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# Chemical Neuroanatomy of the Hypothalamo-Hypophyseal System in Sturgeons

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#### Abstract

The preoptic-hypothalamo-hypophyseal system of sturgeons, located at the base of the brain, has a neurosecretory role exerted by hypophysiotropic neurons most of them located in the preoptic and hypothalamic periventricular region. The majority of those cells are of the cerebrospinal fluid-contacting type and exhibit short processes reaching the ventricular lumen. Moreover, the processes of those hypophysiotropic neurons course along the hypothalamic floor toward the hypophysis forming a preoptic-hypothalamo-hypophyseal tract. This chapter summarizes available data on the distribution of several hypophysiotropic factors, such as galanin, neurophysin, somatostatin, or gonadotropin-releasing hormone, in the preoptic-hypothalamo-hypophyseal system of sturgeons obtained by the use of immunohistochemical techniques. Immunoreactive neurons to those substances were found in the preoptic and hypothalamic nuclei, and immunoreactive fibers were observed along the preoptic-hypothalamo-hypophyseal tract and in the hypophysis, indicating their hypophysiotrophic role in the brain of sturgeons. Thus, most of the neuropeptides and neurohormones found in tetrapods are also present in sturgeons, suggesting that their common ancestors already possessed such regulatory systems. Unfortunately, because of the difficulty in approaching the physiology of sturgeons (size, cost, etc.), the number of experimental studies aiming at deciphering the roles of such neuropeptides and

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neurohormones is very limited, although we can speculate that part of the functions supported by these neurohormones would be similar.

**Keywords** 

Sturgeon • Hypothalamus • Hypophysis • Galanin • Somatostatin • GnRH

## 13.1 The Anatomy of the Preoptic Area and Hypothalamus of Sturgeons

Studies concerning the cytoarchitecture of the diencephalon of chondrosteans, and in particular of sturgeons, are scarce, and current knowledge concerning the organization of this encephalic region is based on anatomical studies carried out at the beginning of the nineteenth century by Johnston (1901) although it has been more recently analyzed in detail by Nieuwenhuys (1998), Rupp and Northcutt (1998), and Rustamov (2006a, b).

The diencephalon is a complex brain region bounded rostrally by the telencephalon and caudally by the mesencephalon, although there is a long-lasting controversy about where exactly are those boundaries. Briefly, there are two different models of forebrain organization based on developmental studies: the *His-Herrick model* which proposed that the origin of all brain regions is in a series of longitudinal

Fig. 13.1 Micrographs of hematoxylin-eosin-stained sagittal (a) and transverse (b-j) sections through the brain of the Siberian sturgeon Acipenser baerii. (a) Sagittal section through the entire brain of *Acipenser*. Lines with the letters at the top indicate the levels of the figures  $(\mathbf{b}-\mathbf{j})$ . (b) Section through the rostral preoptic area showing the small cells of the parvocellular preoptic nucleus (NPOp) arranged in a few rows parallel to the ventricular surface around the preoptic recess (PR). (c) Detail of figure (a) showing the NPOp. (d) Section through the caudal preoptic area showing the small cells of the NPOp and the large cells of the magnocellular preoptic nucleus (NPOm) which occupy a central position in the preoptic region dorsal to the rostral portion of the optic chiasm (OC). Abundant cells are located along the ventral part of the anterior wall of the preoptic recess, in the organum vasculosum of the terminal lamina (OVLT). (e) Detail of figure (d) showing the abundant cells in the NPOp and in the OVLT. (f) Section through the preoptic area at a more caudal level than figure (d) showing the NPOp and the NPOm (arrowheads). (g) Section through the rostral hypothalamus showing the inferior hypothalamic lobes (HL), which surround the hypothalamic lateral recesses (LR). Along the ventromedial walls of the lateral recesses, the third ventricle gives rise to the infundibulum (i) in which more rostral walls the anterior tuberal nucleus (NAT) is located. (h) Detail of the figure (g) showing the major part of hypothalamic neurons located in the ventricular surface around the infundibulum and the lateral recesses. (i) Section through the hypothalamus showing the position of the cells of the lateral tuberal nucleus (NLT) at rostral levels. (i) Section through the caudal hypothalamus showing the NLT surrounding the posterior recess (POR), the median eminence (ME), the hypophysis (H), and the saccus vasculosus (SV). Inset: coronet cells in the floor of the hypothalamus. Abbreviations: CB, corpus cerebelli; h, habenula; H, hypophysis; HL, hypothalamic lobes; *i*, infundibulum; *LR*, lateral hypothalamic recess; *ME*, median eminence; *MO*, medulla oblongata; NAT, anterior tuberal nucleus; NLT, lateral tuberal nucleus; NPOm, magnocellular preoptic nucleus; NPOp, parvocellular preoptic nucleus; OB, olfactory bulb; OC, optic chiasm; OT, optic tectum; OVLT, organum vasculosum of the terminal lamina; POR, posterior recess; PR, preoptic recess; PT, posterior tubercle; SV, saccus vasculosus; T, telencephalon; vc, valvula cerebelli. Scale bars:  $2 \text{ mm}(\mathbf{a})$ ;  $1 \text{ mm}(\mathbf{g})$ ;  $500 \mu \text{m}(\mathbf{b}, \mathbf{d}, \mathbf{h})$ ;  $200 \mu \text{m}(\mathbf{c}, \mathbf{e}, \mathbf{i}-\mathbf{j})$ ;  $100 \mu \text{m}(\mathbf{f})$ ;  $50 \mu \text{m}(\text{inset in j})$ 



columns separated by longitudinal sulci and divides the diencephalon into four longitudinally arranged zones, epithalamus, dorsal thalamus, ventral thalamus, and hypothalamus (Herrick 1910, 1933), and the neuromeric model which suggests that the origin of all brain regions is in a series of transverse regions (neuromeres) separated by vertical sulci and that the diencephalon arises from a rostral parencephalic neuromere but does not include the preoptic area and the hypothalamus which together with the telencephalon are considered part of the secondary prosencephalon (Puelles and Rubenstein 1993). Thus, as in chondrosteans there are no data on neither embryological nor gene expression which could delimitate diencephalic boundaries; most authors have organized the diencephalon of sturgeons as suggested by Braford and Northcutt (1983) for the diencephalon of ray-finned fishes. Braford and Northcutt (1983) follow the His-Herrick model and thus subdivide the diencephalon into the epithalamus, thalamus, and hypothalamus and include the entire preoptic region in the diencephalon. However, Nieuwenhuys (1998), although basically following His-Herrick model for the rest of the diencephalic regions, assigns the preoptic region to the telencephalon, following classic anatomical studies by Johnston (1901). In this review we will follow the organization suggested by Braford and Northcutt (1983) for the diencephalon of ray-finned fishes, i.e., we will include the entire preoptic region in the diencephalon.

#### 13.1.1 Preoptic Area

The preoptic area is the most rostral part of the diencephalon. It surrounds the preoptic recess of the third ventricle and lies between the anterior commissure rostrally and the optic chiasm caudally (Fig. 13.1a). This area is characterized by the periventricular position of most of its cells, containing three periventricular nuclei located around the preoptic recess: the parvocellular preoptic nucleus, the most rostral diencephalic nucleus with small cells arranged in a few rows parallel to the ventricular surface (Fig. 13.1b-f); the magnocellular preoptic nucleus, with large neurosecretory cells occupying a central position in the preoptic region dorsal to the rostral portion of the optic chiasm (Fig. 13.1f); and the suprachiasmatic nucleus, with small densely arranged cells situated dorsal to the optic chiasm. Moreover, there is a migrated nucleus, the entopeduncular nucleus, with small loosely arranged cells. In the parvocellular preoptic nucleus, Rupp and Northcutt (1998) distinguished an anterior and a posterior part. Along the ventral part of the anterior wall of the preoptic recess is located the organum vasculosum of the lamina terminalis (OVLT, Fig. 13.1d, e), one of the circumventricular organs present in all vertebrate groups.

#### 13.1.2 Hypothalamus

During brain ontogenesis, the hypothalamus differentiates relatively late in sturgeons showing the normal histological pattern of the adult at 90 days post-hatching



**Fig. 13.2** (a) Detail of Fig. 13.1a showing a hematoxylin-eosin-stained sagittal section through the hypothalamus of the Siberian sturgeon *Acipenser baerii*. (b) Topography of the hypothalamo-hypophyseal neurosecretory system in Acipenseridae. Figure (b) was modified from Polenov and Garlov (1971). Abbreviations: *i*, infundibulum; *Nh*, neurohypophysis; *OC*, optic chiasm; *PA*, preoptic area; *Pd*, pars distalis of the hypophysis; *Pi*, pars intermedia of the hypophysis; *PNCR*, proximal neurosecretory contact region; *POR*, posterior recess; *PR*, preoptic recess; *PT*, posterior tubercle; *SV*, saccus vasculosus. Scale bar: 500  $\mu$ m

and reaching a considerable size compared to other parts of the brain (Vázquez et al. 2002; Gómez et al. 2009). Due to its extremely enlarged ventricle, the hypothalamus forms the largest and the most ventral diencephalic structure in sturgeons (Figs. 13.1a and 13.2), and it comprises a large paired rostral region which is bordered dorsally by the preoptic area and by the posterior tubercle and a much smaller unpaired caudal portion which is continuous with the pituitary and the saccus vasculosus (Figs. 13.1a, g–j and 13.2). The major part of hypothalamic neurons of the sturgeons is located adjacent to the ventricular surface, with only a few migrated cells situated more laterally (Figs. 13.1g–j and 13.2a). Most of the neurons located in the periventricular zone are of the cerebrospinal fluid-contacting (CSF-C) type. Such neurons exhibit an apical dendrite that ends by a ventricular bulb (Fig. 13.1c, e–f). These CSF-C cells are really abundant in the hypothalamus of the sturgeons, but they represent a "primitive" character that tends to disappear in the course of evolution. Bony fish exhibit much less CSF-contacting cells.

In the rostral hypothalamus, the walls are rather thin and laterally evaginate to form the inferior or lateral hypothalamic lobes, which surround the hypothalamic lateral recesses, a pair of diverticula in the midrostral portion of the third ventricle (Fig. 13.1g-h). In sturgeons, these inferior hypothalamic lobes are much larger than in other chondrosteans and in other fish groups (Fig. 13.1g-h) (Nieuwenhuys 1998; Rupp and Northcutt 1998). Different nomenclatures for the diverse hypothalamic regions of sturgeons have been used in cytoarchitectonic studies. Thus, Nieuwenhuys (1998) divided the rostral hypothalamus of the shovelnose sturgeon (*Scaphirhynchus*) into two longitudinal periventricular regions: a hypothalamic dorsal part, extending along the dorsal and lateral walls of the lateral recesses, which corresponds to the dorsal and lateral parts of the periventricular hypothalamus of Acipenser (Fig. 13.1a, g-h, Rupp and Northcutt 1998), and an hypothalamic ventral part, extending along the ventromedial walls of the lateral recesses where the third ventricle gives rise to the infundibulum (Fig. 13.1a, g-i) in which more rostral walls the anterior tuberal nucleus is located (Fig. 13.1g-h). This ventral part of Scaphirhynchus corresponds to the ventral part of the periventricular hypothalamus in Acipenser (Rupp and Northcutt 1998).

The caudal portion of the hypothalamus is unpaired and surrounds the hypothalamic posterior recess, located in the caudal portion of the third ventricle, which displays small, laterally directed diverticula (Figs. 13.1a, j and 13.2). The caudoventral region of the posterior recess suffers narrowness in the most ventral region which leads to a cavity lined by a thin and strongly folded epithelium, named saccus vasculosus (SV). This structure whose function remains unclear is present in many jawed fish, including chondrosteans (Figs. 13.1a, j and 13.2). The epithelium forming the wall of this organ contains CSF-C cells, supporting cells, and numerous coronet cells, a highly specialized cell type exclusive to the saccus vasculosus of jawed fishes and which is probably glial in nature (Fig. 13.1j) (Arochena et al. 2004; Sueiro et al. 2007). Coronet cells are characterized by a round or pear-shaped perikarya with a short, thick apical process that protruded into the ventricle bearing a crown of globule-tipped cilia (inset in Fig. 13.1j). Unlike other fishes, coronet cells of sturgeons are not confined to the saccus vasculosus, and they are distributed over the entire floor of the hypothalamus and also on the preoptic recess (Kotrschal et al. 1983). The function of this organ remained intriguing for a long time, and it has been suggested to be involved in sensory and transport functions as well as secretory functions (e.g., liquor pressure perception, osmoregulation, calcium homeostasis, glucose loading, and transcellular ion exchange between blood vessels and CSF). However, recently, it has been suggested that the SV is implicated in the regulation of photoperiodism in fish (Nakane et al. 2013). However, we cannot exclude the possibility that the SV serves other physiological functions such as neuroendocrine, as suggested by the localization of thyroid-stimulating hormone in the coronet cells (Nakane et al. 2013) or the expression of brain aromatase shown in trout (Menuet et al. 2003). Additionally, the SV and the hypothalamus are connected to each other by afferent and efferent fiber systems (Yáñez et al. 1997; Sueiro et al. 2007).

In the dorsolateral and ventral periventricular walls of the posterior recess of *Scaphirhynchus* lies the *lateral tuberal nucleus* (Nieuwenhuys 1998), which corresponds to the caudal zone of the periventricular hypothalamus of *Acipenser* (Fig. 13.1i–j, Rupp and Northcutt 1998). Caudally, the dorsal area progressively forms the *posterior tuberal nucleus* in both sturgeon species (Nieuwenhuys 1998; Rupp and Northcutt 1998).

The hypothalamic organization described for sturgeons, characterized by laterally expanded inferior lobes and thin hypothalamic walls, also exists in chondrichthyans (Smeets et al. 1983), but not in other ray-finned fishes, so the lateral expansions in sharks and sturgeons must be viewed as independently evolved parallel features rather than as homologous structures as it was suggested by Northcutt (1995). However, in the sturgeons, as in all ray-finned fishes, the most conserved feature of the hypothalamus is the periventricular cellular zone which exhibits basically the same type of organization in other fish groups (Rustamov 2006b).

## 13.1.3 Hypothalamo-Hypophyseal Relationships

In sturgeons, as in all vertebrates, the hypophysis or pituitary gland is attached to the caudoventral region of the hypothalamus (Figs. 13.1a, g–j and 13.2). The hypophysis of sturgeons, flat and elongated in the rostral-caudal direction, is composed of the adenohypophysis located rostrally and the neurohypophysis located caudally close to the transition of the infundibulum to the saccus vasculosus. The adenohypophysis is the glandular part and is mainly composed of secretory cells, while the neurohypophysis represents the neural part of the gland and consists of neurosecretory terminals originating from the hypothalamus and other brain regions (Fig. 13.2) (Grandi and Chicca 2004). During brain ontogenesis, although the hypothalamus differentiates relatively late, the adenohypophysis is already evident on the floor of the diencephalon at hatching time but reaches the adult morphology at 5 months of age, while the neurohypophysis does not begin its development until 80 days posthatching and does not reach the adult morphology before 9 months of age (Grandi and Chicca 2004; Gómez et al. 2009).

A comprehensive description of the hypothalamo-hypophyseal system was reported in the classical studies of Russian researchers (Sathyanesan and Chavin 1967; Polenov and Garlov 1971, 1973; Polenov et al. 1972, 1976, 1983, 1997; Polenov and Pavlovic 1978; Belenky et al. 1985). The adenohypophysis in sturgeons consists in a pars distalis and a pars intermedia, while the neurohypophysis is included in a neurointermediate lobe consisting in tubular rootlike processes of the bottom of the infundibular wall that penetrate among the cell cords of the pars intermedia (Fig. 13.2b). The distribution of the pituitary endocrine cells was studied by immunocytochemical techniques in the adenohypophysis of different sturgeon species, and seven types of endocrine cells were identified: the adrenocorticotropic, prolactin, growth hormone, gonadotropic and thyroid-stimulating hormone cells in the pars distalis, and the melanocyte-stimulating hormone and somatolactin cells in

the pars intermedia (Hansen 1971; Hansen and Hansen 1975; Pelissero et al. 1988; Joss et al. 1990; Amemiya et al. 1999).

Moreover, in chondrosteans, the hypothalamic floor, located rostroventrally just dorsal to the pars distalis of the adenohypophysis, differentiates into a typical median eminence named *proximal neurosecretory contact region* (Fig. 13.2) (Polenov et al. 1976; Kotrschal et al. 1985). In the space between this region and the pars distalis, there are blood vessels that form part of a hypothalamo-hypophyseal portal system where numerous unmyelinated neurosecretory fibers form synaptic endings and, as in other vertebrates, discharge their products into the portal circulation. There are two types of those fibers that are also found among the processes of the neurohypophysis: Type A, peptidergic and originate in the preoptic area (magnocellular preoptic nucleus) and Type B, monoaminergic and presumably originate in the hypothalamus (lateral tuberal nucleus, Polenov et al. 1972). Thus, both the peptide and monoamine neurohormones along the way hypothalamic neurons regulate the activity of the glandular cells in the pars distalis (Polenov et al. 1976).

## 13.2 Hypophysiotropic Factors in the Preoptic-Hypothalamo-Hypophyseal System of Sturgeons

The presence of numerous cells and fibers containing different hypophysiotrophic factors, such as corticoliberin (Belenky et al. 1985), corticotropin-releasing factor (CRF, González et al. 1992), gonadotropin-releasing hormone (GnRH, Leprêtre et al. 1993; Amiya et al. 2011), neuropeptide Y (NPY, Chiba and Honma 1994; Amiya et al. 2011), methionine-enkephalin (Met-enk, Rodríguez-Moldes et al. 1997), melanin-concentrating hormone (MCH, Baker and Bird 2002), serotonin (5-HT, Adrio et al. 1999; Piñuela and Northcutt 2007), tyrosine hydroxylase (TH, Adrio et al. 2002), neurophysin (NPH, Adrio et al. 2005), galanin (GAL, Adrio et al. 2005; Amiya et al. 2011), substance P, dopamine and leucine-enkephalin (SP, DA, Leu-enk, Piñuela and Northcutt 2007), and somatostatin (SOM, Adrio et al. 2008), has been observed in the preoptic region and the rostral and caudal hypothalamus of the sturgeons by the use of immunohistochemical techniques. All these neuromodulators showed high concentrations and had a similar distribution in the hypothalamus of all the sturgeon species studied. Although some neurons immunoreactive to those factors were observed in nuclei located away from the ventricle, most of them were located in the periventricular region, and they were of the CSF-C type. These CSF-C cells containing those factors were observed both in the preoptic area and in the hypothalamus of all the sturgeon species studied, and they were very abundant in the parvocellular preoptic nucleus; in the dorsal, lateral, and ventrolateral walls of the lateral recesses (lateral and dorsal periventricular hypothalamus of Rupp and Northcutt 1998); and in the tuberal and caudal hypothalamus where they were located in the ventromedial walls of the infundibulum, corresponding to the position of the anterior and lateral tuberal nuclei (ventral periventricular hypothalamus of Rupp and Northcutt 1998). CSF-C cells are considered

phylogenetically ancient in type and may play an important role in the neurotransmission and/or neuromodulation of neuroendocrine pathways in fish (Vigh-Teichmann et al. 1983). In fact, these hypothalamic CSF-C cells showed an intense staining to the different hypophysiotrophic factors studied in both the subventricular perikarya and ventricular processes.

Furthermore, the basal processes of these CSF-C neurosecretory cells coursed ventrolaterally toward the external surface and along the hypothalamic floor toward the hypophysis forming a preoptic-hypothalamo-hypophyseal tract, where fibers immunoreactive to neuropeptides (corticoliberin (Belenky et al. 1985), CRF (González et al. 1992), GnRH (Leprêtre et al. 1993), NPY (Chiba and Honma 1994), Met-enk (Rodríguez-Moldes et al. 1997), MCH (Baker and Bird 2002), GAL and NPH (Adrio et al. 2005), SOM (Adrio et al. 2008), and Leu-enk (Adrio, unpublished results) were observed in different sturgeon species. Some of these fibers innervate the proximal neurosecretory contact region, and others coursed more caudally in the thin floor of the hypothalamus and the hypophyseal stalk toward the neurointermediate lobe of the neurohypophysis, where they appear close to glandular cells of the pars intermedia. Although the origin of the hypothalamus-hypophyseal projections in the sturgeon has not been studied experimentally, these fibers could arise, at least in part, from neurosecretory neurons observed in the preoptic and/or the hypothalamic region, such as those of the anterior and lateral tuberal nuclei, as previously reported in the hypothalamus of teleosts (Holmqvist and Ekström 1995). In fact, the preoptic nuclei and the lateral tuberal nucleus were described in Acipenser fulvescens as neurosecretory nuclei by Sathyanesan and Chavin (1967) who used Gomori's aldehyde fuchsin method for neurosecretion (a classical marker of the hypothalamo-hypophyseal neurosecretory system), and, more recently, cells immunoreactive to neurophysin (NPH-ir) were described in the preoptic (magnocellular preoptic nucleus, Figs. 13.3b, c and 13.4k, l) and hypothalamic (anterior and lateral tuberal nuclei, Figs. 13.3d-f and 13.5e) areas in Acipenser baerii suggesting that both regions contain neurosecretory cells related with the hypothalamohypophyseal system (Adrio et al. 2005). Therefore, the presence of different hypophysiotrophic factors in those nuclei appears general to fishes (see references in Adrio et al. 2005).

In addition, the presence of cells immunoreactive to hypophysiotrophic factors such as CRF (González et al. 1992), NPY (Chiba and Honma 1994), Met-enk (Rodríguez-Moldes et al. 1997), MCH (Baker and Bird 2002), and SOM (Adrio et al. 2008), in the pars distalis of the sturgeon, suggests that these factors are released to the blood in the adenohypophysis and have peripheral functions. Alternatively, some of these factors could have local actions in the pituitary.

Therefore, the hypothalamus of the sturgeons contains neurosecretory cells related to the hypophysis and most likely acting as hypophysiotropic factors modulating the release of adenohypophyseal hormones. However, the hypophysis-related CSF-C neuronal groups of the sturgeon hypothalamus are heterogeneous in terms of their neurochemical content, and, therefore, different types of CSF-C cells could play different roles in neurosecretion and neurotransmission (Adrio et al. 2005).

## 13.2.1 Galaninergic System

Galanin is a 29-amino acid peptide widely distributed in the central nervous system of vertebrates, and the hypothalamus is particularly rich in galanin-synthesizing neurons and nerve processes. Depending on the destination of galanin in nerve terminals, this neuropeptide may function as a neuromodulator/neurotransmitter when it innervates other neurons or as a hypophysiotropic messenger when it is released into the hypothalamo-hypophyseal portal circulation and reaches the anterior pituitary (Merchenthaler et al. 2013). The presence of galaninergic structures in the preoptic-hypothalamic regions seems to be highly conserved among vertebrates. Thus, the location of most of the galanin-immunoreactive (GAL-ir) cell bodies in the preoptic-hypothalamic area and the high galaninergic innervation observed in the hypophysis of all of the vertebrates studied so far (fish, amphibians, reptiles, birds, and mammals; see Adrio et al. (2005) and Mensah et al. (2010) for a review), and the observation that galanin may directly influence hormone release from the pituitary gland (Murakami et al. 1987; Maiter et al. 1990; López et al. 1991; Rao et al. 1996), has led to consider it as a hypophysiotropic peptide in both mammal and nonmammalian vertebrates, including humans (see Mechenthaler (2008), Merchenthaler et al. (2013) and Mensah et al. (2010) for a review). Moreover, galanin expression appears to be modulated by gonadal steroids both in mammals (Park et al. 1997; Rugarn et al. 1999; Shen et al. 1999; Scheffen et al. 2003; Splett et al. 2003) and in teleosts (Olivereau and Olivereau 1991b), which suggests that

Fig. 13.3 Schematic drawings of transverse sections (a-h) through the preoptic region and hypothalamus of Acipenser baerii (from rostral to caudal) showing the distribution of neurons (solid circles) and fibers (dotted areas) immunoreactive to galanin (GAL), serotonin (5-HT), tyrosine hydroxylase (TH), or somatostatin (SOM). On the left, neurons (solid circles) and fibers (dotted areas) immunoreactive to neurophysin (NPH) are shown, and the main anatomical regions are also indicated. The levels of the sections are indicated in a lateral view of the brain on the top. Correspondence with photomicrographs in other figures is indicated by boxed areas. Schematic drawings were modified from Adrio et al. (1999, 2002, 2005, 2008). Abbreviations: CB, corpus cerebelli; CP, choroid plexus; Dd, dorsal part of the dorsal telencephalon; Dl, lateral part of the dorsal telencephalon; FR, fasciculus retroflexus; h, habenula; H, hypophysis; HL, hypothalamic lobes; i, infundibulum; III, third ventricle; IIIn, oculomotor nucleus; IV, fourth ventricle; IVn, trochlear nucleus; LR, lateral hypothalamic recess; ME, median eminence; MLF, medial longitudinal fascicle; MO, medulla oblongata; MPT, medial nucleus of the posterior tubercle; NAT, anterior tuberal nucleus; NIL, neurointermediate lobe of the hypophysis; NLT, lateral tuberal nucleus; NPOm, magnocellular preoptic nucleus; NPOp, parvocellular preoptic nucleus; NPT, posterior tuberal nucleus; NRP, posterior recess nucleus; OB, olfactory bulb; OC, optic chiasm; OT, optic tectum; OVLT, organum vasculosum of the terminal lamina; P, pineal organ; PC, posterior commissure; Pd, pars distalis of the hypophysis; Pi, pars intermedia of the hypophysis; POR, posterior recess; PR, preoptic recess; Pt, pretectum; PT, posterior tubercle; SV, saccus vasculosus; T, telencephalon; Td, dorsal thalamus; TG, mesencephalic tegmentum; tl, torus longitudinalis; TPp, periventricular nucleus of the posterior tubercle; vc, valvula cerebelli; VM, ventromedial thalamic nucleus. Scale bars = 1 mm (lateral view), 500  $\mu$ m (sections)





Fig. 13.3 (continued)



Fig. 13.3 (continued)

this peptide is involved in sexual and reproductive behavior. Therefore, fish galanin is implicated in the regulation of various physiological functions, such as feeding, growth, reproduction, or hormone release from the pituitary gland and gonads, and has an important role in the neuroendocrine integration of those functions in fishes (see Mensah et al. (2010) for a review).

Immunohistochemical studies on the presence of galanin in the brain of nonmammalian vertebrates mainly used fish as the model organism. In fact, the distribution of GAL-ir cells and fibers was studied in the central nervous system of cyclostomes, elasmobranchs, chondrosteans, and teleosts (see references in Mensah et al. 2010), and the majority of the galaninergic neurons were located in the preoptic-hypothalamic regions in all fish species studied. Thus, the highest density of GAL-ir neurons, most of them CSF-C cells, was observed in the preoptic area



**Fig. 13.4** Transverse sections through the preoptic region of *Acipenser*. (**a**–**e**) Sections at the rostral level of the preoptic region showing CSF-C cells immunoreactive to GAL (**a**–**b**), 5-HT (**c**), TH (**d**) or SOM (**e**) in the parvocellular preoptic nucleus (NPOp, note the typical apical dendrite of these CSF-C cells, *arrowheads* in **b**–**e**) and the dense GAL-ir innervation in the ventrolateral region (**a**, *asterisk*). (**f**–**l**) Sections at the caudal level of the preoptic region showing abundant CSF-C cells immunoreactive to GAL (**f**–**g**), 5-HT (**h**), TH (**i**), or SOM (**j**) in the parvocellular preoptic nucleus (NPOp) and to NPH in the rostral (**k**) and caudal (**l**) magnocellular preoptic nucleus (NPOm). In the NPOm not all NPH-ir cells were of the CSF-C type (*arrows* in **k**–**l**). Note GAL-ir fibers in the organum vasculosum of the lamina terminalis (**f**, OVLT) and the dense GAL-ir innervation in the ventrolateral region (**f**, *asterisk*). The levels of the sections correspond to those of Fig. 13.3a (**a**–**e**), 13.3b (**f**–**k**), and 13.3c ((**l**)). Abbreviations: *NPOm*, magnocellular preoptic nucleus; *NPOp*, parvocellular preoptic nucleus; *OVLT*, organum vasculosum of the terminal lamina; *PR*, preoptic recess. Scale bars = 500 µm (**f**), 250 µm (**a**), 100 µm (**b**–**c**, **g**–**i**, **k**–**l**), 50 µm (**d**–**e**, **j**)

and the hypothalamus of the sturgeon brain (Adrio et al. 2005). In the periventricular region, GAL-ir cells extended along the parvocellular preoptic nucleus bordering the preoptic recess (Figs. 13.3a, b and 13.4a, b, f, g); the lateral, ventrolateral, and dorsal walls of the lateral recesses (Fig. 13.3d-f); along the laterodorsal walls of the posterior recess (posterior recess nucleus, Fig. 13.3g); and in the ventromedial walls of the infundibulum corresponding to the position of the anterior (Figs. 13.3d, e and 13.5a, b) and lateral (Figs. 13.3f, g and 13.6a, b) tuberal nuclei (Adrio et al. 2005). The basal processes of these GAL-ir cells coursed ventrolaterally toward the external surface and along the ventral hypothalamus probably contributing to the dense plexus of GAL-ir fibers observed at the level of the median eminence (Figs. 13.3d–g, 13.5a, b and 13.6a–c) and more caudally in the neurointermediate lobe of the hypophysis (Figs. 13.3h and 13.7a, b) (Adrio et al. 2005). These GAL-ir fibers projecting from the preoptic-hypothalamic region onto the pituitary observed in the sturgeon are well characterized in fish (Cornbrooks and Parsons 1991a, b; Moons et al. 1991; Olivereau and Olivereau 1991a; Anglade et al. 1994; Power et al. 1996; Rodríguez et al. 2003; Rodríguez Díaz et al. 2011) and mammals (Ch'ng et al. 1985; Arai et al. 1990; Gai et al. 1990).

Numerous studies in mammals indicate that galanin is functionally related to other neuroactive substances, and the activity of GAL-ir neurons is regulated by afferents containing different neuropeptides, catecholamines, and indolamines and by hormones acting via their corresponding membrane or nuclear receptors (see Merchenthaler 2010 for a review).

Anatomical relations between galanin and other hypophysiotrophic factors, such as NPH, 5-HT, and catecholamines (Adrio et al. 2005) or NPY (Amiya et al. 2011), were studied in the sturgeon brain. GAL, NPH, 5-HT, and catecholamines (TH) are related in the hypophysiotrophic nuclei, such as preoptic (Figs. 13.3a, b and 13.4a–d, f–l) and tuberal nuclei (Figs. 13.3d–g, 13.5a–e and 13.6a–f) and hypophysis (Figs. 13.3g, h and 13.7a–e) (Adrio et al. 1999, 2002, 2005). These cell populations are clearly overlapped



**Fig. 13.5** Transverse sections through the rostral hypothalamus of *Acipenser*. (**a**–**b**) Sections showing GAL-ir CSF-C cells in the anterior tuberal nucleus (NAT). The basal process of these GAL-ir cells appeared to end in the median eminence (*asterisk*) close to the pars distalis of the hypophysis (Pd). (**c**) Section showing abundant 5-HT-ir fibers that innervate the NAT and scarce 5-HT-ir fibers in the median eminence (*asterisk*). (**d**) While TH-ir fibers are very abundant in the median eminence (*asterisk*), only a few innervate the NAT. (**e**) Detail of scarce NPH-ir CSF-C cells in the NAT (*arrows*) and abundant NPH-ir fibers in the median eminence (*asterisk*). (**f**) Detail of SOM-ir CSF-C cells in the NAT. Note the abundant SOM-ir fibers in the median eminence (*asterisk*) and the presence of SOM-ir cells in the Pd (*arrowheads*). The level of the sections corresponds to that of Fig. 13.3e. Abbreviations: *i*, infundibulum; *NAT*, anterior tuberal nucleus; *Pd*, pars distalis of the hypophysis. Scale bars = 200 µm (**a**), 100 µm (**b**-**f**)



Fig. 13.6 Transverse sections through the caudal hypothalamus of Acipenser. (a) Section through the tuberal region showing abundant GAL-ir CSF-C cells in the lateral tuberal nucleus (NLT) and GAL-ir fibers coursing in the hypothalamic floor toward the neurohypophysis (arrows). (b) Section through the caudal hypothalamus showing some GAL-ir CSF-C cells in the NLT (empty arrow*heads*) and GAL-ir fibers coursing in the hypothalamic floor toward the neurohypophysis (*arrows*). Note also the typical thick apical process of coronet cells, which were not GAL-ir (arrowheads). (c) Detail of GAL-ir fibers coursing in the hypothalamic floor toward the neurohypophysis. Note that coronet cells were not GAL-ir (asterisk). (d) Detail of 5-HT-ir CSF-C cells in the NLT and dense serotoninergic innervation in the median eminence (ME). (e) Detail of TH-ir CSF-C cells in the NLT. Note the very long apical dendrites exhibited by these cells (arrowheads). (f) Detail of TH-ir fibers coursing in the hypothalamic floor toward the neurohypophysis. (g) SOM-ir CSF-C cells in the NLT and SOM-ir cells in the pars distalis of the hypophysis (arrowheads). Note the dense SOM-ir fibers in lateral regions and in the ME. (h) Detail of very scarce SOM-ir fibers coursing in the hypothalamic floor toward the neurohypophysis. Coronet cells were not SOM-ir (asterisk). The level of the sections corresponds to that of Fig. 13.3g. Abbreviations: ME, median eminence; *NLT*, lateral tuberal nucleus; *POR*, posterior recess. Scale bars = 100  $\mu$ m (**a-b**, **d-f**), 50  $\mu$ m (**c**, **h**)



**Fig. 13.7** Transverse sections through the caudal region of the hypophysis of *Acipenser* showing fibers immunoreactive to GAL (**a**–**b**), 5-HT (**c**), TH (**d**), NPH (**e**), or SOM (**f**) in the neurointermediate lobe (NIL) of the neurohypophysis near the glandular cells of the pars intermedia (Pi) of the adenohypophysis. The level of the sections corresponds to that of Fig. 13.3g. Scale bars = 100  $\mu$ m (**a**, **d**, **e**), 50  $\mu$ m (**c**, **f**), 25  $\mu$ m (**b**)

in the sturgeon (Figs. 13.3, 13.4, 13.5, 13.6 and 13.7), but double immunolabeling experiments which have compared the location of GAL-ir neurons with that of these NPH-ir neurons have revealed no coexistence of GAL and NPH in preoptic and tuberal cells of Acipenser, although GAL-ir buttons are surrounding NPH-ir cells in the NPOp (see Fig. 9A–C already published in Adrio et al. 2005). However, the comparison of the location of GAL-ir neurons with that of these 5HT-ir or TH-ir neurons shows partial codistribution in some cells of the NPOp (see Figs. 9D-F and I already published in Adrio et al. 2005), but not in the hypothalamus, although in the rodent brain most of the GAL-ir neurons located in the hypothalamic arcuate nucleus also contained TH (Melander et al. 1986) or GAL-ir fibers made direct contact on TH-ir neuronal cell bodies of that nucleus (Kageyama et al. 2008; Merchenthaler et al. 2013). As far as we know, there are no studies that evidence a functional or anatomical relationship of galaninergic, serotoninergic, and catecholaminergic cells of the vertebrate preoptic/ hypothalamic region, although it has been demonstrated that galanin modulates the metabolism of serotonin and dopamine in several brain areas of mammals (Fuxe et al. 1988; Jansson et al. 1989) and catecholaminergic fibers regulate the activity of GAL-ir hypothalamic neurons in rodents and humans (Merchenthaler et al. 2013). Therefore, the relationship between galaninergic, serotoninergic, and catecholaminergic cells observed in the preoptic and tuberal areas of the sturgeon could represent a primitive condition, but more studies in different vertebrate species will be necessary to prove this.

Galanin and NPY are among the most abundant neuropeptides in the hypothalamus of vertebrates, and their role in the regulation of the secretory activity of the anterior pituitary has been well established (see Merchenthaler et al. 2010 for a review). Although in the sturgeon hypothalamus both neuropeptides have a similar distribution (Chiba and Honma 1994; Adrio et al. 2005), the study of the interaction between galanin and NPY did not show neurons containing both neuropeptides, but NPY-ir fibers in close contact with GAL-ir neurons of the anterior tuberal nucleus were observed (Amiya et al. 2011). These results suggest the existence of reciprocal connections between the NPY-ir and GAL-ir neurons in the brain of the sturgeon which may mediate effects of NPY on neuronal systems innervated by galanin and therefore may play a pivotal role in the regulation of reproduction, growth, energy, and metabolism, as it was suggested for teleosts (Volkoff et al. 2005; Amano et al. 2009) and mammals (Horvath et al. 1996; Takenoya et al. 2002; Merchenthaler et al. 2010) where numerous NPY-ir nerve terminals also surrounded the majority of the GAL-ir neurons in the hypothalamus.

Finally, a possible coexistence of GAL and other neuroactive substances in nerve terminals in the median eminence and in the neurohypophysis must also be considered taking in account that GAL-ir, NPH-ir, 5-HT-ir, TH-ir, and NPY-ir cell populations are overlapped in hypophysiotrophic nuclei of the sturgeon and which basal processes coursed ventrolaterally and along the hypothalamic floor toward the pituitary (Figs. 13.3g, h, 13.4a, f, 13.5a–e, 13.6a–e, f and 13.7a–e) (Chiba and Honma 1994; Adrio et al. 1999, 2002, 2005; Amiya et al. 2011). There are no data about this possible colocalization which will indicate an interaction of those substances in the neuroendocrine system of chondrosteans. For instance, the presence of GAL-ir and NPY-ir fibers in the sturgeon hypothalamic floor and the median eminence (Chiba and Honma 1994; Adrio et al. 2005) could indicate that both neuropeptides play roles in the neuronal circuitry regulating the secretion of hormones and have a similar effect on the hypothalamo-pituitary-gonadal axis as it was reported in mammals (see Merchenthaler et al. 2010 for a review).

### 13.2.2 Somatostatinergic System

Somatostatin (SOM) is a neuropeptide that is widely distributed in the central nervous system of vertebrates. In mammals, two major forms of SOM (SOM-14 and SOM-28) are produced by tissue-dependent processing of the same precursor protein (Bohlen et al. 1980; Patzelt et al. 1980; Schindler et al. 1996). The primary structure of SOM-14 has been strongly conserved during evolution, although different molecular forms with similar biological activity have been found (Tostivint et al. 2004). Two isoforms of SOM-14 (SS1, which is identical to mammalian S14, and SS2, which is a variant with one amino acid changed ([Pro2] S14)) have been characterized in sturgeon (Nishii et al. 1995; Kim et al. 2000; Li et al. 2009). Moreover, two SOM precursors, which are encoded by two distinct genes, have been characterized in sturgeons: PSS1, which generates SOM-14, and PSS2, which gives rise to the [Pro2] SOM-14 variant (Trabucchi et al. 2002). In situ hybridization studies have demonstrated that the two SOM precursors (PSS1 and PSS2) are differentially expressed in numerous regions of the sturgeon brain (Trabucchi et al. 2002).

Numerous immunohistochemical studies have demonstrated the wide distribution of SOM in the central nervous system of many vertebrate taxa, including fishes (see references in Adrio et al. 2008 and Coveñas et al. 2011). SOM-immunoreactive (SOM-ir) cells and fibers are widely distributed throughout the central nervous system of the Siberian sturgeon (Acipenser baerii) where most SOM-ir cells were found in the preoptic area and hypothalamus as observed in the brain of other fish and tetrapods, mainly at the level of hypothalamic regions, where the majority of these SOM-ir cells in the sturgeon were CSF-C, as previously reported in the hypothalamus of several fish and amphibians (see references in Adrio et al. 2008). Thus, in the periventricular region, SOM-ir CSF-C cells were found in the parvocellular preoptic nucleus bordering the preoptic recess (Figs. 13.3a, b and 13.4e, j), the lateral walls of the lateral recesses (Figs. 13.3d-f), along the laterodorsal walls of the posterior recess (posterior recess nucleus, Fig. 13.3g), and in the anterior and lateral tuberal nuclei (Figs. 13.3d-h, 13.5f and 13.6g) (Adrio et al. 2008). The evolutionarily conserved expression pattern of SOM suggests that, at least in the preoptic area and hypothalamus, this peptide serves a basic function that was already present in ancestral vertebrates. Moreover, the abundance of SOM-ir CSF-C cells observed in the brain of Acipenser (Figs. 13.4e, j, 13.5f and 13.6g) (Adrio et al. 2008) suggests that SOM may act as a neurotransmitter of neuroendocrine pathways, as reported in fish (Vigh-Teichmann et al. 1983), or as a regulator of neural circuits related to cerebrospinal fluid homeostasis as observed in amphibians (Mathieu et al. 2004). SOM-ir adenohypophysial cells were also observed in the pars distalis of the hypophysis of A. baerii, which suggests that SOM is released to the blood in the adenohypophysis, and has peripheral functions (Figs. 13.3e, f, 13.5f and 13.6g) (Adrio et al. 2008).

In situ hybridization studies have demonstrated that mRNAs of the two SOM precursors (PSS1 and PSS2) are differentially expressed in neurons of the brain of the white sturgeon (Trabucchi et al. 2002). Thus, both precursors are expressed in cells of some hypothalamic regions, but only PSS1 mRNA is expressed in the preoptic region (Trabucchi et al. 2002), so observations in *A. baerii* with immunohistochemical techniques indicate that the used antiserum by Adrio et al. (2008) probably only reveals the SS1 isoform in the Siberian sturgeon brain.

Abundant SOM-ir fibers, presumably arising from preoptic and tuberal cells, coursed along the hypothalamic floor toward the median eminence, where SOM-ir innervation was very dense (Figs. 13.3d–g, 13.5f and 13.6g, h), and some of them reaching the neurointermediate lobe of the neurohypophysis (Figs. 13.3h and 13.7f) (Adrio et al. 2008). The presence of SOM in the hypothalamo-hypophyseal system of *Acipenser* (Adrio et al. 2008) indicates that this peptide has a role in the regulation of secretion of pituitary hormones, as reported in other vertebrates (Eigler and Ben-Shlomo 2014) including teleosts, in which the projection of SOM-ir cells to the pituitary was related to the control of prolactin (Grau et al. 1985), growth hormone

(Marchant et al. 1989; Lin et al. 1993), or adrenocorticotropic hormone (Langhorne 1986) secretion. In fact, the distribution of SOM-ir elements observed in the hypothalamus of *A. baerii* (Adrio et al. 2008) is similar to the distribution of hypophysiotrophic neurons containing other peptides in the hypothalamus of other sturgeon species (CRF: González et al. 1992; GnRH: Leprêtre et al. 1993; NPY: Chiba and Honma 1994; MCH: Baker and Bird 2002; GAL: Adrio et al. 2005), which again suggests a hypophysiotrophic role for this peptide.

Finally, and as it was indicated previously for galanin, several neuropeptides, such as somatostatin, often exert their actions together with catecholamines and other classical neurotransmitters. In fact, the overlapping between distributions of SOM-ir cells and fibers (Figs. 13.3d–h, 13.5f, 13.6g, h and 13.7f) (Adrio et al. 2008) and catecholaminergic cells and fibers (Figs. 13.3d–h, 13.5d, 13.6e and 13.7d) (Adrio et al. 2002) in the hypothalamus and the median eminence of *Acipenser* suggests interaction between these systems which could influence each other's functions, as has been shown in mammals (Ibata et al. 1982; Sakanaka et al. 1990) and amphibians (González et al. 2003).

#### 13.2.3 Gonadotropin Releasing-Hormone System

Gonadotropin-releasing hormone (GnRH) plays a major role in growth regulation in fish and is one of the key regulators of the reproduction in all vertebrates and some invertebrates, since it acts in the brain-pituitary-gonad axis inducing synthesis and release of gonadotropins in the pituitary. Gonadotropins in turn stimulate synthesis of the steroid hormones in gonads, and some of these steroids, besides regulating steroidogenesis and gametogenesis, also exert feedback regulation upon the hypothalamus and/or pituitary gland in order to complete the reproduction cycle as it was reported in teleosts (Weltzien et al. 2004; Kim et al. 2006; Chang et al. 2009; Taranger et al. 2010; Hildahl et al. 2011).

Using a combination of HPLC and radioimmunoassay, two variants of gonadotropin-releasing hormone (GnRH) have been identified in the brain of the white sturgeon (Acipenser transmontanus) and other phylogenetically ancient bony fish (Sherwood et al. 1991). One of these forms corresponds to the mammalian decapeptide (mGnRH; pGlu-His-Trp-Ser-His-Gly-Trp-Tyr-Pro-Gly-NH2) and the other to chicken GnRH-II (cGnRH-II; pGlu-His-Trp-Ser-Tyr-Gly-Leu-Arg-Pro-Gly-NH2). The presence of these two forms was confirmed in other sturgeon species such as the Siberian (Acipenser baerii, Leprêtre et al. 1993), the Russian (Acipenser gueldenstaedtii, Lescheid et al. 1995), the Beluga (Huso huso, Gharaei et al. 2010), and the Chinese sturgeon (Acipenser sinensis, Yue et al. 2013). Only two studies examined the distribution of the GnRH neurons in the brain of sturgeons revealed by immunohistochemical techniques (Leprêtre et al. 1993; Amiya et al. 2011). Cell bodies mGnRH-immunoreactive (mGnRH-ir) were observed in the olfactory nerves and bulbs, the telencephalon, the preoptic region, and the mediobasal hypothalamus (Fig. 13.8) (Leprêtre et al. 1993; Amiya et al. 2011). In the preoptic area, mGnRH-ir cells were located in the parvocellular preoptic nucleus

and the organum vasculosum of the terminal lamina (Fig. 13.8a, b) and in the anterior and lateral tuberal nuclei in the hypothalamus (Fig. 13.8d, e). Most of these mGnRH-ir neurons were of the CSF-C type and exhibited short processes reaching the ventricular lumen (Fig. 13.8a, b, d, e). All these cell bodies were observed along mGnRH-ir fiber tracts that could be followed from the olfactory nerve to the hypothalamo-pituitary interface. Thus, numerous mGnRH-ir fibers were observed in all brain regions, in particular in the anterior brain (Fig. 13.8a-e), although mGnRH-ir fibers were not observed in the anterior lobe of the pituitary, but a few were seen to enter the neurointermediate lobe (Fig. 13.8f), similar to the situation existing in teleosts (Kah et al. 1986, 1991). In contrast, cGnRH-II was more abundant in the posterior brain, although a few fibers could be detected in the preoptic region and the hypothalamus (Fig. 13.8d, e). The only cGnRH-II-positive cells, which were negative for mGnRH, were consistently observed in the midbrain located close to the nucleus of the medial longitudinal fasciculus (Fig. 13.8f), similar to what has been reported in many teleosts or even tetrapods (see references in Leprêtre et al. 1993). These observations suggest that in sturgeons, mGnRH has a hypophysiotrophic role regulating the release of gonadotropin and also functions as a neuromodulator, whereas cGnRH-II has only neuromodulatory functions (Leprêtre et al. 1993) as it was reported for salmon GnRH (sGnRH) and cGnRH-II in the masu salmon (Amano et al. 1991).

Despite the fact that the sturgeon specimens used in Leprêtre et al. (1993) and Amiya et al. (2011) studies were immature, both reported the presence of an overall distribution of mGnRH in the brain that was very close similar to that of the distribution of salmon GnRH in teleosts (Kah et al. 1986, 1991; Oka and Ichikawa 1990; Amano et al. 1991), which suggests that this GnRH system is established early during development as shown in other vertebrate species and is probably activated by increasing level of sex steroids at the time of puberty.

**Fig. 13.8** Schematic drawings of transverse sections through the preoptic region (a-c) and hypothalamus (d-f) of Acipenser baerii (from rostral to caudal) showing the distribution of neurons (solid circles) and fibers (dotted areas) immunoreactive to mammalian (mGnRH) and chicken (cGnRH-II) gonadotropin-releasing hormone. At the *left*, anatomical regions are summarily indicated. The levels of the sections are indicated in a lateral view of the brain on the top. Schematic drawings were modified from Leprêtre et al. (1993). Abbreviations: CP, choroid plexus; Dd, dorsal part of the dorsal telencephalon; Dl, lateral part of the dorsal telencephalon; FR, fasciculus retroflexus; h, habenula; H, hypophysis; HL, hypothalamic lobes; Hyp, hypothalamus; i, infundibulum; III, third ventricle; IV, fourth ventricle; IVn, trochlear nucleus; LR, lateral hypothalamic recess; ME, median eminence; MLF, medial longitudinal fascicle; MPT, medial nucleus of the posterior tubercle; NAT, anterior tuberal nucleus; NIL, neurointermediate lobe of the hypophysis; NLT, lateral tuberal nucleus; NPOp, parvocellular preoptic nucleus; OB, olfactory bulb; OC, optic chiasm; OT, optic tectum; OVLT, organum vasculosum of the terminal lamina; P, pineal organ; PC, posterior commissure; Pd, pars distalis of the hypophysis; POR, posterior recess; PR, preoptic recess; SV, saccus vasculosus; T, telencephalon; Td, dorsal thalamus; tl, torus longitudinalis; TPp, periventricular nucleus of the posterior tubercle; vc, valvula cerebelli; VM, ventromedial thalamic nucleus. Scale bars = 1 mm (lateral view), 500  $\mu$ m (sections)



In the brain of the Siberian sturgeon, reciprocal connections were reported between the NPY and GnRH neurons (Amiya et al. 2011). NPY-ir profiles were observed in close contact with GnRH-ir cell bodies in the preoptic area, while NPY-ir cell bodies were contacted by GnRH-ir fibers. This suggests that NPY and GnRH neural activities are reciprocally regulated in the brain of sturgeons (Amiya et al. 2011).

#### Conclusions

In conclusion, the hypothalamus of sturgeons is characterized by the importance of a very large ventricle and the presence of a majority of CSF-C cells most likely representing a basal character that can be also observed in teleosts such as the eel. In early teleosts, such as the zebrafish, the hypothalamic ventricle is not so large, although CSF-C cells are also very abundant. On another hand, most of the neuropeptides and neurohormones found in tetrapods are present in sturgeons, suggesting that their common ancestors, before the split between sarcopterygians and actinopterygians, already possessed such regulatory systems. Unfortunately, because of the difficulty in approaching the physiology of sturgeons (size, cost, etc.), the number of experimental studies aiming at deciphering the roles of such neuropeptides and neurohormones is very limited, although we can speculate that part of the functions supported by these neurohormones would be similar.

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