**RESEARCH ARTICLE**

# The myodural bridge in the common rock pigeon (*Columba livia*): Morphology and possible physiological implications

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Liaoning Province Department of Education Funds, Grant/Award Number: L2016012, L2015156; Natural Science Foundation of China, Grant/Award Number: NSFC31600972, NSFC31571234

The dense connective tissue that connects muscles to the cervical spinal dura mater is known as the myodural bridge in human anatomy and has been a subject of interest to anatomists and clinicians. The myodural bridge was originally discovered in humans, and also has been observed in other mammals and in reptilian sauropsids. We investigated the existence of the myodural bridge in a bird, that is, the Common Rock Pigeon *Columba livia*, to expand the understanding of the structure and function of the myodural bridge. Gross anatomical dissection of seven specimens and histological analyses of the suboccipital region of eight specimens were performed. The rectus capitis dorsalis minor muscle joins occipital periosteal extensions and inserts with several dense connective tissue cords on the dorsal side of the dura mater of the cervical spinal cord. The myodural bridge consists primarily of collagen Type I fibres, suggesting that the myodural bridge can transmit strong tensional forces generated by the contraction of *M. rectus capitis dorsalis minor* to the dura mater. The pull on the dura mater may affect the circulation of the cerebrospinal fluid in the subarachnoid space of the spine.

**KEYWORDS**

bird, cerebrospinal fluid, connective tissue, Dura mater, histological sections, rectus capitis dorsalis minor muscle

## 1 | INTRODUCTION

The myodural bridge consists of dense connective tissue bridging the cervical spinal dura mater on the one hand with the *Ligamentum nuchae* and *Mm. rectus capitis posterior minor*, *rectus capitis posterior major* and *obliquus capitis inferior* conversely. It is a well-documented anatomical structure in humans (Palomeque-del-Cerro et al., 2017; Yuan et al., 2017; Enix, Scali, & Pontell, 2014; Zheng et al., 2014; Pontell, Scali, Marshall, & Enix, 2013; Scali, Pontell, Enix, & Marshall, 2013; Mitchell, Humphreys, & O'Sullivan, 1998; Hack et al., 1995). A recent study revealed this structure also in five other mammalian taxa, that is, *Macaca mulatta*, *Oryctolagus cuniculus*, *Canis familiaris*, *Felis catus*, *Ratus norvegicus*, *Cavia porcellus* and Indoasian finless porpoise, and hypothesized that it may be widespread among mammals (Zheng et al., 2017). In addition, it was shown that the posterior occipital muscles insert on the dorsal side of the dura mater of the spinal cord by multiple trabeculae in the Siamese crocodiles, *Crocodylus siamensis* (Zhang et al., 2016).

Biomechanical studies have shown that contraction of the *M. rectus capitis posterior minor* produces a posterior displacement of the dura mater via the myodural bridge and would increase the tension on the cervical dura mater (Venne, Rasquinha, Kunz, & Ellis, 2017). This may prevent an in-folding of the spinal dura mater during head extension, or stimulate cervical neck extensor muscles that would resist hyperflexion or hypertranslation (Hack et al., 1995; Nakagawa, Mikawa, & Watanabe, 1994; Scali et al., 2013). The presence of a myodural bridge has clinical implications for cervicogenic headache (Alix & Bates, 1999; Hack & Hallgren, 2004). It is believed that a pathologically tense *M. rectus capitis posterior minor* may produce improper forces that are transmitted through the myodural bridge to the pain-sensitive dura mater. Clinical studies by Yuan et al. (2017) revealed that patients of chronic cervicogenic headache have a hypertrophic *M. rectus capitis posterior minor* and that the myodural bridge may be implicated in this type of headache. Other hypothesized functions of the myodural bridge is the maintaining of the integrity of the cerebello-medullary cistern (Scali et al., 2013; Scali, Pontell, Nash, & Enix, 2015) and acts as a cerebrospinal fluid pump (Hallgren, Hack, & Lipton, 1997; Sui et al., 2013; Xu et al., 2016).

Okoye Chukwuemeka Samuel and Nan Zheng contributed equally to this work.

Since the myodural bridge is currently known only in mammals and reptilian sauropsids, we investigated whether this structure exists also in birds to expand the understanding of the structure and function of the myodural bridge and to provide insights into its evolution. The Common Rock Pigeon [*Columba livia* (Gmelin, 1789)] was chosen as a representative of birds.

## 2 | MATERIAL AND METHODS

### 2.1 | Animal handling

Fifteen, one year-old specimens of *Columba livia* (Gmelin, 1789) were provided by a local supplier. They were housed in cages and fed with bird pet food. They were euthanized with an overdose of avertin. Approval for this study was granted by the Ethics Committee of Animal Experiments of Dalian Medical University (AEE18035), and the experiments were performed according to the regulations and guidelines stipulated by the American National Institutes of Health.

### 2.2 | Gross anatomical studies

Seven specimens were used for gross anatomical dissection, which was performed using a stereomicroscope. The upper dorsal cervical region of the specimens was dissected to expose the deep suboccipital muscles by cutting through the biventer cervicis and complexus muscles. The *M. rectus capitis dorsalis major* was detached from its occipital attachment to reveal the *M. rectus capitis dorsalis minor* which lies deep to it. The *M. rectus capitis dorsalis minor* was cut from its occipital attachment and reflected to observe its connection with the dorsal atlanto-occipital membrane. Subsequently, an incision was made through the dorsal atlanto-occipital membrane along the dorsal border of the foramen magnum, or lamina of the atlas, to observe the connection between the dorsal atlanto-occipital membrane and the dorsal spinal dura mater. Specimens were fixed and stored in 10% formalin between subsequent examinations. Photographic documentation was carried out using Canon D-40 camera.

### 2.3 | Histological studies

Eight specimens were used for histological studies. Tissue samples of the occiput and the cervical region were fixed in 10% formalin for 10 days. Subsequently, they were transferred to a 10% ethylenediamine tetraacetic acid (EDTA) solution for decalcification for about 8–12 days. The EDTA solution was changed at three-day intervals. The decalcified tissue samples were washed overnight in running water and subsequently dehydrated in increasing grades of alcohol, cleared in xylene, infiltrated in melted paraffin and embedded. A rotary microtome was used to cut 10- $\mu$ m-thick sections. Sections were mounted on microscope slides. These tissue slices were divided into three groups: Group 1 for haematoxylin and eosin (H & E) stain; group 2 for Masson trichrome stain; and group 3 for sirius red (SR) in saturated carbozotic acid staining (see Supporting Information for detailed staining methods). Microscopic examinations and photography were carried out under a NIKON Eclipse80i research light microscope. Multiple images from each section were stitched together

using microsoft image composite editor of NIKON Eclipse80i image processing and analysis software. The results of the sirius red in saturated carbozotic acid staining was acquired using light and polarizing microscopes. Different staining methods were used to validate the myodural bridge fibre properties. The H and E stain is a conventional standard in histological staining. Masson trichrome stain can be used for detecting collagen fibers in tissues. Sirius red staining in saturated carbozotic acid can also detect collagen fibers in tissues and most importantly can distinguish the collagen type under a polarizing microscope. Information on the myodural bridge collagen type is useful in ascertaining the strength of the myodural bridge.

## 3 | RESULTS

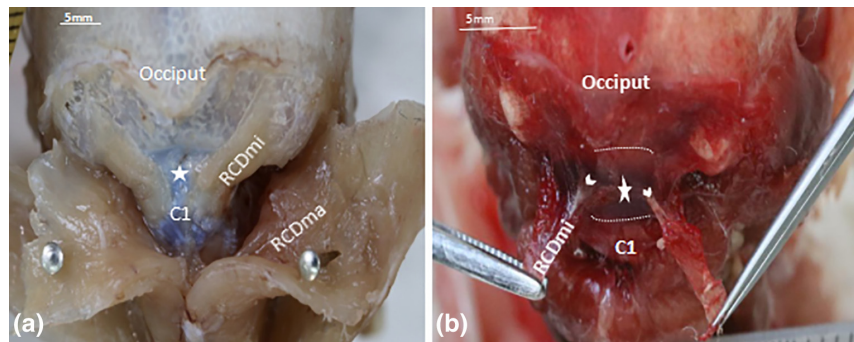
### 3.1 | Gross anatomy

The *M. rectus capitis dorsalis major* has a large superficial part and a smaller deep part. The cranial attachment is at the occiput and the caudal attachment is at the processus spinosus of vertebra C2. The *M. rectus capitis dorsalis minor* is obliquely oriented with its cranial attachment on the occiput, below the transverse nuchal crest and its caudal attachment on the dorsal side of the arcus vertebrae of C1 (Figure 1a). The ventral side of the *M. rectus capitis dorsalis minor* has dense connective tissue connections with the dorsal atlanto-occipital membrane (Figure 1b). The connection is so strong that manual traction on the *M. rectus capitis dorsalis minor* pulls the dorsal atlanto-occipital membrane dorsally. The dorsal atlanto-occipital membrane originates from the dorsal margin of the foramen magnum and inserts on the upper margin of the arcus vertebrae of C1. The dorsal atlanto-occipital membrane adheres tightly to the dorsal spinal dura mater by fibrous cords of dense connective tissue that emanates from the arc-shaped connective tissue on the ventral surface of the dorsal atlanto-occipital membrane that was engorged with blood in the occipital and cervical sinus (see Figure 2a,d). The myodural bridge, dorsal atlanto-occipital membrane, and spinal dura mater were present in all the seven specimens that underwent gross anatomical examinations.

### 3.2 | Light microscopic histology

#### 3.2.1 | Hematoxylin–eosin stained sections

In these sections, the dorsal atlanto-occipital membrane has its proximal attachment on the margin of the foramen magnum of the occipital bone and the distal attachment to the arcus of the atlas (Figure 3b,d). The tendon of *M. rectus capitis dorsalis minor* terminates at the caudal part of the arcus of the atlas (Figure 3d). However, dense fibrous bundles arise from the tendon of the RCDmi muscle and the occiput, run ventrally, and transversely through the DAO membrane. Emerging in the epidural space, the dense connective tissue receives connective tissue from the deep aspect of the occiput (this is the arc shaped connective tissue in Figure 1d) and continues as a dense cord-like structure (Figure 3b,d). This structure extends ventrally through the epidural space, which contains the occipital and cervical sinuses, then bifurcates before inserting into the dorsal spinal dura mater adjacent to the cerebello-medullary cistern (Figure 3b,d). Figure 3d shows that



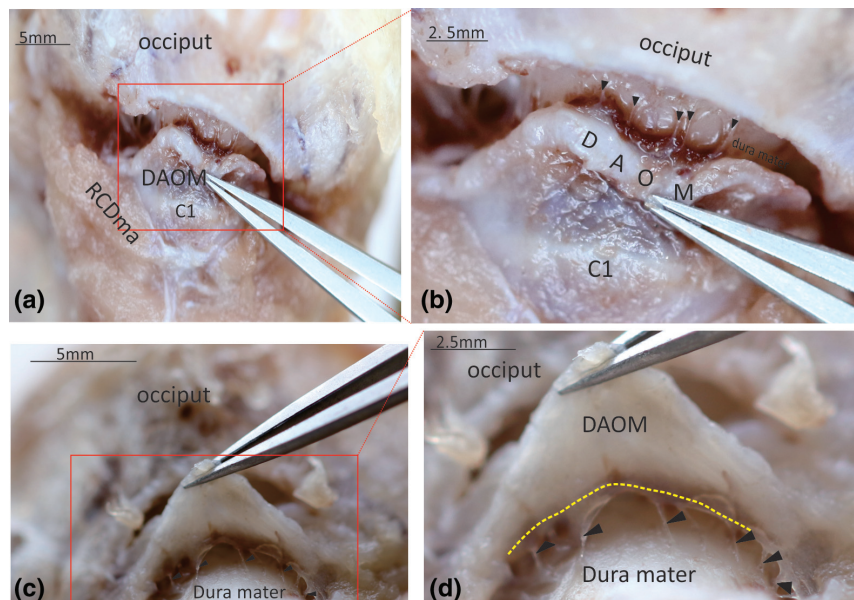
**FIGURE 1** *Columba livia*, dorsal views of an anatomical dissection of the deep suboccipital space. (a) Superficial view of the deep suboccipital region. The RCDmi lies obliquely on the dorsal atlanto-occipital membrane (star) and deep to the RCDma (reflected). (b) The deep suboccipital space. The RCDmi muscle is reflected caudally. The ventral surface of the RCDmi muscle is connected by dense connective tissue (arrow head) to the dorsal atlanto-occipital membrane (star). The white line indicates the extent of the dorsal atlanto-occipital membrane from the foramen magnum cranially and the atlas (C1) caudally. Abbreviations: C1 = atlas; RCDma = rectus capitis dorsalis major muscle; RCDmi = rectus capitis dorsalis minor muscle

the dense cord-like structure repeatedly bifurcates before inserting into the spinal dura mater. Thus, the myodural bridge fibers merge with connective tissues fibers from the deep aspect of the occiput and then insert on the spinal dura mater. The cervical sinus abuts the dense connective connection between the dorsal atlanto-occipital membrane and the cervical spinal dura mater (Figures 3a,c and 6).

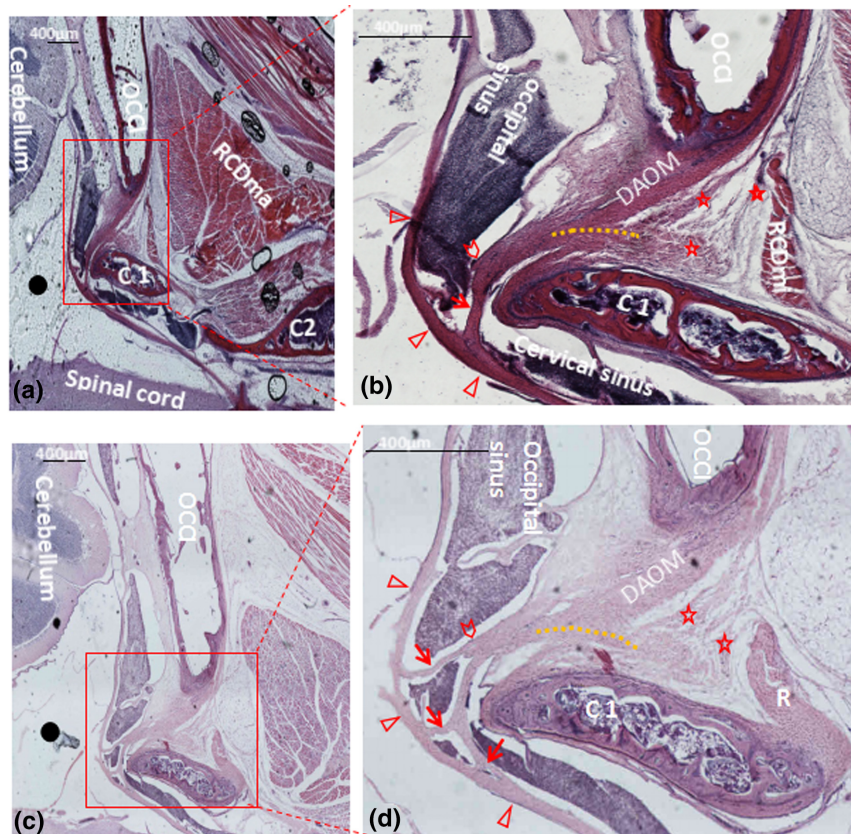
**3.2.2 | Masson trichrome stained sections**

Connective tissue with numerous collagen fibers that originate from the rectus capitis dorsalis minor muscle and tendon extend ventrally through the dorsal atlanto-occipital membrane (Figure 4b,d). The

dorsal atlanto-occipital membrane is a dense connective tissue structure lying between the occiput and atlas. The *M. rectus capitis dorsalis minor* myodural bridge emerging from the deep part of the dorsal atlanto-occipital membrane receive additional connective tissue fibers from the deep aspect of the occiput. These fibers then extend ventrally through the epidural space as a densely packed cord of collagenous connective tissue that inserts on the dorsal spinal dura mater (Figures 4b,d and 6). The dorsal atlanto-occipital membrane, the tendon of the *M. rectus capitis dorsalis minor*, the myodural bridge and the bridging structure are densely stained blue, indicating they consist of dense collagenous connective tissue (Figure 4b,d). The cervical sinus



**FIGURE 2** *Columba livia*, anatomical dissection showing the connection between the dorsal atlanto-occipital membrane and the Dura mater. (a) Dorsal view of the dorsal atlanto-occipital membrane, occiput, and atlas. The dorsal atlanto-occipital membrane (DAOM) was separated from its cranial attachment at the foramen magnum and reflected caudally. (b) Magnified view of the rectangular region in figure a. (c) Dorsal view of the dorsal spinal dura mater. The DAOM was separated from its caudal attachment on the arcus of the atlas and reflected cranially. (d) Magnified view of the rectangular region in figure c. Multiple cord-like dense connective tissue connections (triangle arrow) exist between the DAOM and the dura mater (c, d). These cords arose from a crest-shaped connective tissue (dotted line) beneath the DAOM (d). Abbreviations: C1 = atlas; DAOM = dorsal atlanto-occipital membrane; RCDma = rectus capitis dorsalis major muscle



**FIGURE 3** *Columba livia*, hematoxylin–eosin stained sections of the suboccipital region. (a) Oblique section along the RCDmi muscle. (b) a magnification of figure a. (c) Sagittal section of the medial part of the RCDmi muscle. (d) a magnification of figure c. The DAOM runs from the occiput to the arcus of the atlas (C1). The occiput (OCCI) and the RCDmi muscle and tendon send connective tissue fiber bundles (star) that run ventrally and pass (dotted line) through the DAOM (b, d), which emerge on the ventral aspect of the DAOM, receive some connective tissue fibers from the deep aspect of the occiput (arrow head), and continue through the epidural space as cord-like dense connective tissue (arrow) that bifurcates and attaches to the dorsal spinal dura mater (triangle arrow) adjacent to the cerebello-medullary cistern (circle) (b, d). The cervical sinus is shown as a continuation of the occipital sinus (a, c). Abbreviations: DAOM = dorsal atlanto-occipital membrane; OCCI = occiput; R = tendon of the RCDmi muscle; RCDma = rectus capitis dorsalis major muscle; RCDmi = rectus capitis dorsalis minor muscle

arises from the occipital sinus and continues caudally, dorsal to the spinal cord. There are myodural bridge collagenous fibers between these sinuses (Figure 4c).

### 3.2.3 | Sirius red in saturated carbazotic acid sections

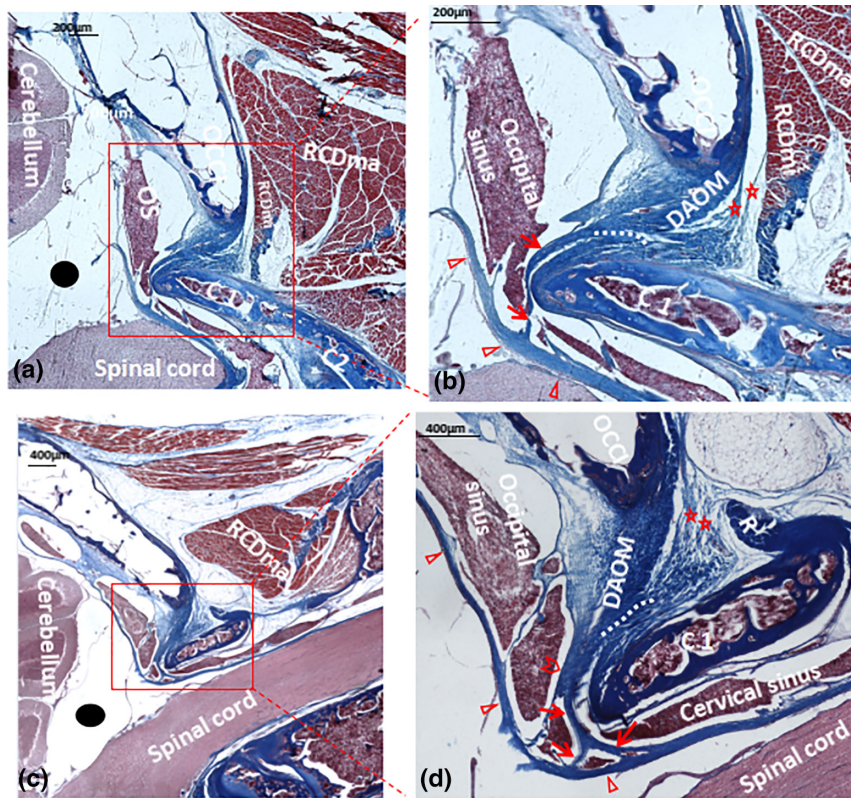
In this staining, connective tissue connecting the *M. rectus capitis dorsalis minor*, dorsal atlanto-occipital membrane, and spinal dura mater are stained dark red. This means that the myodural bridge are collagen fibers (Figure 5a). Using polarizing microscopy, these fibers are red or yellow, which means that they are Type I collagen fibers (Figure 5b,c). The myodural bridge histological features of all the eight specimens were similar.

## 4 | DISCUSSION

The myodural bridge refers to the dense connective tissue structure that connects the *Ligamentum nuchae* and *Mm. rectus capitis posterior minor*, *rectus capitis posterior major* and *obliquus capitis inferior* to the spinal dura mater through the atlanto-occipital and atlanto-axial

interspaces (Hack et al., 1995; Zheng et al., 2014; Scali et al., 2013; Pontell et al., 2013). The existence of this structure in humans is supported by strong evidence (Palomeque-del-Cerro et al., 2017) and has been studied in domestic dogs, finless porpoise, rhesus monkey, rabbit, and rat (Zheng et al., 2017). Thus, it is assumed to be a common structure in placental mammals (Zheng et al., 2017). The present study shows that the myodural bridge exists also in *Columba livia*. Dense connective tissue fibers originating mostly from the ventral aspect of *M. rectus capitis dorsalis minor* run ventrally through the dorsal atlanto-occipital membrane, combine with the connective tissue from the adjoining occiput in the epidural space, and the continuing connective tissue cords then insert into the dorsal cervical spinal dura mater. These bridging structures are composed of closely packed collagen Type I fibers and look like tendons that may resist tension. The cord-like bridging structure bifurcates several times before inserting on the dorsal spinal dura mater, apparently to increase the attachment area on the dura mater.

From an evolutionary point of view, structures that are functionally relevant to an organism are usually preserved (Tsutsumi, Tran, & Cooper, 2017). Conservation of the myodural bridge across the



**FIGURE 4** *Columba livia*, Masson trichrome stained histological section of the suboccipital region. (a) Oblique section along the RCDmi muscle. (b) a magnification of figure a. (c) Sagittal section of the medial part of the RCDmi muscle. (d) a magnification of figure c. The DAOM is a dense connective tissue structure lying between the occiput and atlas. Multiple collagen fibers bundles (star) originating from the occiput, RCDmi muscle and tendon runs ventrally to insert and pass through (dotted lines) the DAOM. Dense collagen fibers emerge on the deep part of the DAOM, receive some connective tissue from the deep side of the occiput (arrow head) and continue ventrally as a cord-like dense collagen bundle (arrow) that bifurcates and attaches to the dorsal spinal dura mater (triangle arrow), adjacent to the cerebello-medullary cistern (circle) (b, d). Abbreviations: DAOM = dorsal atlanto-occipital membrane; OCCI = occiput; OS = occipital sinus; R = tendon of the RCDmi muscle; RCDmi = rectus capitis dorsalis minor muscle

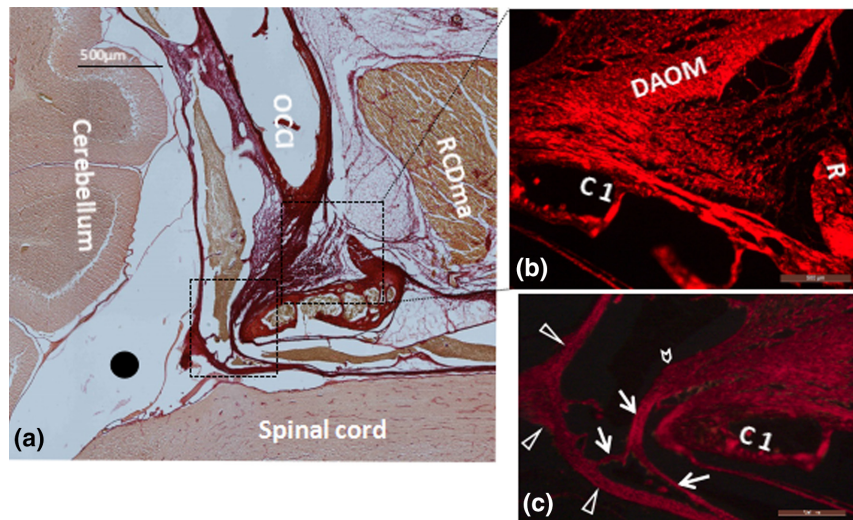
different species of terrestrial vertebrates (sauropsids and mammals) may indicate the functional importance of the myodural bridge. The myodural bridge has been considered to anchor the dura mater, thus, preventing its buckling (Hack et al., 1995; Shinomiya, Dawson, Spengler, Konrad, & Blumenkopf, 1996; Tagil, Ozçakar, & Bozkurt, 2005; Scali et al., 2013).

Considering the location of attachment of the myodural bridge to the dorsal spinal dura mater, adjacent to the cerebello-medullary cistern, which is the largest subarachnoid cistern, we presume that the myodural bridge functions to maintain the integrity of the cerebello-medullary cistern (Scali et al., 2013, 2015) and that the contraction of the myodural bridge via the rectus capitis dorsalis minor muscle may have a function that is related to the circulation of the cerebrospinal fluid (Sui et al., 2013; Xu et al., 2016). A biomechanical study has demonstrated that the contraction of the rectus capitis posterior minor muscle causes posterior displacement of the dura mater via the myodural bridge (Venne et al., 2017). Sui et al. (2013) proposed that the myodural bridge functions as a cerebrospinal fluid pump. They suggested that contractions of the myodural bridge pulls on the dura mater dorsally, thereby decreasing the pressure in the subarachnoid space, which contains the cerebrospinal fluid. This negative pressure

possibly propels cerebrospinal fluid, thus, making the myodural bridge act like a pump that initiates and maintains the flow of the cerebrospinal fluid within the subarachnoid space of the spine.

The myodural bridge of Common Rock Pigeons is composed of closely packed collagen type I fibers, which are found mostly in tendons and have high tensile resistance. Their myodural bridge is thus strong and may produce a significant pull on the spinal dura mater. Following the hypothesis of Sui et al. (2013), the pull of the myodural bridge is likely to provide cerebrospinal fluid propulsion. The Common Rock Pigeon can serve as a good model for testing the hypothesis that myodural bridge can serve as power for cerebrospinal fluid propulsion. However, future biomechanical studies are required to ascertain the function of the myodural bridge in the circulation of cerebrospinal fluid within the subarachnoid space.

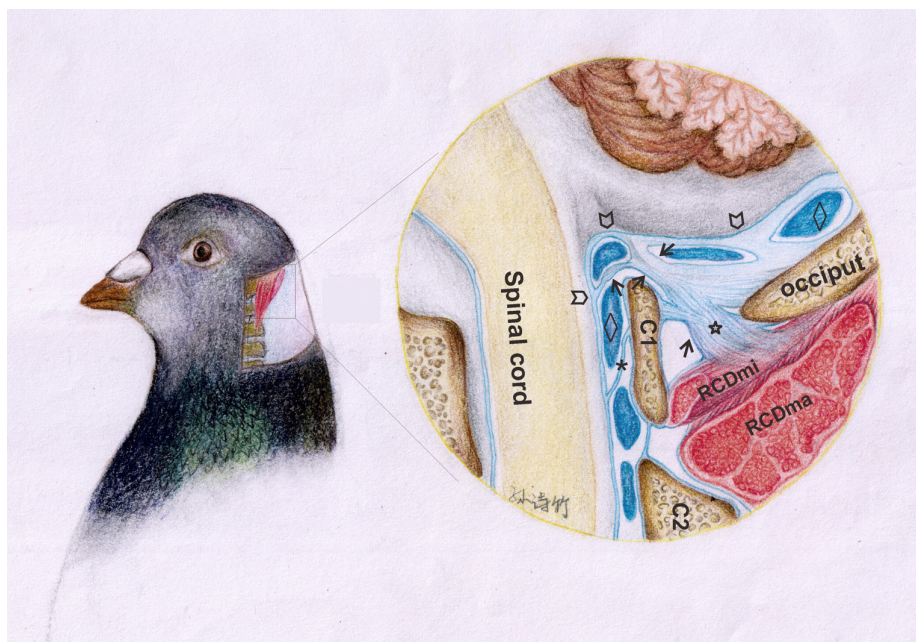
Interestingly, we observed that the myodural bridge in *Columbia livia* and in the Siamese crocodile (Zhang et al., 2016) are similar. In these animals, the myodural bridge connecting with the cervical spinal dura mater are cord-like dense connective tissues, whereas the myodural bridge of humans (Palomeque-del-Cerro et al., 2017) and other mammals (Zheng et al., 2017) consists of dense connective tissue occupying the epidural space. Archosaurs (i.e., birds and crocodiles)



**FIGURE 5** *Columba livia*, sirius red stained (in saturated carbazotic acid) histological sections of the suboccipital region. (a) Light microscopic view of the medial sagittal section. (b, c) magnification of figure b viewed through polarizing microscope. The DAOM (dorsal atlanto-occipital membrane) is made up of dense connective collagen Type I tissues. Dense connective Type I collagen fibers from the RCDmi tendon and the occiput run through the DAOM(B), emerge on its ventral side and receive some dense tissue from the deep aspect of the occiput (arrow head). The bridging collagen Type I tissue continues as a cord-like structure (arrow), which bifurcates before attaching on the dorsal spinal dura mater (triangle arrow) (c). Abbreviations: C1 = atlas; circle = cerebello-medullary cistern; DAOM = dorsal atlanto-occipital membrane; Occi = occiput; R = tendon of RCDmi tendon; RCDmi = rectus capitis dorsalis minor muscle

also have a similar internal vertebral venous plexus (IVVP) pattern. For example, the occipital venous sinus drains into the cervical venous sinus, which continues caudally as a single voluminous spinal vein dorsal to the spinal cord (Baumel, 1975; Zippel, Lillywhite, & Mladinich, 2003). In contrast, the IVVP of terrestrial mammals consists of two longitudinal veins located ventrolaterally in the vertebral canal

(Barnett, Harrison, & Tomlinson, 1958; Hoogland, Vorster, Groen, & Kotze, 2012) so that they possess an anterior IVVP but no posterior IVVP. Although anterior and posterior IVVPs exist in humans, the posterior IVVP is rudimentary in the cervical region, but robust in the thoracolumbar region (Stringer, Restieaux, Fisher, & Crosado, 2012). We hypothesize that the myodural bridge evolved from a cord-like



**FIGURE 6** *Columba livia*, illustration shows the connection between the rectus capitis dorsalis minor muscle and the dura mater. \* = dense fibres of myodural bridge from the rectus capitis dorsalis minor muscle, ↑ = myodural bridge, Δ = dura mater, ◇ = blood in the occipital and cervical sinuses, RCDma = rectus capitis dorsalis major muscle, RCDmi = rectus capitis dorsalis minor muscle

dense connective tissue structure into a dense connective tissue that occupies the epidural space between the dorsal spinal dura mater and the dorsal atlanto-occipital membrane. This modification necessitated a shift of the venous blood flow to the ventrolateral side of the vertebral canal or a reduced posterior IVVP as exemplified in humans. Some researchers have questioned the functional significance of the regional differences in the posterior IVVP in humans (Hoogland et al., 2012). We suggest that the cervical posterior IVVP is reduced to provide more room for the myodural bridge, which was shown in humans to connect the spinal dura mater via the atlanto-occipital and atlanto-axial intervertebral spaces. This may also explain the shift in the venous flow from the dorsal to the ventrolateral aspect of the vertebral canal in other mammals.

Zheng et al. (2014) showed that the atlanto-axial myodural bridge in humans combines with a dense connective complex from the posterior arch of the atlas and the lamina of the axis to connect to the spinal dura mater. Zheng et al. (2014) termed the ligament the vertebro-dural ligament. Scali et al. (2015) demonstrated the existence of similar structures and also showed that the atlanto-occipital myodural bridge combines with ligamentous structures from the posterior arch of the atlas and then connects to the spinal dura mater. Scali et al. (2015) identified the extension from the atlas and axis as dorsal meningo-vertebral ligaments and suggested the term meningo-myovertebral ligament, which describes the structure following the merging of the atlanto-occipital and atlanto-axial myodural bridge with the dorsal meningo-vertebral ligament of the atlas and axis. In the Common Rock Pigeons, the myodural bridge was evident only at the atlanto-occipital interspace and received periosteal connections only from the occiput and not from the vertebral column.

This study has shown that the myodural bridge abuts the cervical sinus. Studies in both humans and other animals have shown that the primary route of blood return from the head during upright position is usually through the internal vertebral plexus. Considering the adjoining position of the myodural bridge with the cervical sinus, we reason that the contractions of the myodural bridge may have an effect on the venous blood flow on the venous blood flow in the cervical sinus.

In conclusion, this study establishes the presence of a myodural bridge in *Columbia livia*, and shows that it is made up of cord-like collagen Type 1 fiber bundles responsible for their high tensile resistance property.

## ACKNOWLEDGMENTS

We thank Dr. Sun ShiZhu for the anatomical illustration in this manuscript. This work was supported by Natural Science Foundation of China (NSFC31600972, NSFC31571234), Liaoning Province Department of Education Funds (L2016012, L2015156).

## AUTHOR CONTRIBUTIONS

S-B. Y., S. H.-J., designed the research, O.C.S and Z.N, data acquisition. O.C.S and S-B. Y. drafted the manuscript. O.C.S., S-B.Y., S. H.-J., critical revision of the manuscript. All authors were involved in data interpretation.

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Okoye CS, Zheng N, Yu S-B, Sui H-J. The myodural bridge in the common rock pigeon (*Columba livia*): Morphology and possible physiological implications. *Journal of Morphology*. 2018;279:1524–1531. <https://doi.org/10.1002/jmor.20890>