to be connected to the tectal ventricle. The valvula cerebelli gradually appeared from 21 days old in the middle of the tectal ventricle (Fig. 8). Bilateral extensions of the tectal ventricle, which was



Figs. 1–4 **1** Frontal section of the brain ventricles (H&E) from 1-day-old *H. huso* larvae. *tv* telencephalic ventricle, *OTV* tectal ventricle, *Crv* cerebellar ventricle, *ep* ependymal cells, *EM* embryonic cells, *OT* optic tectum, *T* telencephalon. **2** Frontal section of the brain ventricles (H&E) from 6-day-old *H. huso* larvae. *Lav* lateral ventricle, *Olbv* olfactory ventricle, *TH* telencephalic hemisphere, *Etv* extension of telencephalic ventricle, *ic* inner cell layer of olfactory bulb, *Olb* olfactory bulb, *ivf* interventricular foramen, *thv* third ventricle, *lr* lateral recess of ventricle, *NAT* anterior tuberal nucleus, *h* habenula, *D* diencephalon. **3** Frontal section of the brain ventricles (H&E) from 54-day-old *H. huso* larvae. *Hypv* hypothalamic ventricle, *Shypv* sulcus hypothalamicus, *Caq* cerebral aqueduct, *Hypr* hypothalamic recess. **4** Frontal section of the brain ventricles (H&E) from 21-day-old *H. huso* larvae. *MO* medulla oblongata, *FV* fourth ventricle, *Crv* cerebellar ventricle, *VC* valvula cerebelli, *Ma* Mauthner cells, *OT* optic tectum, *EOTV* extension of tectal ventricle, *Crc* crown cells

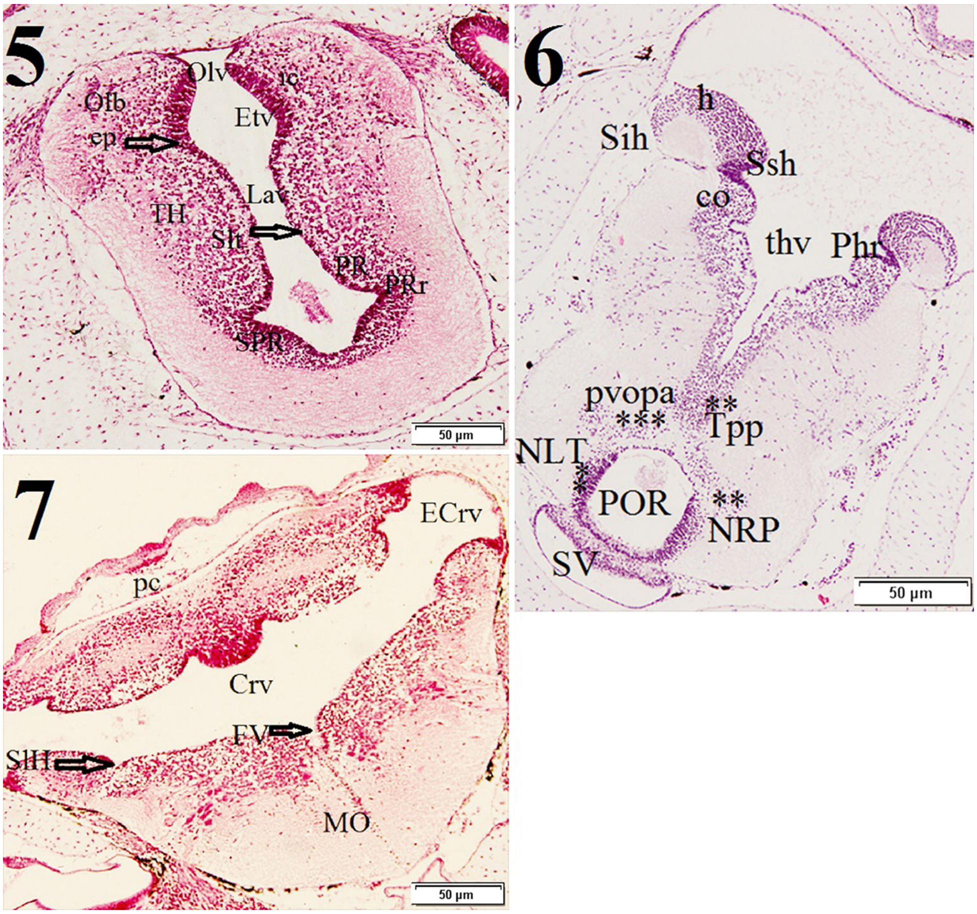
surrounded by ependymal cells, were first observed at 6 days old and expanded with age (Figs. 3, 8).

A special group of ependymal cells named crown cells appeared on the floors of the third and tectal ventricles at 21 days old (Fig. 8). At 15 days old, the tectal ventricle was noted to have extended caudally to the posterior recess (POR), an evagination surrounded by saccus vasculosus (SV) (Fig. 6). At 15 days old, the lateral tubular nucleus (NLT) and nucleus of the posterior recess (NRP) were detected on the lateral and rostral sides of the posterior recess, respectively (Fig. 6).

From the first day of the larval period, the hindbrain contained the two lobes of the cerebellum and the cerebellar ventricle (Fig. 1) and was connected to the hypothalamic recess of the third ventricle via the cerebral aqueduct. The cerebellar ventricle grew with age and presented two bilateral extensions from 6 days old (Fig. 4).

From 6 days old, the choroid plexus and sulcus limitans of HIS (SlH) were recognized at the rostrodorsal and caudomedial parts of the cerebellar ventricle, respectively (Fig. 4). Subsequent expansion of the extensions of the cerebellar ventricle resulted in these structures developed during the next days (Fig. 7). VIIv (the facial viscerosensory lobe) was seen on the lateral side of the caudal border of the cerebellar ventricle from 6 days old (Fig. 4).

The cerebellar and fourth ventricles could be distinguished from each other by 6 days old (Fig. 4). The fourth ventricle grew longitudinally with age (Fig. 8). At 54 days old, an elongated part of the fourth ventricle was visualized in the center of the medulla oblongata (Fig. 10). From 21



Figs. 5–7 **5** Frontal section of the brain ventricles (H&E) from 15-day-old *H. huso* larvae. *MO* medulla oblongata, *Ecrv* extension of cerebellar ventricle, *cp* choroid plexus, *SlH* sulcus limitans of HIS, *FV* fourth ventricle, *Crv* cerebellar ventricle. **6** Frontal section of the brain ventricles (H&E) from 6-day-old *H. huso* larvae. *MO* medulla oblongata, *Ecrv* extension of cerebellar ventricle, *Crv* cerebellar ventricle, *cp* choroid plexus, *SlH* sulcus limitans of HIS, *VIIv* facial viscerosensory lobe, *FV* fourth ventricle. **7** Frontal section of the brain ventricles (H&E) from 15-day-old *H. huso* larvae. *Lav* lateral ventricle, *Olv* olfactory ventricle, *TH* telencephalic hemisphere, *Etv* extension of telencephalon ventricle, *ic* inner cell layer of olfactory bulb, *Olb* olfactory bulb, *ep* ependymal cells, *Slt* sulcus limitans telencephali, *PR* preoptic region, *PRr* preoptic recess, *SPR* sulcus preopticus

days old, bilaterally situated Mauthner cells (Ma) were observed on the caudolateral side of the fourth ventricle (Fig. 8). Vagal viscerosensory lobes (Vnl) were clearly seen on the caudolateral side of the medulla oblongata at 54 days old (Fig. 10). The fourth ventricle continued as the ependymal canal into the spinal cord (Fig. 10).

According to the results of this study, the brain ventricular system in *H. huso* larvae contains three main divisions:

- Forebrain division, including the olfactory, lateral, and third ventricles
- Midbrain division, including the tectal ventricle
- Hindbrain division, including the cerebellar and fourth ventricles

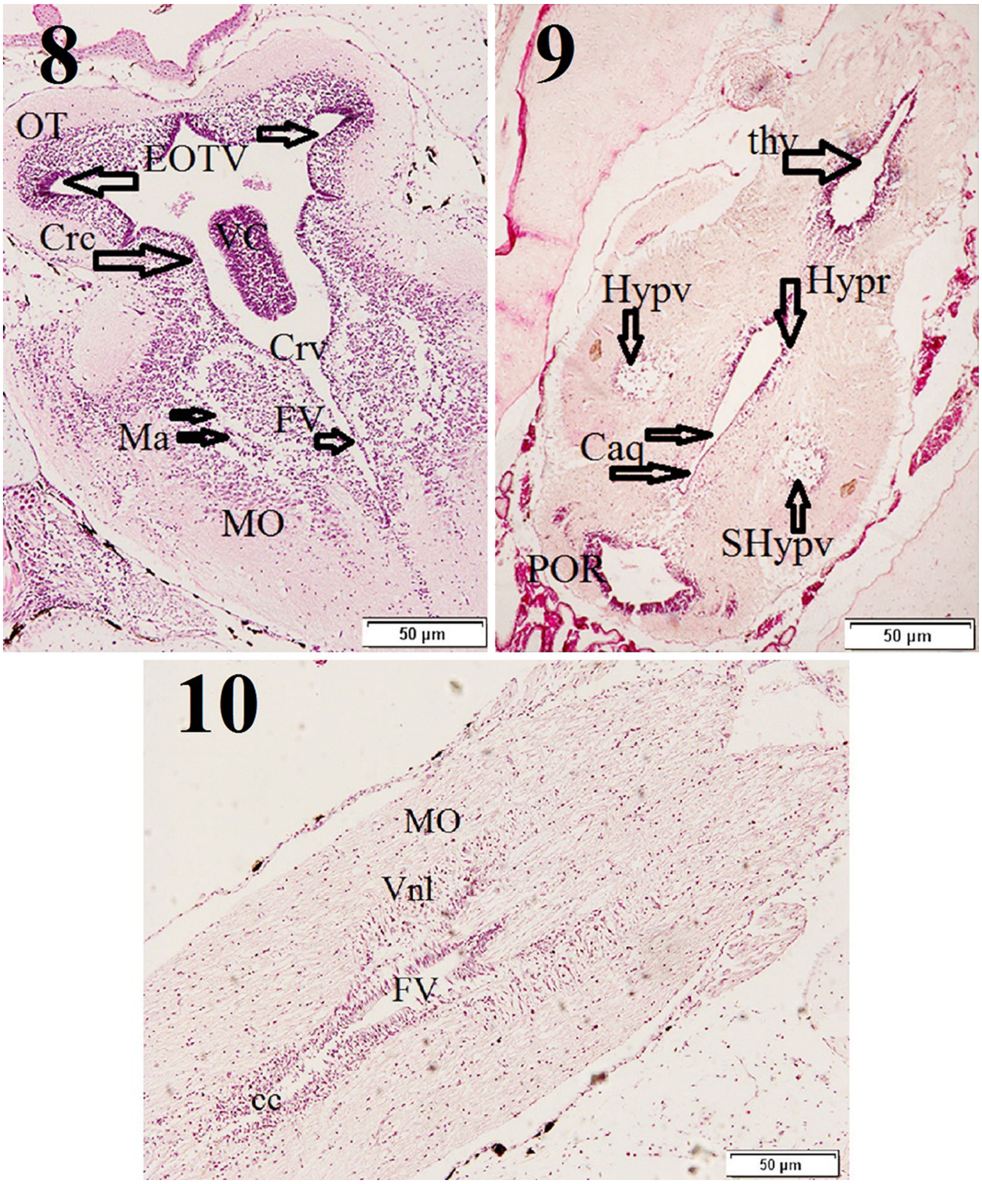
Stereological results

According to the results of the stereological studies performed in this work, among the three divisions of the brain ventricular system defined above, the forebrain ventricular space presented the smallest volume while the hindbrain ventricular space presented the largest volume (Table 1).

Discussion

The ventricular system contains a row of spaces oriented rostrocaudally. Cerebrospinal fluid (CSF) flows inside this system and is in contact with the choroid plexus. Early during the process of development (at 1 and 3 days old), the ventricles were surrounded by a thick layer of embryonic and ependymal cells, but this layer thinned out with age and with increased differentiation of white and gray matter; thus, at 54 days old, a thin layer of ependymal cells and gray matter covered the ventricular spaces.

In fishes, the brain ventricular system consists of three main parts. In Acipenseridae (just as for other actinopterygian fishes), the telencephalon develops an eversion during embryonic growth which leads to the formation of the telencephalic ventricle (Northcutt and Braford 1980). In 1-day-old *H. huso* larvae, no extension of the telencephalic ventricle was observed, whereas it was divided into olfactory and lateral ventricle at 6 days old.



Figs. 8–10 **8** Frontal section of the brain ventricles (H&E) from 15-day-old *H. huso* larvae. *co* commissural organ, *thv* third ventricle, *h* habenula, *POR* posterior recess, *SV* saccus vasculosus, *NLT* lateral tuberal nucleus, *Sih* sulcus intrahabenularis, *Ssh* sulcus subhabenularis, *Phr* posthabenular recess, *pvopa* anterior part of the paraventricular organ, *Tpp* periventricular nucleus of the posterior tuberculum, *NRP* nucleus of posterior recess. **9** Frontal section of the brain ventricles (H&E) from 6-day-old *H. huso* larvae. *OTV* tectal ventricle, *OT* optic tectum, *EOTV* extension of tectal ventricle, *h* habenula, *SV* saccus vasculosus. **10** Frontal section of the brain ventricles (H&E) from 54-day-old *H. huso* larvae. *cc* central canal, *Vnl* vagal viscerosensory lobe, *MO* medulla oblangata, *FV* fourth ventricle

The olfactory ventricle was clearly a bilateral extension of the rostral part of the telencephalic ventricle which developed with age. In *A. naccarii*, as in other sturgeons, this part is very large and wide, and has a wide internal ventricle recess (Johnston 1898 and 1901). The olfactory ventricle continued caudally between the telencephalic hemispheres until it became the lateral ventricle, so the olfactory ventricle and lateral ventricle together formed a T-shaped "telencephalic ventricle." This is due to an eversion in the dorsal wall of the embryonic neural tube in actinopterygians (Nieuwenhuys 1998).

The sulcus limitans telencephali was observed as a shallow depression in the caudomedial part of the lateral ventricle from 15 days old. In all sturgeons, this structure extends from the anterior commissure to the caudal part of the pallium and the level of the preoptic region, and is surrounded by subependymal arteries. This structure connects the pallium and preoptic region (Johnston 1901).

Table 1 Volumes of the three divisions of the brain ventricular system of larval *H. huso*, as estimated via Cavalieri's principle (values shown are in mm^3)

Age of larva (days)	Total volume of ventricles	Ventricular volume of forebrain	Ventricular volume of midbrain	Ventricular volume of hindbrain
1	17.72	5.22	6.06	6.44
3	19.68	6.32	6.58	6.78
6	24.02	7.44	8.26	8.32
15	26.82	8.46	9.22	9.24
21	29.15	9.28	9.93	9.94
54	34.62	10.36	11.96	12.3

At 15 days old, the sulcus preopticus became visible in the caudal part of the preoptic recess. This sulcus is not found in all species of sturgeon and is rarely deep, but its function is not yet clear (Herrick 1910 and 1921).

The caudal part of the telencephalic ventricle was connected with the third ventricle in the diencephalon via the interventricular foramen. In the habenula of the diencephalon of 15-day-old larvae, two sulci were noted. The sulcus interhabenularis is small in all fishes and is inside the habenula ganglion. It is always observed in the lateral part of the habenula and controls the flow of CSF in the habenula–ventricle system. The sulcus subhabenularis is visible on both sides in most sturgeons. It is adjacent to the subcommissural organ and forms the posthabenular recess. It influences the flow of CSF inside the third ventricle (Herrick 1921).

At 6 days old, the third ventricle adjacent to the hypothalamus had a lateral recess on both sides that was surrounded by the sulcus hypothalamicus and formed the hypothalamic ventricle. This ventricular recess and sulcus are visible in all species of ray-finned fishes (Nieuwenhuys 1998). The anterior tubular nucleus (NAT) was found caudally at the junction with the lateral recess. The NAT regulates the secretion of CSF into the recess. The sulcus hypothalamicus in its caudal part is the deepest part and in its rostral part from the view of number sulcus hypothalamicus has variable between fish species (Nieuwenhuys 1964 and 1998).

The floor of the third ventricle in sturgeons is coated with special ependymal cells named crown cells; these may help to produce CSF for the third ventricle (Kotrschal et al. 1983). In some pelagic fishes, on the dorsal surface, the choroid plexus of the third ventricle presents several extensions such as the saccus dorsalis. These sacci, which are associated with light-sensitive pineal gland and other circumventricular organs (Leonhardt 1980), were not observed in the *H. huso* larvae studied in the present work.

The third ventricle was observed to be connected to the tectal ventricle between the lobes of the optic tectum in 1-day-old larvae. By 21 days old, the lateralis valvula cerebelli had become visible in the middle of the tectal ventricle. In sturgeons, the floor of this ventricle is covered with crown cells. The posterior recess in the caudal part of the tectal ventricle was visible at 15 days old. The various nuclei around this recess probably influence the production of CSF. The posterior recess was surrounded by the saccus vasculitis, a circumventricular organ of unknown function (although it most probably influences the production of CSF for the third and tectal ventricles, aided by adjacent nuclei and the thalamus; Kotrschal et al. 1983).

Next, the tectal ventricle was connected to the cerebellar ventricle through the cerebral aqueduct. This ventricle is located within the cerebellum and is quite a large ventricle. In all fishes, the roof of the cerebellar ventricle consists of the choroid plexus, with varying degrees of differentiation (Weiger et al. 1988). In some fish, such as the Cyprinidae, there are columnar sensory cells in the dorsal wall of the cerebellar ventricle, which are related to the senses of hearing, taste, and the lateral line (Kanwal and Finger 1992).

In the medio-internal part of the cerebellar ventricle, the sulcus limitans of HIS was seen from 6 days old. This sulcus is observed adjacent to the cerebellar ventricle in other sturgeons from 10 days old. It relates to one of the somatosensory, viscerosensory and visceromotor or somatomotor centers (Larsell 1967). At 21 days old, Mauthner cells (Ma) were seen bilaterally below the cerebellar ventricle. These cells are linked to octaval nerve action in sturgeons. They are not completely myelinized before 21 days old and are therefore not clearly visible before then (Hernando et al. 2005). The cerebellar ventricle was connected to the fourth ventricle in the medulla oblongata. In all fishes, the roof of this ventricle is covered with the choroid plexus (Butler and Hodos 2005). Facial and vagal lobes are observed around the fourth ventricle in fish species; these are viscerosensory lobes (Butler and Hodos 2005).

Cavalieri's principle has been used to estimate the volumes of various structures in animals, such as kidney, esophagus, and testis (Howard and Reed 1998). According to our stereological study of the brain ventricular spaces in *H. huso* larvae utilizing Cavalieri's principle, the ventricular spaces in the hindbrain were larger in volume than those in either the midbrain or forebrain, which correlates well with the importance of the hindbrain in this fish.

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Compliance with ethical standards

Conflict of interest None.

References

Bemis WE, Findeis EK, Grande L (1997) An overview of Acipenseriformes. Environ Biol Fish 48:25–71

Bergquist H (1932) Zur Morphologic des Zwischenhirns bei niederen Wirbeltieren. Acta Zool 13:57–304

Birstein VJ, Doukakis P, Sorkin B, Desalle R (1998) Population aggregation analysis of three caviar-producing species of sturgeons and implications for the species identification of black caviar. Conserv Biol 12:766–775

Broglio C, Rodriquez R, Salas C (2003) Spatial cognition and its neural basis in teleost fishes. Fish Fish 4:255–274

Butler AB, Hodos W (2005) Comparative vertebrate neuroanatomy: evolution and adaptation, 2nd edn. Wiley, Hoboken

Ekstrom P, Johnsson CM, Ohlin LM (2001) Ventricular proliferation zones in the brain of an adult teleost fish and their relation to neuromeres and migration (secondary matrix) zones. J Comp Neurol 436:92–110

Gundersen HJG, Jensen EB (1987) The efficiency of systematic sampling in stereology and its prediction. J Microsc 147:229–263

Hernando JA, Domezain A, Zabala C, Domezain J, Cabrera R, Soriguer MC (2005) Desarrollo de las aletas pectorales durante la morfogenesis de *Acipenser naccarii*, Bonaparte 1836. Abstr IX Congreso Nacional de Acuiculture, Cadiz, Spain, 12–16 May 2003, pp 81–85

Herrick CJ (1910) The morphology of the forebrain in Amphibia and Reptilia. J Comp Neurol 20:413–547

Herrick CJ (1921) A sketch of origin of the cerebral hemispheres. J Comp Neurol 32:429–454

Howard CV, Reed MG (1998) Unbiased stereology. Three-dimensional measurement in microscopy. BIOS, Oxford, pp 55–68

Johnston JB (1898) The olfactory lobes, forebrain, and habenular tracts of *Acipenser*. Zool Bull 1:221–241

Johnston JB (1901) The brain of *Acipenser*. A contribution to the morphology of the vertebrate brain. Zool Jahrb 15:59–260

Kanwal JS, Finger TE (1992) Central representation and projections of gustatory systems. In: Hara TJ (ed) Chemoreception in fishes. Elsevier, New York, pp 79–102

Kimley AP, Beavers SC, Curtis TH, Jorgensen SJ (2002) Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. Environ Biol Fish 63:117–135

Kotrschal K, Krautgartner WD, Adam H (1983) Crown cells in the diencephalon of *Acipenser ruthenus* (Acipenseridae, Chondrostei). J Hirnforsch 24:109–120

Larsell O (1967) The comparative anatomy and histology of the cerebellum from myixinoids through birds. University of Minnesota, Minneapolis

Leonhardt H (1980) Ependym and circumventricular organ. In: Oksche A, Vollrath L (eds) Neuroglia I. Handbuch der mikroskopischen anatomie des menschen, Bd. Iv: nerve system 10. Springer, Berlin, pp 176–666

Nieuwenhuys R (1962) Trends in the evolution of the actinopterygian forebrain. J Morphol 111:69–88

Nieuwenhuys R (1963) The comparative anatomy of the actinopterygian forebrain. J Hirnforsch 6:171–192

Nieuwenhuys R (1964) Further studies on the general structure of the actinopterygian forebrain. Acta Morphol Neerl Scand 6:65–79

Nieuwenhuys R (1998) Chondrostean fishes. In: Nieuwnhuys R, Ten Donkelaar HJ, Nicholson C (eds) The central nervous system of vertebrates. Springer, Berlin, pp 701–757

Northcutt RG (1978) Brain organization in the cartilaginous fishes. In: Hodgson ES, Mathewson RF (eds) Sensory biology of sharks, skates and rays. Office of Naval Research, Arlington, pp 117–193

Northcutt RG (1996) The Agnathan ark: the origin of craniate brains. Brain Behav. Evolut 48:237–247

Northcutt RG, Braford MR (1980) New observations on the organization and evolution of the telencephalon of actinopterygian fishes. In: Ebbeson SOE (ed) Comparative neurology of the telencephalon. Plenum, New York, pp 41–98

Vazquez M, Rodriguez F, Domezain A, Salas C (2002) Development of the brain of the sturgeon *Acipenser naccarii*. J Appl Ichthyol 18:275–279

Von Kupffer K (1906) Die Morphogenie der Central nerven-systems. In: Hertwig O (ed) Handbuch der vergleichenden un experimentelien Entwicklungsgeschichte der Wirbeltiere, vol 2, part 3. Gustav Fischer Verlag, Jena, pp 1–272

Weiger T, Lametschwandtner A, Kotrschal K, Krautgartner WD (1988) Vascularization of the telencephalic choroid plexus of a ganoid fish [*Acipenser ruthenus* (L.)]. Am J Anat 182:33–41