Connection of the Posterior Occipital Muscle and Dura Mater of the Siamese Crocodile

JING-HUI ZHANG,[1] WEI TANG,[1] ZHAO-XI ZHANG,[2] BING-YI LUAN,[3] SHENG-BO YU,[1]* AND HONG-JIN SUI[1]*
[1]Department of Anatomy College of Basic Medicine, Dalian Medical University, Dalian, Liaoning, China
[2]First Clinical College, Dalian Medical University, Dalian, Liaoning, China
[3]Dalian Hoffen Bio-Technique Co., Ltd, Dalian, Liaoning, China

ABSTRACT

The myodural bridge was proposed initially in 1995. The myodural bridge is a connective tissue bridge that connects a pair of deep muscles at the suboccipital region to the dura mater. There have been numerous studies concerning the morphology and function of the myodural bridge. To determine whether a myodural bridge exists in reptiles, six Siamese crocodiles were investigated using gross anatomy dissection and P45 sheet plastination technologies. As a result, we demonstrated that the posterior occipital muscles of the Siamese crocodile are directly or indirectly connected to the proatlas, atlas, and intermembrane between them. Multiple trabeculae existing in the posterior epidural space extended from the ventral surface of the proatlas, atlas, and intermembrane between them to the dorsal surface of the spinal dura mater. This study showed that the posterior occipital muscle in the suboccipital region of the Siamese crocodile is connected to the spinal dura mater through the proatlas, atlas, and the trabeculae. In conclusion, a myodural bridge-like structure exists in reptiles. This connection may act as a pump to provide cerebrospinal fluid (CSF) circulation at the occipitocervical junction. We hypothesize that a physiologic role of the Siamese crocodile's myodural bridge may be analogous to the human myodural bridge. Anat Rec, 299:1402–1408, 2016. © 2016 Wiley Periodicals, Inc.

Key words: myodural bridge; rectus capitis posterior major muscle; rectus capitis posterior minor muscle; proatlas; spinal dura mater; Siamese crocodile; cerebrospinal fluid circulation

The suboccipital region consists of complex anatomical structures that are of interest to anatomists and clinicians. Soft tissue connections extending from the suboccipital muscles and the nuchal ligament to the spinal dura mater and their role have been studied recently. In 1992, these fascial communications were briefly described by Khan and Kortiké (1992) in a report of the posterior intervertebral spaces of the craniovertebral joint. Hack et al. (1995), who proposed the concept of a myodural bridge in 1995, believed that the myodural bridge is a connective tissue bridge that connected the rectus capitis posterior minor muscle to the spinal dura mater via the posterior atlanto-occipital interspace.

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Hong-Jin Sui and Sheng-Bo Yu contributed equally to this work.

*Correspondence to: Hongjin Sui, Department of Anatomy, College of Basic Medicine, Dalian Medical University, Dalian, China. E-mail: ysbdmu@126.com Hong-Jin Sui, Department of Anatomy, College of Basic Medicine, Dalian Medical University, Dalian, China. Fax: (+86) 0411-86110355. E-mail: suihj@hotmail.com

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Mitchell et al. (1998) verified the existence of the fascial connection between the nuchal ligament and the suboccipital dura mater. Alix and Bates (1999) observed and verified the structure of the myodural bridge described by Hack et al. (1995). Dean and Mitchell (2002) confirmed the connection of the nuchal ligament, dura mater, and suboccipital muscle. However, the studies of Johnson et al. (2000) and Nash et al. (2005) suggested that the nuchal ligament was not distinguishable in the suboccipital region. Zumpano et al. (2006) described the frequency and consistency of the myodural bridge and classified its structure. Myodural bridges extending from the rectus capitis posterior major and obliquus capitis inferior to the cervical dura mater were reported by Scali et al. (2011, 2013a,b) and Pontell et al. (2013a,b). The later studies by Sui et al. (2013), Zheng et al. (2014), and Yuan (2016) solidified the previous findings of the connections between the suboccipital structures and the cervical dura mater, and furthermore found two novel ligaments, termed "the Vertebrodural Ligament" and "the To Be Named Ligament," as a structural supplements for the myodural bridge. Relevant reports in recent years have suggested that the myodural bridge has important pathophysiological functions. Myodural bridges might generally play a role in protecting the spinal cord from dural enfolding (Hack et al., 1995; Alix & Bates, 1999; Nash et al., 2005; Tagil et al., 2005; Scali et al., 2011, 2013b; Pontell et al., 2013b), by placing the dura under tension (Alix & Bates, 1999; Scali et al., 2011,b; Pontell et al., 2013a,b), and also aid in the maintenance of CSF outflow from the cisterna magna (Scali et al., 2011, 2013a,b; Pontell et al., 2013a) by maintaining the integrity of the subarachnoid space. Sui et al. (2013) and Zheng et al. (2014) proposed that the suboccipital muscles-myodural bridge-cervical dural sleeve complex was most likely acting as a pump to provide power for cerebrospinal fluid (CSF) circulation. Several studies (Hack et al., 1995; Kontautas et al., 2005; Nash et al., 2005) suggested that the myodural bridge in the suboccipital region of humans was probably correlated with chronic cervical headache.

Our group has dissected many mammals, including the monkey, dog, cat, rabbit, mouse, and cowfish (*Neophocaena phocaenoides*), and found that each has an anatomical structure that is similar to the human myodural bridge. Compared with other extant reptiles, the Siamese crocodile is a typical representative of the most nonspecialized animals (Cong et al., 1998). Thus, this study selected the Siamese crocodile as a representative reptile and performed an anatomical study on the structure of its nape area to determine whether a myodural bridge-like structure exists in reptiles.

MATERIALS AND METHODS

Experimental Materials

Six fresh Siamese crocodile samples were collected at a zoo after their natural deaths. Two of them were used for studying the gross anatomy dissection, and another four samples were used for P45 sheet plastination evaluations.

The equipment required included a high-speed band saw, acetone-resistant metal mesh, a temperature-controlled refrigerator (minimum temperature −25°C), vacuum pump, small water pump, P45 flat box (full of P45 polyester resin: 1,000 mL P45 monomer, 10 g $P45_a$, 30 mL $P45_b$, and 5 g $P45_c$), polishing machines, pressure gauges, and a Canon EOS 450D single-lens reflex camera. Reagents included P45 monomer, polyurethane foam, and acetone.

Experimental Methods

A U-shaped incision was made along the infraoccipital margin of the Siamese crocodile's shoulder. The skin was reflected to expose cutaneous muscle. Muscles were isolated layer by layer to expose the depressor mandibulare, splenius capitis, semispinalis capitis, and the first cervical nerve. The first cervical nerve was found to pierce superficially between the rectus capitis posterior major and semispinalis capitis. So this two muscles were separated with each other according to the first cervical nerve. The rectus capitis posterior minor was exposed near the midline, medial to the rectus capitis posterior major. Each muscle was transected at its origin along the bone surface of the caudal occipital region of the skull to expose the proatlas. The relations of the proatlas and surrounding tissue were observed and recorded.

The proatlas covering the surface of the atlanto-occipital joint was transected along the bone surface of the caudal occipital region of the skull. The atlanto-occipital joint (ball-and-socket joint) was exposed dorsally. The soft tissue was removed from the atlanto-occipital joint to the dorsal surface of the basioccipital bone, and the atlanto-occipital joint was transected.

The paraspinal muscles were transected to expose the first and second cervical ribs. The pedicle of the vertebral arch was cut on the plane of the costovertebral joint. A ventral vertebra was removed, and the vertebral canal was exposed. The dural sac was cut longitudinally on the ventral side, and the spinal cord was removed. The connection between the posterior of the dura mater and the posterior wall of the vertebral canal was observed.

The P45 sheet plastination technology described by Sui et al. (2013) was used. After fixation (10% formalin solution), the samples were frozen at −70°C for 2 weeks, immersed in polyurethane foam, and frozen again at −70°C for 2 days. They were then serially sectioned into 3 mm-thick sagittal slices with a high-speed band saw. The sections obtained were immersed in 5% hydrogen peroxide overnight and then washed with cold water.

After bleaching, the sections were dehydrated by freeze substitution, using acetone. First, sections were precooled at 5°C, immersed rapidly in −25°C acetone solution and left there for 1 week, and then placed in −15°C acetone solution for 10 days. They were then transferred to 100% acetone solution at room temperature for degreasing. The concentration of the acetone solution was determined daily. If the concentration was above 99.5% three consecutive times, the degreasing step ended.

The next step was vacuum impregnation. The flat box used for impregnation was composed of two 5 mm-thick tempered glass plates, a 4 mm-diameter rubber tube, and large binder clips. Sections were removed from the acetone solution and placed between the two tempered glass plates. The flat box was filled of P45 polyester resin (plasticizing P45 polyester resin; Dalian Hoffen Bio-Technique Co., Ltd, Dalian, Liaoning, China). The resin was prepared according to the following proportions: 1,000 mL P45 monomer, 10 g $P45_a$, 30 mL $P45_b$, and 5 g

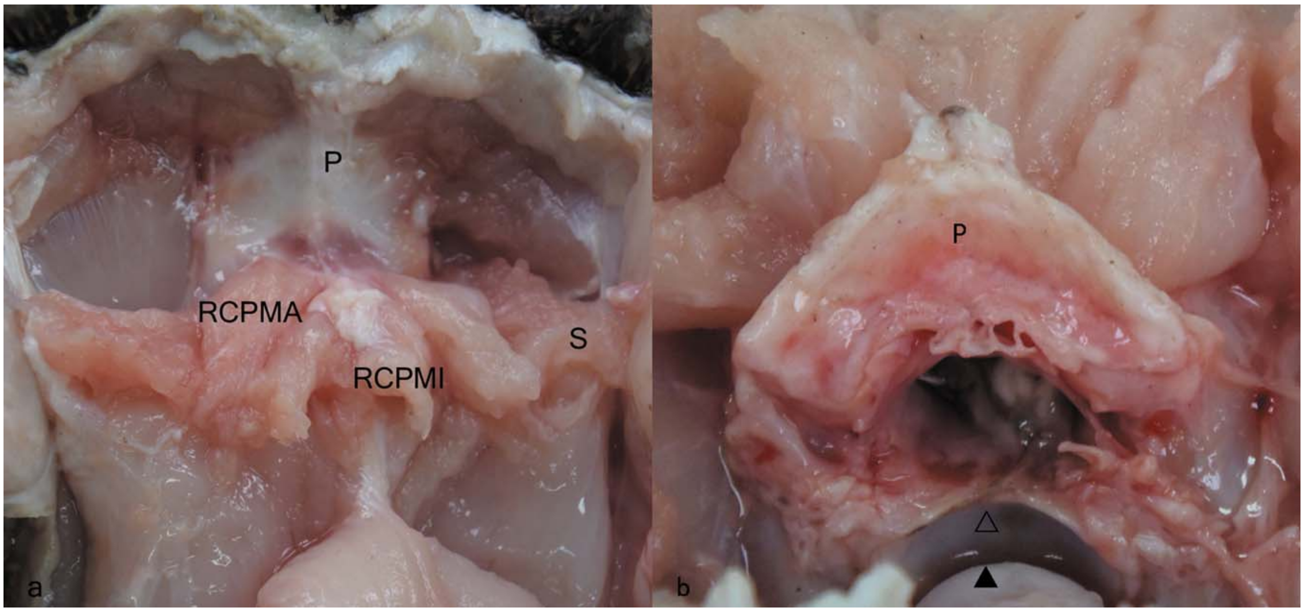

Fig. 1. The dorsal and anterior views of the proatlas. (a) The dorsal view of the proatlas with the vertebral occipital muscles reflected caudally. The proatlas is an arrow-shaped bone chip. The posterior occipital muscles on the surface of proatlas were reflected caudally. (b) The anterior view of the proatlas. The proatlas is a thin crescent-domed bone chip in anterior aspect. Atlanto-occipital joint is a ball-and-socket joint in Siamese crocodile. P, the proatlas; RCPMA, the rectus capitis posterior major; RCPMI, the rectus capitis posterior minor; S, the semispinalis; Open triangle, the cotyloid cavity; Filled triangle, the hemispheric protrusion.

$P45_c$. The $P45_a$ and $P45_c$ are plasticizers. P_{45b} is a hardener. The flat box was placed upright in the vacuum chamber and impregnated at room temperature. According to the degree of bubble release, the pressure of the vacuum chamber was slowly decreased to 20, 10, 5, and then 0 mmHg. At 0 mmHg, when bubbles no longer appeared, the impregnation was terminated. The sections were placed in a water bath heated to 40°C for solidification in the 3 days duration. After solidification, the sections were taken out of the water bath and removed from the glass plates.

RESULTS

Gross Anatomy Dissection

Bone structures in the dorsal suboccipital region of the Siamese crocodile include the skull base, proatlas, atlas, and axis. The proatlas is an arrow-shaped, thin, crescent-domed bone chip (Fig. 1) that obliquely covers the spinal cord from the back of the interspace between the anterior border of the first cervical vertebra (atlas) and the dorsal margin of the foramen magnum of the cranium. There is a membrane-like structure between the proatlas and atlas. The atlas is composed of a pair of separated dorsal arches and a hypocentra, no real centrum, and a spinous process. In addition to the centrum and vertebral arch, there is a massive odontoid process in front of the axis.

Muscles in the deep posterior occipital region include the vertebral occipital muscles (the rectus capitis posterior major and rectus capitis posterior minor) and the semispinalis capitis. The rectus capitis posterior major originates from exoccipital bone and terminates in the anterior end of the C2 spinous process and the atlantal arch. The rectus capitis posterior minor originates from supraoccipital bone and terminates in the anterior end of the C2 spinous process, neural arch of the atlas, proatlas, and the membranous structure between the proatlas and atlas. The first cervical nerve, which runs from the semispinalis capitis and rectus capitis posterior major, is a marker for separations between them. The proatlas is covered by three muscles, from the midline laterally, which are the rectus capitis posterior minor, the rectus capitis posterior major, and semispinalis capitis (Figs. 1a, 2). In addition, deep to the above-mentioned muscles, a dense connective tissue was found to connect these muscles with the proatlas, atlas and membranous structure in this study (Fig. 2).

The atlanto-occipital joint of the Siamese crocodile is a ball-and-socket joint (Fig. 1b). The posterior atlanto-occipital membrane merges dorsally with the proatlas. The posterior atlanto-occipital membrane is tightly connected to the dura mater near the midline, forming a fibrous tissue bridge. At the region bounded by the proatlas anteriorly and the anterior border of the lamina of the vertebral arch of C2 posteriorly, there are many trabecular connective tissue structures in the "inverted triangle" area (wide cephalic region, narrow caudal region) in the posterior wall of the spinal canal. These trabeculae connected the dural sac to the posterior wall of the spinal canal (Fig. 3). Uniform, dense trabeculae were observed between the proatlas and dural sac, with only a few trabeculae between the axis and dural sac. Caudal and lateral to the "inverted triangle" area, a Y-shaped potential lacuna was present between the posterior wall of the spinal canal and the dura mater (Fig. 4). The potential lacuna extended cranially along two sides of the "inverted triangle" and reached the interspace between the atlas and occipital bone (for the first cervical nerve root). On both sides of the potential lacuna distal to the axis, there were discontinuous sheet-like structures connecting the lateral posterior wall of the spinal canal and the dura mater. These sheet-like structures existed near to the posterior intervertebral spaces (Fig. 5). Moreover, the trabeculae near to the interspace between the occipital bone and the atlas were more concentrated (Fig. 3). When the vertebral occipital muscles were pulled, the movement of the proatlas could move the anterior cervical dura mater.

Results of P45 Sheet Plastination Technology

Median sagittal sections of four Siamese crocodile samples showed that the vertebral occipital muscles originated from the occipital bone and extended caudally. Dense connective tissue in the deep region of the muscles was connected to the proatlas. At the level of the proatlas to the anterior border of the C2 lamina of the vertebral arch, the dural sac was connected to the posterior wall of the spinal canal (including the proatlas, atlas, and membrane between them) through the trabeculae (Figs. 6, 7).

DISCUSSION

Structure of the Human Myodural Bridge

Since Hack et al. (1995) proposed the concept of a human myodural bridge, relevant studies have been frequently reported. These studies suggest that the human myodural bridge is the connective tissue bridge between deep structures in the suboccipital region and dura mater. The myodural bridge in the epidural cavity is formed from the rectus capitis posterior minor, the rectus capitis posterior major, obliquus capitis inferior and the nuchal ligament and inserted to the dura mater (Khan and Kortiké, 1992; Hack et al., 1995; Tagil et al., 2005; Scali et al., 2011, 2013a,b; Pontell et al., 2013a,b). Many mammals, including the monkey, dog and cowfish, were investigated by our research team and a myodural bridge was found in each of them (unpublished findings). Thus, we postulated that the myodural bridge might be a normal and universal structure in mammals. Furthermore, the results of this study showed that a myodural bridge-like connection also exists in reptiles.

Myodural Bridge-Like Structure and Its Characteristics in the Siamese Crocodile

After studying the anatomical structure of the dorsal occipital regions of two Siamese crocodiles, layer by layer, we demonstrated that the vertebral occipital muscles (the rectus capitis posterior minor and rectus capitis posterior major) and the semispinalis capitis of the Siamese crocodile covered the proatlas. Dense connective tissue deep to these three muscles is connected to the deep structure (with the proatlas, atlas and the membrane-like structure between them). Contraction of these muscles could move the proatlas. At the level of the proatlas to the anterior border of the C2 lamina of the vertebral arch, the dura mater connects to the posterior wall of the spinal canal via a lot of trabeculae of connective tissue. The trabeculae are more concentrated near to the proatlas and the intervertebral foramen of the atlas. Because of the presence of uniform, dense trabeculae connecting the proatlas and dura mater, the cervical dura mater could move following the movement of the proatlas. Median sagittal sections showed that the dense connective tissue in the deep areas of the muscles is connected to the proatlas. At the level of the proatlas to the anterior border of the C2 lamina of the vertebral arch, the dural sac is connected to the posterior wall of the spinal canal through trabecular connective tissue. Moreover, dense trabecular connective tissue is visible between the proatlas and dura mater.

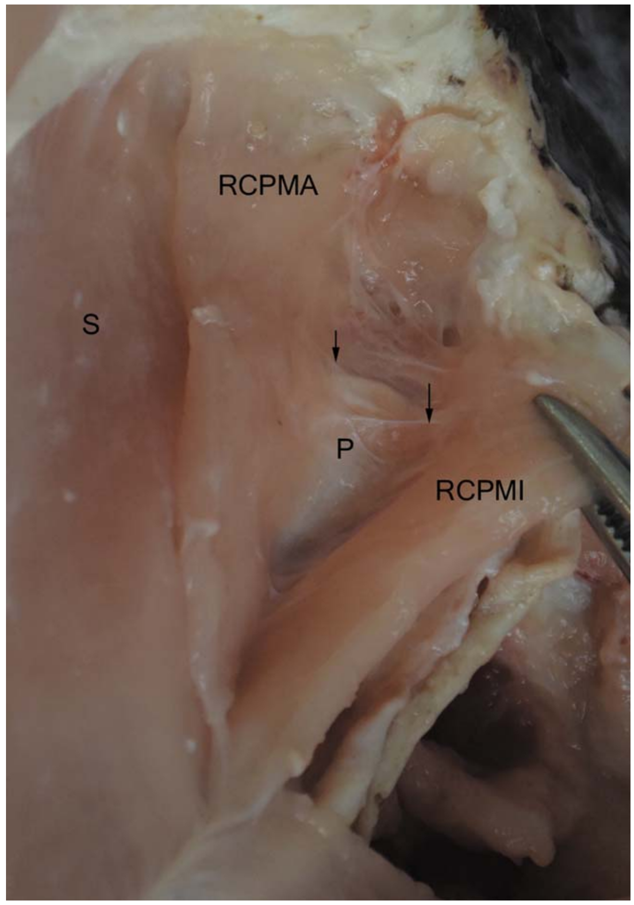

Fig. 2. Connections of dense connective tissue between the vertebral occipital muscles and the proatlas. P, the proatlas; RCPMA, the rectus capitis posterior major; RCPMI, the rectus capitis posterior minor; S, the semispinalis; Arrows, the connections of dense connective tissue between the RCPMA, RCPMI, and the proatlas.

The gross anatomy dissection of the Siamese crocodile is consistent with the results of P45 sheet plastination technology. In the present study, the vertebral occipital muscle is connected to the proatlas, atlas, and membrane structure via dense connective tissue. In addition, the proatlas, atlas, and membranous structure connect to the dura mater through trabecular connective tissue. The findings of this study indicate that a reptile (Siamese crocodile) has a myodural bridge-like structural connection: vertebral occipital muscle (rectus capitis posterior major and rectus capitis posterior minor) is connected to the proatlas, and then the proatlas is connected to the dura mater via the trabeculae. We suggest that this structural complex might play a similar function to the human myodural bridge.

Effects of the Myodural Bridge

Studies of the myodural bridge over the past several decades have fully verified its presence, but its origin

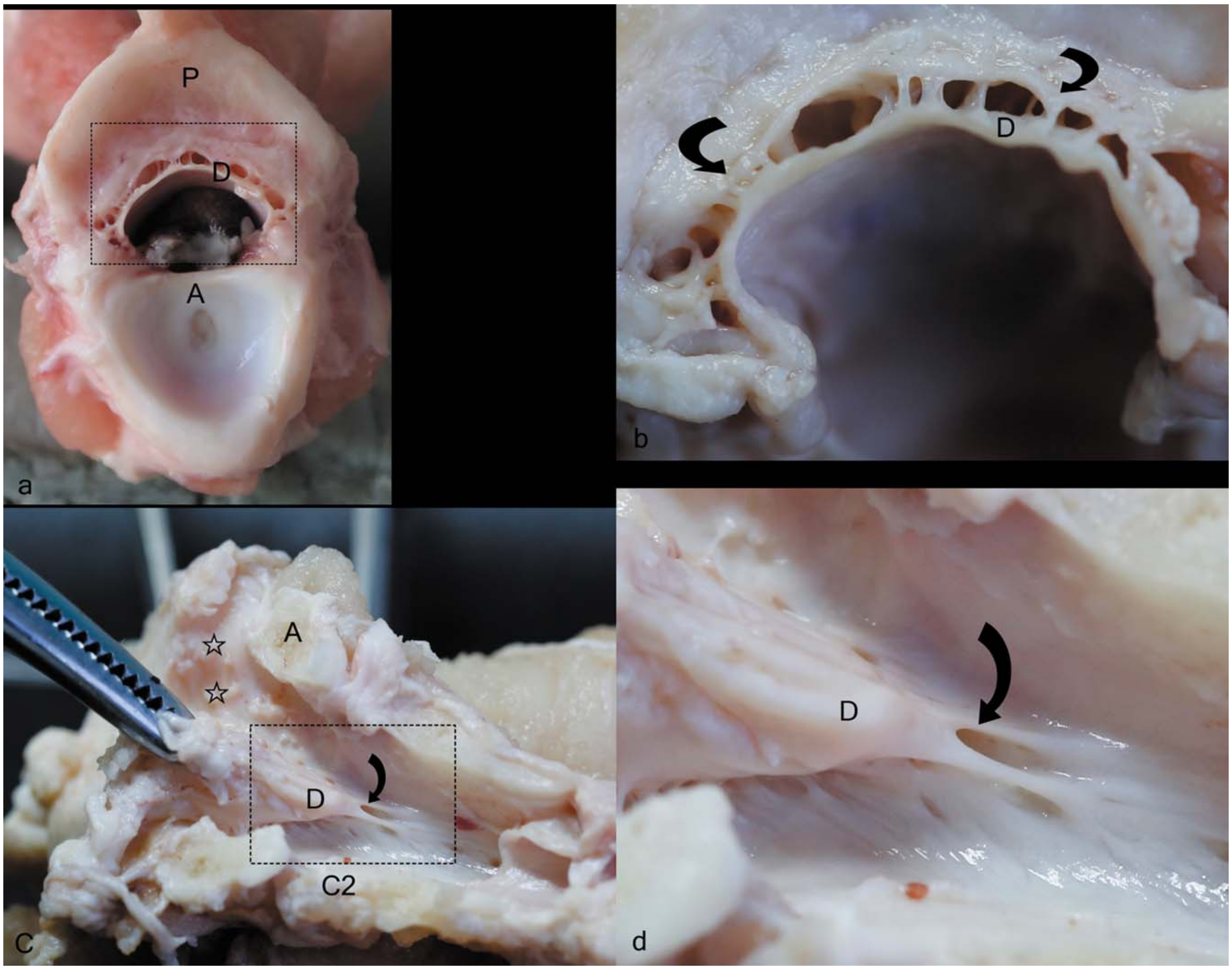

Fig. 3. Trabeculae between the posterior wall of the spinal canal and the spinal dura mater. (a) The anterior view of the proatlas, atlas, and the section of the vertebral canal. (b) A magnified picture of the rectangular region of the figure a. (c) The ventral view of the posterior wall of the spinal canal from the proatlas to the C2 with the spinal dural sac drawn anteriorly. (d) The magnified picture of the rectangular region of the figure c. The trabeculae were dense between the proatlas and the spinal dura mater (a, b). And at the level of the proatlas to the anterior border of the C2 lamina of the vertebral arch, there are many trabecular connective tissue structures in this “inverted triangle” area (wide cephalic region, narrow caudal region) in the posterior wall of the spinal canal (c). The transections of the trabeculae were showed at the left part of the “triangle” area (c). So, there were a lot of trabeculae connecting the dural sac to the posterior wall of the spinal canal (c, d). Arrows, the trabeculae. P, the proatlas; A, the atlas; D, the dura mater; C2, the axis; Stars, the cutting end of the trabeculae.

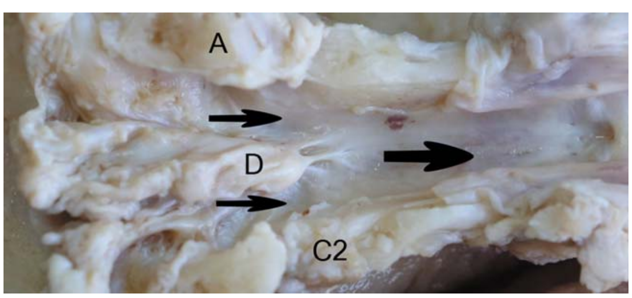

Fig. 4. Epidural space lateral and distal to the trabeculae area. Caudal to the atlas, a Y-shaped potential lacuna (arrows) was present between the posterior wall of the spinal canal and the dura mater. A, the atlas; C2, the axis; D, the spinal dural sac reflected anteriorly.

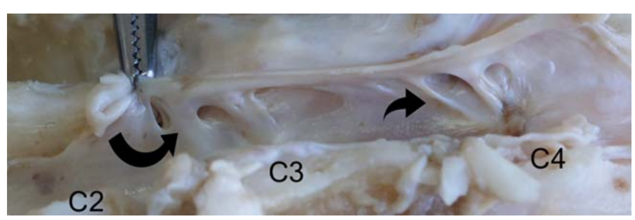

Fig. 5. The sheet-like structures between the dura mater and the lateral posterior wall of spinal canal at the lateral epidural space distal to the axis. The sheet-like structures (arrows) were concentrated a little near to the posterior intervertebral spaces. C2, the axis; C3, the third vertebra; C4, the fourth vertebra.

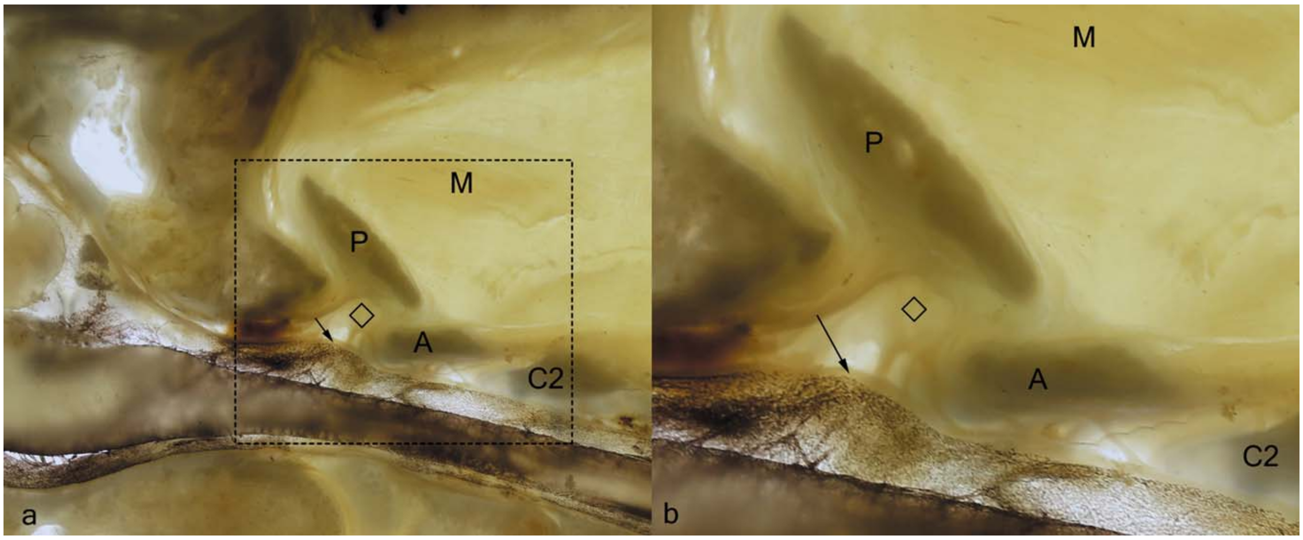

Fig. 6. The trabeculae between the proatlas, atlas and the posterior wall of the dura mater. (a) The median sagittal section of head and neck of the Siamese crocodile using the P45 sheet plastination. (b) The magnified pictures of the rectangular region of the figure a. The trabeculae were present in the posterior epidural space at the level of the proatlas to the anterior border of the C2 lamina of the vertebral arch, which were extended from the posterior wall of the spinal canal to the dural sac (a). Uniform, dense, trabeculae were extended from the proatlas, atlas and the dura mater (b). P, the proatlas; A, the atlas; C2, the axis; Open diamond, the trabeculae; Arrow, the spinal dura mater; M, the vertebral occipital muscles.

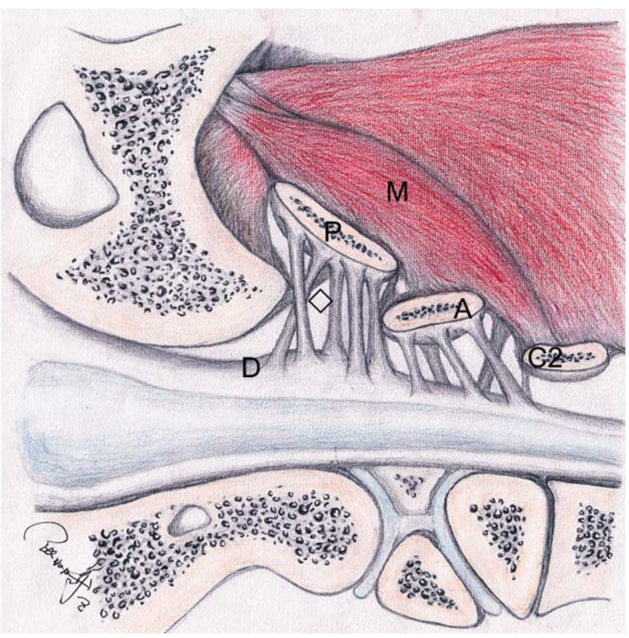

Fig. 7. Diagram of the connection from the post-occipital muscles to the dura mater based on the gross and sectional anatomy of the post-occipital region. Vertebral occipital muscles were inserted to the proatlas, atlas, and membranous structure between them. The proatlas, atlas, and the membranous structure were connected to the dura mater via trabeculae. P, the proatlas; A, the atlas; C2, the axis; Open diamond, the trabeculae; D, the spinal dura mater; M, the vertebral occipital muscles.

and function have remained unknown. Many scholars believe that the myodural bridge is an extension of the deep muscles in the suboccipital region at the joint and is directly or indirectly connected to the dura mater (Hack et al., 1995; Mitchell et al., 1998; Alix & Bates, 1999; Dean & Mitchell, 2002; Scali et al., 2013a; Sui et al., 2013).

There are a variety of viewpoints concerning the function of the myodural bridge. Hack et al. (1995) believed that it protects the dura mater and spinal cord. They also stated that vertical fiber arrangement of the myodural bridge prevents infolding of the dura mater.

Rutten et al. (1997) proposed that the myodural bridge could maintain the flow of the CSF in the subarachnoid cavity and cerebellomedullary cistern, protecting the dura mater during head movement.

McPartland and Brodeur (1999) verified that the rectus capitis posterior minor muscle could prevent the infolding of the dura mater during head movement, which might inhibit CSF flow. Scali et al. (2011, 2013a,b) and Pontell et al. (2013a) also suggest that the myodural bridge was related to the maintenance of CSF outflow from the cisterna magna by maintaining the integrity of the subarachnoid space.

Recently, Sui et al. (2013) and Zheng et al. (2014) proposed a new hypothesis addressing CSF circulation. They proposed that when the rectus capitis posterior minor contracted, the dura mater was pulled by the myodural bridge, thereby inducing alterations in the subarachnoid volume and then producing negative pressure. As a result, the CSF circulation could be affected by these changes. They thought that this effect of the myodural bridge is possibly an important power source of the CSF circulation as a pump. Yu et al. (2014) investigated the CSF flow before and after head rotation using a phase-contrast cine magnetic resonance method. They demonstrated that head rotation affected the mean velocity, flow rate, and flow direction of CSF at the occipitocervical junction.

In a reptile, the trabeculae, similar to the myodural bridge in humans, connected the dura mater to the proatlas, and caused the dura mater to move easily following the movement of the proatlas. Meanwhile, the proatlas was a freely sliding chip bone filling in the posterior interspace between the occipital bone and the atlas. So it is strongly suggested that the vertebral occipital muscle-proatlas-trabeculae-dura mater complex is more likely to be an important circulation power for the CSF at the occipitocervical junction. The results of the present study support the hypothesis by Sui et al. (2013) and Zheng et al. (2014).

CONCLUSIONS

- The posterior occipital muscle of the Siamese crocodile is composed of the rectus capitis posterior major and the rectus capitis posterior minor.
- The posterior occipital muscle of the Siamese crocodile is directly or indirectly connected to the proatlas, atlas, and the membranous structure between them.
- Multiple trabeculae are present in the triangular region ventral to the proatlas, atlas, and the membranous structure between them. Acting as connections, they integrate the cervical dura mater with the proatlas primarily and atlas secondarily.
- A myodural bridge is also present between the posterior occipital muscle and the dura mater. This connection shows that muscle is connected to the membrane between the proatlas and atlas via dense connective tissue. The membranous structure is connected to the dura mater through the trabeculae.
- The complex of vertebral occipital muscle-proatlas-trabeculae-dura mater probably plays a myodural bridge-like role in reptiles. It is suggested that this structural complex might be an important power for the CSF circulation at the occipitocervical junction.

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