Systematic Morphology and Evolutionary Anatomy of the Autonomic Cardiac Nervous System in the Lesser Apes, Gibbons (*Hylobatidae*)

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ABSTRACT

We examined the morphology of the autonomic cardiac nervous system (ACNS) on 20 sides of 10 gibbons (Hylobatidae) of three genera, and we have inferred the evolution of the anatomy of the primate ACNS. We report the following. (1) Several trivial intraspecific and interspecific variations are present in gibbons, but the general arrangement of the ACNS in gibbons is consistent. (2) Although the parasympathetic vagal cardiac nervous system is extremely consistent, the sympathetic cardiac nervous system, such as the composition of the sympathetic ganglia and the range of origin of the sympathetic cardiac nerves, exhibit topographical differences among primates. (3) The vertebral ganglion, seldom observed in the Old World monkeys (Cercopithecidae), was consistently present in gibbons as well as in humans. (4) There are fewer thoracic ganglia contributing to the cervicothoracic ganglion in humans than in gibbons and in gibbons than in Old World monkeys. (5) The superior cardiac nerve originating from the superior cervical ganglion, rarely observed in Old World monkeys but commonly observed in humans, was present in 13 of 20 sides (65%), mostly on the left. Accordingly, the ACNS morphology exhibits evolutionary changes within the primate lineage. These evolutionary differences between Old World monkeys, gibbons, and humans are most parsimoniously interpreted as resulting from regular changes in the lineages leading from their common ancestor to the extant species that we dissected. They include the reduction in the number of thoracic ganglia contributing to the cervicothoracic ganglion and the expansion of the range of the cardiac nervous origin. Anat Rec, 291:939–959, 2008. © 2008 Wiley-Liss, Inc.**

Key words: cardiac nerve; cardiac branch; heart; comparative anatomy; cervical ganglion; vertebral ganglion; cervicothoracic ganglion

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TABLE 1. Examined materials

Species	Specimen no.	Sex	Stage	Institute	Remark
Genus *Hylobates* (2n=44)					
White-handed gibbon (*H. lar*)	No. 1	Male	Adult	Primate Research Institute, Kyoto University, Japan	#970904–7
	No. 2	Male	Infant	Dokkyo Medical University, Japan	
Agile Gibbon (*H. agilis*)	No. 3	Female	Adult	Primate Research Institute, Kyoto University, Japan	
	No. 4	Male	Adult	Dokkyo Medical University, Japan	#791
Müller's gibbon (*H. muelleri*)	No. 5	Male	Infant	Berlin Museum of Natural History, Germany	
(*H. muelleri funereus*)	No. 6	Female	Subadult	Smithsonian National Museum of Natural Hitory, USA	#255967
Genus *Symphalangus* (2n=50)					
Siamang (*S. syndactylus*)	No.7	Male	Adult	Primate Research Institute, Kyoto University, Japan	
	No. 8	Male	Subadult	Smithsonian National Museum of Natural Hitory, USA	#255980
Genus *Nomascus* (2n=52)					
Black crested gibbon (*N. concolor*)	No. 9	Male	Adult	Smithsonian National Museum of Natural Hitory, USA	#397380
	No. 10	Male	Infant	Smithsonian National Museum of Natural Hitory, USA	#538794
Total		20 sides of 10 bodies			

The autonomic cardiac nervous system (ACNS) has been the subject of much biomedical research because it is crucial for important life-maintaining cardiac functions such as heart rate, blood pressure, blood flow, and pain delivery. Our study of the ACNS has been conducted to further knowledge about this system, particularly its evolution.

In a previous study, we revisited the anatomy of the human ACNS to facilitate function-preserving operations aimed at improving patient quality of life (Kawashima, 2005). In that research, numerous variations in humans were explained in terms of their morphogenesis. The topographical changes of the human ACNS which occur in the cases of branchial arterial anomalies such as the retroesophageal right subclavian arteries and the anomalous left vertebral artery originating directly from the aortic arch were also reported (Kawashima and Sasaki, 2005, 2007). We then reported new ACNS arrangements which contradicted the previous theory that the ACNS shifts caudally following ontogenetic changes of the great artery (Horiguchi et al., 1982). These results suggest the importance of morphogenesis in the ACNS. However, numerous points remain to be clarified not only in human ACNS morphology but also in its evolution. It is necessary to examine this evolution using phylogenetic methods based on our research and the descriptive and comparative anatomical investigations conducted by others (van den Broek, 1908; Riegele, 1926; Nonidez, 1939; Kuntz, 1946; Mitchell, 1953; Mizeres, 1955, 1958; Pick, 1970; Fukuyama, 1982; Tanaka et al., 1998; Tanaka et al., 2007).

We have already studied the comparative anatomy of the ACNS in Asian and African Old World monkeys (Cercopithecidae; Kawashima and Sato, 2000; Kawashima et al., 2001, 2005, 2007), finding meaningful morphological differences between humans and Old World monkeys. Although mouse, rat, rabbit, and dog have been used as animal models, it is questionable to extrapolate functional results from these to humans because of their phylogenetic distances. Because Old World monkeys are much closer phylogentically to humans than rats and mice, one can more readily extrapolate functional results from them to humans. To better understand functional experiments, it is essential to examine the morphological differences in the ACNS in various primates and to infer the evolutionary changes that have occurred in the primate lineage. A firm understanding of comparative anatomy can facilitate a more nuanced interpretation of experimental studies.

In our previous reports, the ACNS morphology in the Old World monkeys was found to be different from humans. Consistently, the superior cervical, the middle cervical, and the cervicothoracic (stellate) ganglia (composed of the inferior cervical and the first and second thoracic ganglia), and the third to twelfth (thirteenth) thoracic ganglia were present, but the vertebral ganglion was usually absent. Although the superior, inferior, and thoracic cardiac branches of the parasympathetic vagal cardiac nerves were consistently observed, the sympathetic cardiac nerves tended to have a narrow range of origin. The superior cardiac nerve originating from the superior cervical ganglion was infrequently observed and the thoracic cardiac nerve was rarely present.

These differences between the Old World monkeys and humans raise the following questions. (1) When did the vertebral ganglion consistently appear in primate evolution? (2) How is the composition of the cervicothoracic ganglion associated with primate evolution? When did the thoracic contributions to the cervicothoracic ganglion seen in Old World monkeys change to the reduced contributions from the thoracic ganglia seen in humans, in which they are limited to the inferior cervical and the first thoracic ganglia? (3) When, in primate evolution, did the middle cervical ganglion develop the communicating branches with the spinal cervical nerves? (4) When did the superior cardiac nerve origi-

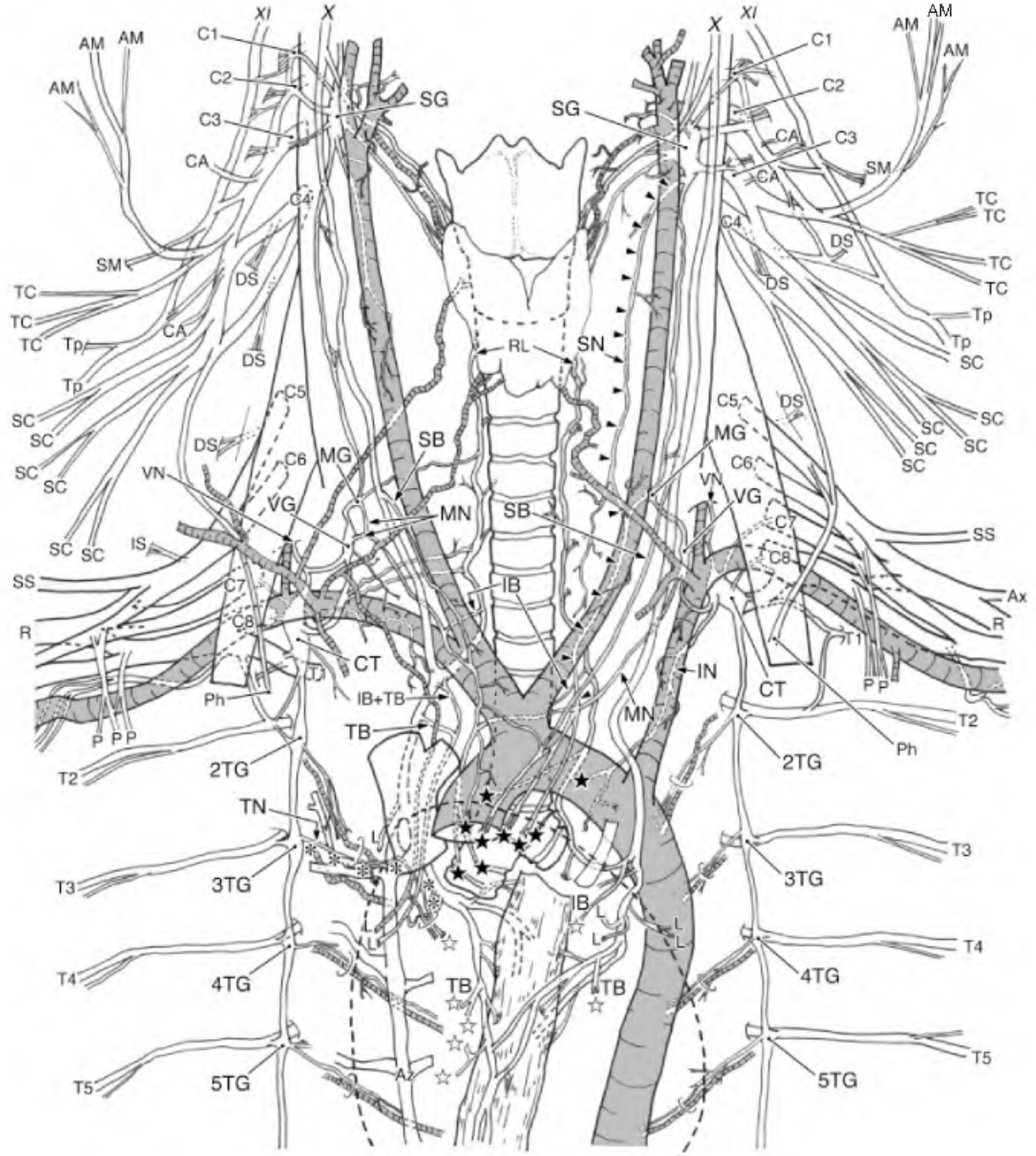

Fig. 1. The autonomic cardiac nervous system and its surrounding structure in the white-handed gibbon (*Hylobates lar*, No. 2). Viewed from the ventral aspect. The black and white stars show the cardiac nerves/branches entering from the arterial and venous parts of the pericardium reflection, respectively. The arrowheads and asterisks show the superior cardiac nerve originating from the superior cervical ganglion and the thoracic cardiac nerve, respectively. AM, greater auricular nerve; Ax, axillary nerve; Az, azygos vein; CA, cervical ansa; CT, cervicothoracic (stellate) ganglion; DS, dorsal scapular nerve; IB, inferior (vagal) cardiac branch; IN, inferior cardiac nerve; IS, subscapular nerve; L, nerve branches to lung; MG, middle cervical ganglion; MN, middle cardiac nerve; P, pectoral nerve; Ph, phrenic nerve; R, radial nerve; RL, recurrent laryngeal nerve of vagus nerve; SB, superior (vagal) cardiac branch; SC, supraclavicular nerve; SG, superior cervical ganglion; SM, nerve branch to sternocleidomastoid muscle; SN, superior cardiac nerve; SS, suprascapular nerve; TB, thoracic (vagal) cardiac branch; TC, transverse cervical nerve; TN, thoracic cardiac nerve; Tp, nerve branch to trapezius muscle; VG, vertebral ganglion; VN, vertebral nerve; *X*, vagus nerve; *XI*, accessory nerve; 2–5TG, second to fifth thoracic ganglia.

nating from the superior cervical ganglion and the thoracic cardiac nerve appear consistently?

To answer these questions, we examined the systematic morphology of 20 sides of 10 gibbons of three genera, summarized the general morphology of the gibbon ACNS, compared it with our and previous reports in primates, and discussed the anatomical differences and the evolutionary changes they represent.

MATERIALS AND METHODS

Materials

Twenty sides of 10 bodies including three genera of the gibbons: Genera *Hylobates* (2n = 44), *Symphalangus* (2n = 50), and *Nomascus* (2n = 52), were used in this study, as shown in Table 1. Specifically, four sides of two white-handed gibbons (*Hylobates lar* [Linnaeus, 1771]), four sides of two Agile gibbons (*H. agilis* [Cuvier, 1821]), four sides of two Müller's Bornean gibbons (*H. muelleri* [Martin, 1841]), four sides of two Siamangs (*Symphalangus syndactylus* [Raffles, 1821]), and four sides of two Black Crested gibbons (*Nomascus concolor* [Harlan, 1826]) were examined. The identification of the gibbons was determined from Groves (2001), Kunimatsu (2003), and Geissmann (1994, 1995, 2007). The taxonomy follows Groves (2005). A phylogeny of the family Hylobatidae is provided by Whittaker et al. (2007), based on the mitochondrial D-loop, behavioral characteristics, and morphological features. They found *Bunopithecus* (not dissected) to be the most basal genus, with the next branch of the tree including the sister groups *Nomascus* and *Symphalangus*, and the terminal branches including the members of the genus *Hylobates*, including the species *H. lar*, *H. muelleri*, and *H. agilis*. All specimens were obtained from museums, institutions, or universities (Table 1) and were fixed by 10% formaldehyde solution by means of the femoral artery and/or preserved in 70% alcohol for more than 10 years.

Dissection Methods

All dissections were performed using forceps for optic surgery (World Precision Instruments, New Haven, CT, Dumont #4) under a neurosurgical stereomicroscope (Olympus, Lake Success, NY, OME 5000) or using a surgical head loupe (OPTAS Co., Osaka, Japan, BMX-40). The major stages were recorded in detailed drawings made from the lateral and ventral aspects in a step-by-step manner to preserve the relationships among the vessels, the nerves, and the surrounding structures. In addition, the dissection steps were documented with digital images taken with a Canon digital camera (Canon, Tokyo, Japan, IXY digital 800IS).

Discrimination of the Fine Peripheral Cardiac Nervous Branches

The intrapericardial peripheral autonomic nerve distribution to the heart was examined with Sudan black stain. After carefully examining the origin and course of the autonomic cardiac nervous system, we removed the heart with the autonomic nerves from the bodies. The specimens were kept overnight at room temperature in Sudan black solution (Sudan black B [Wako Pure Chemical, Japan] 0.5 g and 70% ethyl alcohol to make 1,000 ml). Although this staining method is not specific for the autonomic nerves, it can be used to contrast them with the other connective tissues. It stains all other structures such as muscles, vessels, and connective tissues black, but it stains the nerve fibers a whitish color because only they are covered by nerve sheaths such as the epinerium.

The protocol for the present research did not include any specific issue requiring approval from the Ethics Committees of our university. The present work conformed to the provisions of the 1995 Declaration of Helsinki (revised in Edinburgh, 2000).

Terms: Cardiac Nerves/Branches

Our definitions follow Fukuyama (1982) modified as follows. Within the cardiac nerves connecting to the cardiac plexus or distributing to the heart, each cardiac nerve is named according to its site of origin as follows: *superior cardiac nerves*, cardiac nerves originating from the superior cervical ganglion or the sympathetic trunk between the superior and the middle cervical ganglia; *middle cardiac nerves*, cardiac nerves originating from the (accessory) middle cervical or vertebral ganglia or the sympathetic trunk between the middle and inferior cervical ganglia (or the cervicothoracic ganglion), including the *ansa subclavia*; *inferior cardiac nerves*, cardiac nerves originating from the inferior cervical or cervicothoracic (stellate) ganglia; *thoracic cardiac nerves*, cardiac nerves originating from the thoracic ganglia or the thoracic sympathetic trunk below the inferior cervical or the cervicothoracic ganglia.

Each cardiac branch is named according to its site of origin from a developmental viewpoint, as follows: *superior cardiac branch*, cardiac branch arising from the vagus nerve in the upper (proximal) portion of the recurrent laryngeal nerve; *inferior cardiac branch*, cardiac branch originating from the recurrent laryngeal nerve; and *thoracic cardiac branch*, cardiac branch originating from the vagus nerve in the lower (distal) portion of the recurrent laryngeal nerve.

Fig. 2. The autonomic cardiac nervous system and its surrounding structure in the agile gibbon (*Hylobates agilis*, No. 3). Viewed from the ventral aspect. The black and white stars show the cardiac nerves/branches entering from the arterial and venous parts of the pericardium reflection, respectively. The arrowheads and asterisks show the superior cardiac nerve originating from the superior cervical ganglion and the thoracic cardiac nerve, respectively. AM, greater auricular nerve; aMG, accessory middle cervical ganglion; CA, cervical ansa; CT, cervicothoracic (stellate) ganglion; DS, dorsal scapular nerve; IB, inferior (vagal) cardiac branch; IN, inferior cardiac nerve; IVC, inferior vena cava; L, nerve branches to lung; MG, middle cervical ganglion; MN, middle cardiac nerve; P, pectoral nerve; Ph, phrenic nerve; RL, recurrent laryngeal nerve of vagus nerve; SB, superior (vagal) cardiac branch; SC, supraclavicular nerve; SG, superior cervical ganglion; SM, nerve branch to sternocleidomastoid muscle; SN, superior cardiac nerve; SS, suprascapular nerve; TB, thoracic (vagal) cardiac branch; TC, transverse cervical nerve; TN, thoracic cardiac nerve; Tp, nerve branch to trapezius muscle; VG, vertebral ganglion; VN, vertebral nerve; *X*, vagus nerve; *XI*, accessory nerve; 2–6TG, second to sixth thoracic ganglia.

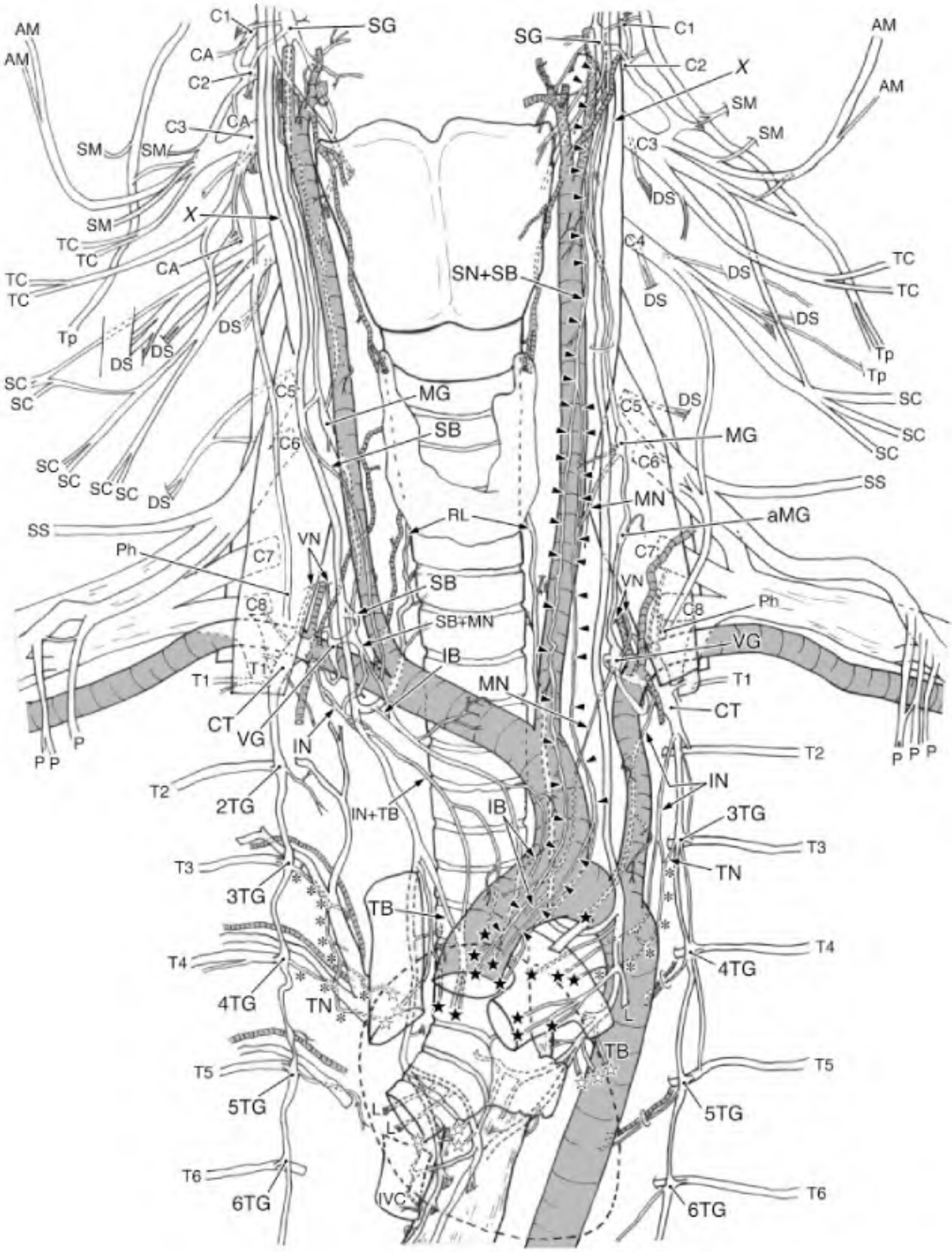

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Figure 2.

RESULTS

Observations

Representative observations for each species are shown in the figures.

White-handed gibbon (Hylobates lar). The superior cervical and middle cervical ganglia, the vertebral ganglion, the cervicothoracic (stellate) ganglion, and the thoracic ganglia are present on both sides (No. 2, Fig. 1). Both cervicothoracic ganglia are composed of the inferior cervical and the first thoracic ganglia.

The superior cervical ganglia communicate with each of the first three cervical nerves (C1–3) and the middle cervical ganglia did not communicate with any cervical nerve. Both vertebral ganglia ramify into the vertebral nerves following the vertebral artery, entering into the foramen transversarium and communicating with some cervical nerves. In addition to branching into the vertebral nerves, the right and the left cervicothoracic ganglia communicate with C7–T2 and C8–T1, respectively.

On the right side, the middle cardiac nerve originates from the middle cervical and vertebral ganglia; the thoracic cardiac nerve originates from the third thoracic ganglion by means of nerves along the azygos vein and right superior vena cava; and the superior cardiac branches, inferior cardiac branches, and thoracic cardiac branches are present. On the left side, the superior cardiac nerve originates from the superior cervical ganglion; the middle cardiac nerves originate from the middle cervical and vertebral ganglia; the inferior cardiac nerves originate from the cervicothoracic ganglion; and the superior cardiac branches, the inferior cardiac branch, and thoracic cardiac branches are present.

Agile gibbon (Hylobates agilis). The superior cervical and middle cervical ganglia, the vertebral ganglion, the cervicothoracic (stellate) ganglion, and the thoracic ganglia are present on both sides (No. 3, Fig. 2). On the left side, an additional ganglion, the accessory middle cervical ganglion, between the middle cervical and cervicothoracic ganglia also is present. The right cervicothoracic ganglia are composed of the inferior cervical and the first thoracic ganglia, whereas the left cervicothoracic ganglia are composed of the inferior cervical and the first and second thoracic ganglia.

The superior cervical ganglia communicate with each of the first two cervical nerves (C1–2) and the (accessory) middle cervical ganglia do not communicate with any cervical nerve. Both vertebral ganglia ramify into the vertebral nerves following the vertebral artery, entering into the foramen transversarium and communicating with some cervical nerves. In addition to branching into the vertebral nerves, the right and the left cervicothoracic ganglia communicate with C8–T1 and C7–T3, respectively.

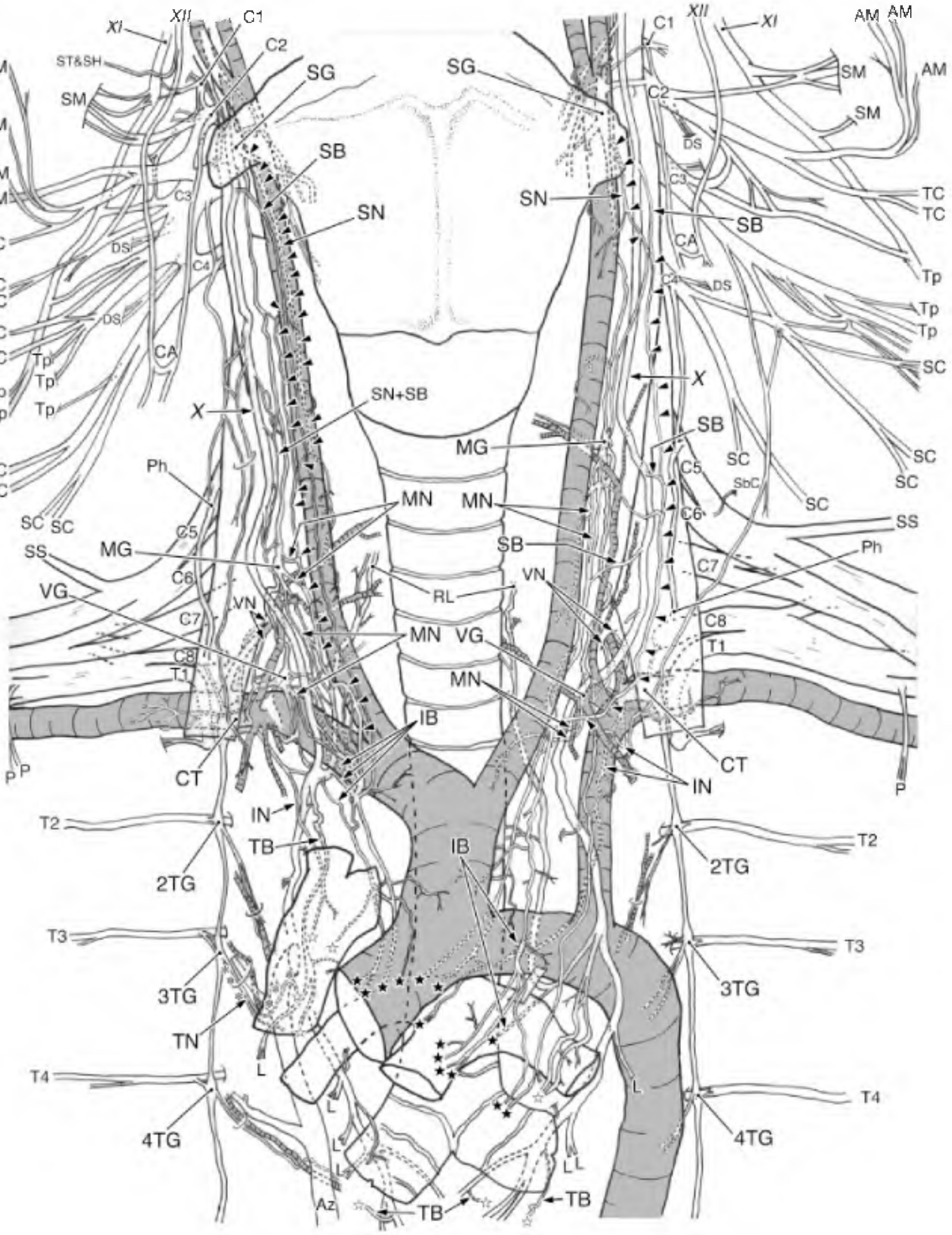
On the right side, the middle cardiac nerves originate from the vertebral ganglion and the sympathetic trunk between the vertebral and cervicothoracic ganglia; the inferior cardiac nerve originates from the cervicothoracic ganglion; the thoracic cardiac nerves originate from the third and fourth thoracic ganglia by means of nerves along the azygos vein and right superior vena cava; and the superior cardiac branches, inferior cardiac branches, and thoracic cardiac branches are present. On the left side, the superior cardiac nerve originates from the superior cervical ganglion; the middle cardiac nerves originate from the middle cervical and vertebral ganglia; the inferior cardiac nerves originate from the cervicothoracic ganglion; the thoracic cardiac nerve originates from the third thoracic ganglion by means of a root the aortic arch; and the superior cardiac branches, the inferior cardiac branch, and thoracic cardiac branches are present.

Müller's Bornean gibbon (Hylobates muelleri). The superior cervical and middle cervical ganglia, in the vertebral ganglion, the cervicothoracic (stellate) ganglion, and the thoracic ganglia are present on both sides (No. 6, Fig. 3). Both cervicothoracic ganglia are composed of the inferior cervical and the first thoracic ganglia.

The right and left superior cervical ganglia communicate with C1–3 and C1–2, respectively. Both middle cervical ganglia did not communicate with any cervical nerve. Both vertebral ganglia ramify into the vertebral nerves following the vertebral artery, entering into the foramen transversarium and communicating with some cervical nerves. In addition to branching into the vertebral nerves, both cervicothoracic ganglia communicate with C8–T1.

On the right side, the superior cardiac nerves originate from the superior cervical ganglion and the sympathetic trunk between the superior and middle cervical ganglia; the middle cardiac nerves originate from the middle cervical and vertebral ganglion; the inferior cardiac nerve originates from the cervicothoracic ganglion; the thoracic cardiac nerve originates from the third thoracic ganglion by means of roots along the azygos vein and right superior vena cava; and the superior cardiac branches, inferior cardiac branches, and thoracic cardiac branches are present. On the left side, the superior cardiac nerve originates from the superior cervical ganglion; the middle cardiac nerves originate from the mid-

Fig. 3. The autonomic cardiac nervous system and its surrounding structure in the Müller's Bornean gibbon (*Hylobates muelleri*, No. 6). Viewed from the ventral aspect. The black and white stars show the cardiac nerves/branches entering from the arterial and venous parts of the pericardium reflection, respectively. The arrowheads and asterisks show the superior cardiac nerve originating from the superior cervical ganglion and the thoracic cardiac nerve, respectively. AM, greater auricular nerve; Az, azygos vein; CA, cervical ansa; CT, cervicothoracic (stellate) ganglion; DS, dorsal scapular nerve; IB, inferior (vagal) cardiac branch; IN, inferior cardiac nerve; L, nerve branches to lung; MG, middle cervical ganglion; MN, middle cardiac nerve; P, pectoral nerve; Ph, phrenic nerve; RL, recurrent laryngeal nerve of vagus nerve; SB, superior (vagal) cardiac branch; SbC, nerve to subclavian muscle; SC, supraclavicular nerve; SG, superior cervical ganglion; SM, nerve branch to sternocleidomastoid muscle; SN, superior cardiac nerve; SS, suprascapular nerve; TB, thoracic (vagal) cardiac branch; TC, transverse cervical nerve; TN, thoracic cardiac nerve; Tp, nerve branch to trapezius muscle; VG, vertebral ganglion; VN, vertebral nerve; *X*, vagus nerve; *XI*, accessory nerve; *XII*, hypogastric nerve; 2–4TG, second to fourth thoracic ganglia.



XI
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Figure 3.

dle cervical and vertebral ganglia and the sympathetic trunk; the inferior cardiac nerves originate from the cervicothoracic ganglion; and the superior cardiac branches, the inferior cardiac branch, and thoracic cardiac branches are present.

Siamang (Symphalangus syndactylus). The superior cervical, middle cervical ganglia, the vertebral ganglion, the cervicothoracic (stellate) ganglion, and the thoracic ganglia are present on both sides (No. 7, Fig. 4). On the left side, an additional ganglion, the accessory middle cervical ganglion, between the superior and middle cervical ganglia also is present. Both cervicothoracic ganglia are composed of the inferior cervical and the first thoracic ganglia.

Both superior cervical ganglia communicate with each of the first two cervical nerves (C1–2). On the right sides, the middle cervical ganglion did not communicate with any cervical nerve, whereas the sympathetic trunk between the middle cervical and vertebral ganglia communicates with C5 and C6. On the left sides, accessory middle and main middle cervical ganglia communicate with C5 and C6, respectively. Both vertebral ganglia ramify into the vertebral nerves following the vertebral artery, entering into the foramen transversarium and communicating with some cervical nerves. In addition to branching into the vertebral nerves, the right and the left cervicothoracic ganglia communicate with C7–T1 and C8–T1, respectively.

On the right side, the middle cardiac nerves originate from the middle cervical and vertebral ganglia; the inferior cardiac nerve originates from the cervicothoracic ganglion; the thoracic cardiac nerves originate from the second and third thoracic ganglia by means of branches along the azygos vein and right superior vena cava; and the superior cardiac branches, inferior cardiac branches, and thoracic cardiac branches are present. On the left side, the superior cardiac nerve originates from the superior cervical ganglion and sympathetic trunk between the superior and middle cervical ganglia; the middle cardiac nerves originate from the (accessory and main) middle cervical and vertebral ganglia; the inferior cardiac nerve originates from the cervicothoracic ganglion; and the superior cardiac branches, the inferior cardiac branch, and thoracic cardiac branches are present.

Black crested gibbon (Nomascus concolor). The superior cervical and middle cervical ganglia, the vertebral ganglion, the cervicothoracic (stellate) ganglion, and the thoracic ganglia are present on both sides (No 9, Fig. 5). On the right side, an additional ganglion, the accessory middle cervical ganglion, between the superior and middle cervical ganglia also is present. Both cervicothoracic ganglia are composed of the inferior cervical and the first thoracic ganglia.

The superior cervical ganglia communicate with each of the first two cervical nerves (C1–2) and the (accessory) middle cervical ganglia did not communicate with any cervical nerve. Both vertebral ganglia ramify into the vertebral nerves following the vertebral artery, entering into the foramen transversarium and communicating with some cervical nerves. In addition to branching into the vertebral nerves, both cervicothoracic ganglia communicate with C8–T1.

On the right side, the middle cardiac nerves originate from the middle cervical and vertebral ganglia; the inferior cardiac nerves originate from the cervicothoracic ganglion; the thoracic cardiac nerve originates from the second thoracic ganglion by means of roots along the azygos vein and right superior vena cava; and the superior cardiac branches, inferior cardiac branches, and thoracic cardiac branches are present. On the left side, the superior cardiac nerve originates from the superior cervical ganglion and sympathetic trunk between the superior and middle cervical ganglia; the middle cardiac nerves originate from the middle cervical and vertebral ganglia; the inferior cardiac nerve originates from the cervicothoracic ganglion; the thoracic cardiac nerve originates from the second thoracic ganglion; and the superior cardiac branches, the inferior cardiac branch, and thoracic cardiac branches are present.

Positions of the Cervical and Upper Thoracic Ganglia and Relationship With the Spinal Nerves

In most cases, three cervical ganglia were present, and one thoracic ganglion around each thoracic spinal nerve outlet was present (Table 2). The inferior cervical ganglion and first thoracic ganglion tend to fuse as the cervicothoracic (stellate) ganglion in the thoracic outlet region.

The superior cervical ganglion is consistently positioned behind (dorsal to) the bifurcation of the common carotid artery and between the first and second cervical vertebrae. The superior cervical ganglion exhibits communicating branches with the spinal nerves on all sides (100%), communicating with C1–2 (14/20 sides, 70.0%) or C1–3 (6/20 sides, 30.0%).

The middle cervical ganglion is situated in the cervical sympathetic trunk and between the fifth and seventh vertebrae. The accessory middle cervical ganglion around the middle cervical ganglion was observed on three sides (15.0%; on the right side in one, on the left side in two). The (accessory) middle cervical ganglion rarely has communicating branches with the lower cervical nerves (1 of 3 sides for the accessory middle cervical ganglion, 33.3%; 1 of 16 sides for the middle cervical ganglion, 6.2%) depending on their positions.

The vertebral ganglion is situated on or medial to the vertebral artery and gives origin to the vertebral nerve. This ganglion was observed in all sides (20/20 sides, 100.0%). Only one side has communicating branches with C5–6, whereas these ganglia always ramified into the vertebral nerve (100.0%).

The cervicothoracic ganglion was observed in all cases (20/20 sides, 100.0%). The cervicothoracic ganglion is composed of the inferior cervical and first thoracic ganglia in 19 of the 20 sides (95.0%), and of the inferior cervical and first and second thoracic ganglia in one side (5.0%). The cervicothoracic ganglion exhibits communicating branches with the spinal nerves on all sides (100.0%), communicating with C7–T1 (3/20 sides, 15.0%), C7–T2 (1/20 sides, 5.0%), C8–T1 (14/20 sides, 70.0%), C8–T2 (1/20 sides, 5.0%) and C7–T3 (1/20 sides, 5.0%).

A vertebral nerve, consisting of a nerve following the vertebral artery and entering into the *foramen transversarium*, does not originate from the (accessory) middle cervical ganglion (0%), but from a vertebral ganglion

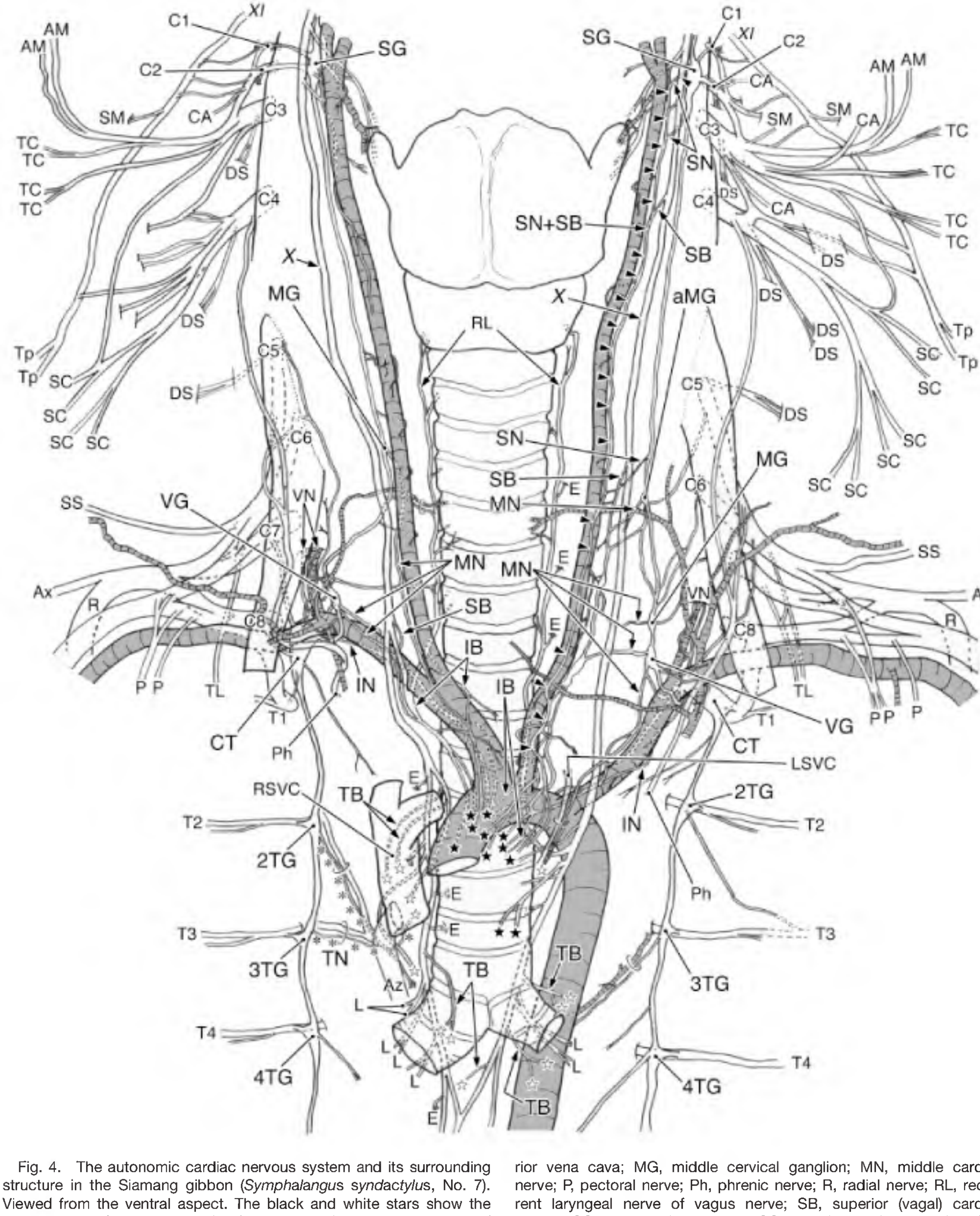
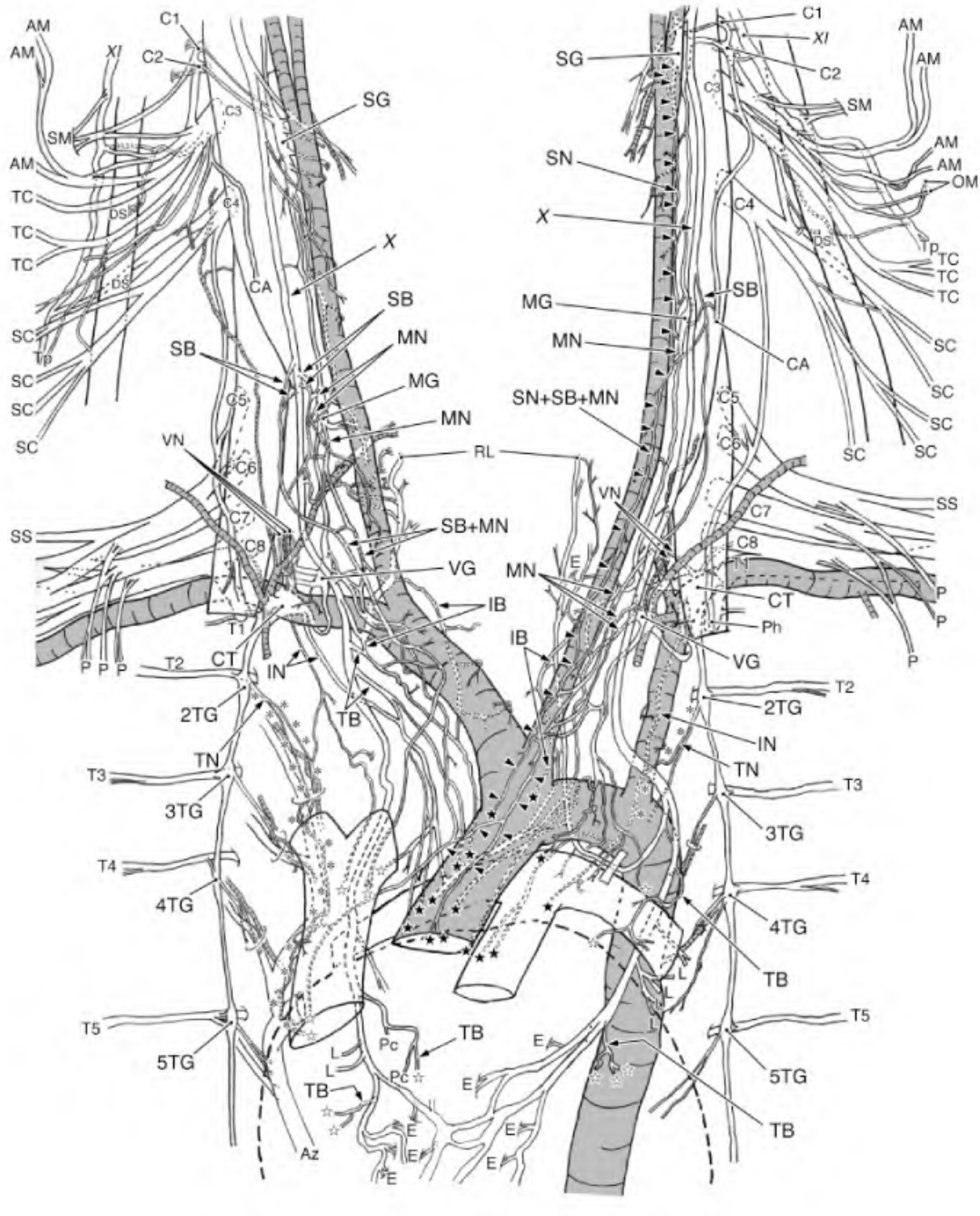


Fig. 4. The autonomic cardiac nervous system and its surrounding structure in the Siamang gibbon (*Symphalangus syndactylus*, No. 7). Viewed from the ventral aspect. The black and white stars show the cardiac nerves/branches entering from the arterial and venous parts of the pericardium reflection, respectively. The arrowheads and asterisks show the superior cardiac nerve originating from the superior cervical ganglion and the thoracic cardiac nerve, respectively. AM, greater auricular nerve; aMG, accessory middle cervical ganglion; Ax, axillary nerve; Az, azygos vein; CA, cervical ansa; CT, cervicothoracic (stellate) ganglion; DS, dorsal scapular nerve; IB, inferior (vagal) cardiac branch; IN, inferior cardiac nerve; L, nerve branches to lung; LSVC, left superior vena cava; MG, middle cervical ganglion; MN, middle cardiac nerve; P, pectoral nerve; Ph, phrenic nerve; R, radial nerve; RL, recurrent laryngeal nerve of vagus nerve; SB, superior (vagal) cardiac branch; SC, supraclavicular nerve; SG, superior cervical ganglion; SM, nerve branch to sternocleidomastoid muscle; SN, superior cardiac nerve; SS, suprascapular nerve; TB, thoracic (vagal) cardiac branch; TC, transverse cervical nerve; TN, thoracic cardiac nerve; TL, lateral thoracic nerve; Tp, nerve branch to trapezius muscle; VG, vertebral ganglion; VN, vertebral nerve; *X*, vagus nerve; *XI*, accessory nerve; 2–4TG, second to fourth thoracic ganglia.



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OM

Figure 5.

(20/20 sides, 100.0%) and the cervicothoracic ganglion on all sides (20/20 sides, 100.0%).

Origins and Frequencies of the Cardiac Nerves/Branches

The superior cardiac nerve originating from the superior cervical ganglion was observed in more than half the sides (13/20 sides, 65.0%; right, 4 sides; left, 9 sides) as shown in Figure 6A–C (Table 3). In addition, the superior cardiac nerve originating from the sympathetic trunk was observed in 10 sides (50%; right 5 sides, left 5 sides).

In contrast, the middle cardiac nerve originating from the middle cervical or the vertebral ganglia was consistently observed in 15 of 16 sides (93.8%) and 20 of 20 sides (100.0%), respectively. Additionally, the middle cardiac nerve originating from the accessory middle cervical ganglion or the sympathetic trunk was also observed in one of three sides (33.3%) and 11 of 20 sides (55.0%), respectively. The inferior cardiac nerve and the thoracic cardiac nerve were observed in 17 sides (85.0%, 7 right sides, 10 left sides) and 13 sides (65.0%; 9 right sides, 4 left sides), respectively. The superior, inferior, and thoracic cardiac branches of the vagus nerve were consistently observed in 19 (95.0%), 20 (100.0%), and 20 sides (100.0%), respectively. Thus, the cardiac nerves and branches are numerous, including the left superior, both middle, both inferior, right thoracic cardiac nerves and all vagal cardiac branches.

Inlet/Outlet of the Cardiac Nerves/Branches From the Pericardium

In innervating the heart, the ACNS enters the heart only through reflected portions of the pericardium, because elsewhere the heart is covered with the pericardium (Fig. 7). The reflected portions of the pericardium are located at the bases of the aorta and pulmonary trunk and the superior and inferior venae cavae and pulmonary veins. A relatively large venous hilum between the oblique and transverse sinuses of the pericardium is present in humans, but it is present only in immature animals in most other primates including gibbons, and in adults a venous hilum is present only at the connection between the right and left pulmonary veins.

In all figures, the cardiac nerves and branches entering and leaving the arterial and venous portions are shown as black stars for arterial and white stars for venous portions.

Generally, the inlet and outlet of the ACNS were distinguishable in two courses. One was a relatively thick descending nerve group originating from the cervical, cervicothoracic sympathetic, and vagal nerves and entering or leaving from the arterial and superior vena cava portions (Fig. 7A,B). The other comprised relatively thin nerves and branches originating from the thoracic sympathetic and vagal nerves that tended to run individually, entering the pulmonary venous portion (Fig. 7C,D).

Intrapericardial Peripheral Cardiac Nervous Distribution

After entering and/or leaving the pericardium, the mixtures of parasympathetic and sympathetic nerve branches run along the great vessels and/or heart muscle itself (Fig. 8). The majority of the arterial portion ran in the groove between the aorta and pulmonary trunk, then formed the coronary plexus around both the coronary arteries, and was distributed to the atriums, ventricles, and coronary plexus depending on the branches of the coronary arteries (Fig. 8A–D).

The majority of the venous group, especially nerve branches from the pulmonary veins, were extremely fine and it was difficult to trace their final distribution at the submacroscopic level. However, the hilum of the venous group was relatively visible. Importantly, numerous large cardiac ganglia, like those seen in humans (Pauza et al., 2000), were observed on the left atrium (Fig. 8E,F).

DISCUSSION

General Morphology of the Sympathetic Ganglia in Gibbons and Comparison With Other Primates

In the comparative anatomical reports of the ACNS in primates, many studies have focused on the relationship between the sympathetic ganglia and the spinal nerves (van den Broek, 1908; Riegele, 1926; Botar, 1932; Kolesnikov, 1935; Zuckerman, 1938; Sheehan and Pick, 1943; Pick, 1970). For lemurs (*Strepsirrhini*) and New World monkeys (*Platyrrhini*), there is only one study by van den Broek (1908), who dissected a black lemur (*Lemur macaco* = *Eulemur macaco*) and a spider monkey (*Ateles ater* = *Ateles paniscus*). In *Eulemur macaco*, the superior cervical ganglion did not communicate with any cervical nerve, the middle cervical ganglion communicated with the vertebral nerve, the vertebral ganglion communicated with C4–C8 by means of the vertebral nerve, and the cervicothoracic ganglia was composed of the inferior cervical and the first and second thoracic ganglia and communicated with T1–T2. In *Ateles paniscus*, the superior cervical ganglion communicated with C1–2, the middle cervical ganglion communicated with C3–6 by means of the vertebral nerve, and the cervicothoracic ganglion was composed of the inferior cervical and the

Fig. 5. The autonomic cardiac nervous system and its surrounding structure in the black crested gibbon (*Nomascus concolor*, No. 9). Viewed from the ventral aspect. The black and white stars show the cardiac nerves/branches entering from the arterial and venous parts of the pericardium reflection, respectively. The arrowheads and asterisks show the superior cardiac nerve originating from the superior cervical ganglion and the thoracic cardiac nerve, respectively. AM, greater auricular nerve; Az, azygos vein; CA, cervical ansa; CT, cervicothoracic (stellate) ganglion; DS, dorsal scapular nerve; IB, inferior (vagal) cardiac branch; IN, inferior cardiac nerve; L, nerve branches to lung; MG, middle cervical ganglion; MN, middle cardiac nerve; OM, minor occipital nerve; P, pectoral nerve; Ph, phrenic nerve; RL, recurrent laryngeal nerve of vagus nerve; SB, superior (vagal) cardiac branch; SC, supraclavicular nerve; SG, superior cervical ganglion; SM, nerve branch to sternocleidomastoid muscle; SN, superior cardiac nerve; SS, suprascapular nerve; TB, thoracic (vagal) cardiac branch; TC, transverse cervical nerve; TN, thoracic cardiac nerve; Tp, nerve branch to trapezius muscle; VG, vertebral ganglion; VN, vertebral nerve; *X*, vagus nerve; *XI*, accessory nerve; 2–5TG, second to fifth thoracic ganglia.

TABLE 2. Sympathetic ganglia

Species		Side	Composition of Ganglia	Comunication between ganglia and spinal nerves
White-handed gibbon (*H. lar*)	No. 1	R	SG,VG,CT(1G+1TG), 2TG-	SG(C1,2), VG(VN), CT(VN,C8,T1), 2TG(T2)-
		L	SG, MG, VG, CT(1G+1TG), 2TG-	SG(C1,2), MG(−), VG(VN), CT(VN,C8,T1), 2TG(T2)-
	No.2	R	SG, MG, VG, CT(1G+1TG), 2TG-	SG(C1,2,3), MG(−), VG(VN), CT(VN,C7,8,T1,2), 2TG(T2)-
		L	SG, MG, VG, CT(1G+1TG), 2TG-	SG(C1,2,3), MG(−), VG(VN), CT(VN,C7,8,T1), 2TG(T2)-
Agile gibbon (*H. agilis*)	No.3	R	SG, MG, VG, CT(1G+1TG), 2TG-	SG(C1,2), MG(−), VG(VN), CT(VN,C8,T1), 2TG(T2)-
		L	SG, MG, aMG, VG, CT(1G+1TG+2TG), 3TG-	SG(C1,2), MG(−), aMG(−), VG(VN), CT(VN,C7,8,T1,2,3), 3TG(T3,4)-
	No.4	R	SG, VG, CT(1G+1TG), 2TG-	SG(C1,2,3), MG(−), VG(VN), CT(VN,C8,T1,2), 2TG(T2)-
		L	SG, MG, VG, CT(1G+1TG), 2TG-	SG(C1,2,3), MG(−), VG(VN), CT(VN,C8,T1), 2TG(T2)-
Müller' gibbon (*H. muelleri*) (*H. muelleri funereus*)	No.5	R	SG, VG, CT(1G+1TG), 2TG-	SG(C1,2), VG(C5,6,VN), CT(VN,C8,T1), 2TG(T2)-
		L	SG, VG, CT(1G+1TG), 2TG-	SG(C1,2), VG(VN), CT(VN,C7,8,T1), 2TG(T2)-
	No.6	R	SG, MG, VG, CT(1G+1TG), 2TG-	SG(C1,2,3), MG(−), VG(VN), CT(VN,C8,T1), 2TG(T2)-
		L	SG, MG, VG, CT(1G+1TG), 2TG-	SG(C1,2), MG(−), VG(VN), CT(VN,C8,T1), 2TG(T2)-
Siamang (*S. syndactylus*)	No.7	R	SG, VG, CT(1G+1TG), 2TG-	SG(C1,2), ST(C5,6), MG(−), VG(VN), CT(VN,C7,8,T1), 2TG(T2)-
		L	SG, aMG, MG, VG, CT(1G+1TG), 2TG-	SG(C1,2), aMG(C5), MG(C6), VG(VN), CT(VN,C8,T1), 2TG(T2)-
	No.8	R	SG, MG, VG, CT(1G+1TG), 2TG-	SG(C1,2), MG(−), VG(VN), CT(VN,C8,T1), 2TG(T2)-
		L	SG, MG, VG, CT(1G+1TG), 2TG-	SG(C1,2), MG(−), VG(VN), CT(VN,C8,T1), 2TG(T2)-
Black crested gibbon (*N. concolor*)	No.9	R	SG, aMG, MG, VG, CT(1G+1TG), 2TG-	SG(C1,2), aMG(−), MG(−), VG(VN), CT(VN,C8,T1), 2TG(T2)-
		L	SG, MG, VG, CT(1G+1TG), 2TG-	SG(C1,2), MG(−), VG(VN), CT(VN,C8,T1), 2TG(T2)-
	No.10	R	SG, MG, VG, CT(1G+1TG), 2TG-	SG(C1,2,3), MG(−), VG(VN), CT(VN,C8,T1), 2TG(T2)-
		L	SG, MG, VG, CT(1G+1TG), 2TG-	SG(C1,2), MG(−), VG(VN), CT(VN,C8,T1), 2TG(T2)-
	Frequency (%)			Communication
Total (20 sides)			SG:20/20 sides (100.0%)	SG: ⟨C1,2⟩: 14/20 sides (70.0%)
				: ⟨C1,2,3⟩: 6/20 sides (30.0%)
			MG: 16/20 sides (80.0%)	ST: ⟨C5,6⟩: 1/20 sides (5.0%)
			aMG: 3/20 sides (15.0%)	: ⟨no communication⟩: 19/20 sides (95.0%)
				aMG: ⟨C5⟩: 1/3 sides (33.3%)
				: no communication: 2/3 sides (66.7%)
			VG: 20/20 sides (100.0%)	MG: ⟨C6⟩: 1/16 sides (6.2%)
				: ⟨no communication⟩: 15/16 sides (93.8%)
			IG: 0/20 sides (0.0%)	VG: ⟨VN⟩: 19/20 sides (95.0%)
				⟨C5,6,VN⟩: 1/20 sides (5.0%)
			CT: 20/20 sides (100.0%)	CT: ⟨VN,C7,8,T1⟩: 3/20 sides (15.0%)
	composition		: 1G+1TG: 19/20 sides (95.0%)	: ⟨VN,C7,8,T1,2⟩: 1/20 sides (5.0%)
			: 1G+1−2TG: 1/20 sides (5.0%)	: ⟨VN,C8,T1⟩: 14/20 sides (70.0%)
				: ⟨VN,C8,T1,2⟩: 1/20 sides (5.0%)
				: ⟨VN,C8,T1,2,3⟩: 1/20 sides (5.0%)

Abbreviations: aMG, accessory middle cervical ganglion; CT, cervicothoracic ganglion; IB, inferior cardiac branch; IG, inferior cervical ganglion; IN, inferior cardiac nerve; MG, middle cervical ganglion; MN, middle cardiac nerve; SB, superior cardiac branch; SG, superior cervical ganglion; SN, superior cardiac nerve; ST, sympathetic trunk; TB, thoracic cardiac branch; TG, thoracic ganglion; TN, thoracic cardiac nerve; VG, vertebral ganglion; VN, vertabral nerve.

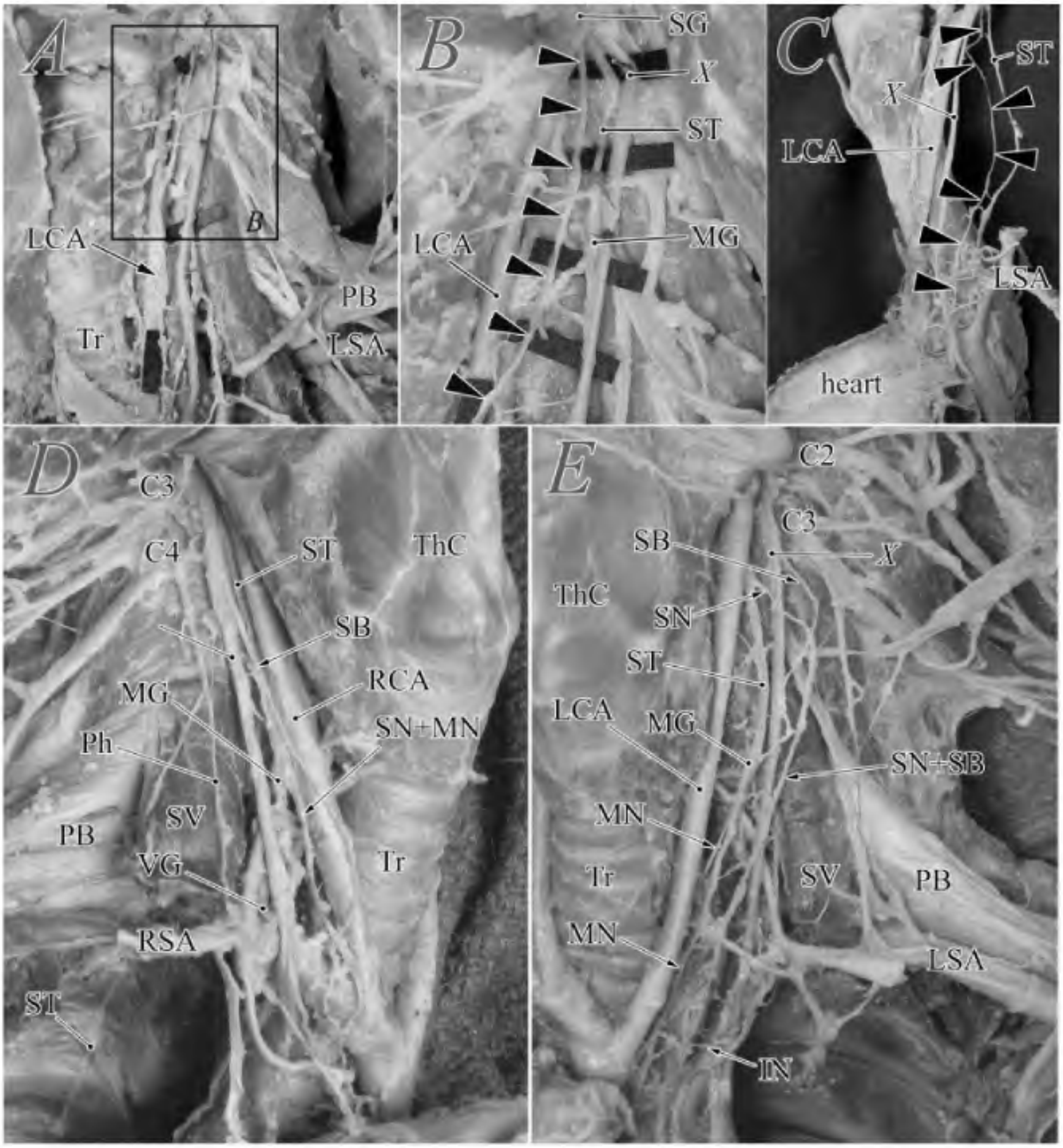

Fig. 6. Photographs showing the autonomic cardiac nervous system (ACNS) in the gibbons. **A:** Left ACNS and its surrounding structures in agile gibbon (No.3). **B:** The regional enlargement of (A). The superior cardiac nerve originating from the superior cervical ganglion as shown in arrowheads. **C:** The left superior cardiac nerve originating from the superior cervical ganglion in the white-handed gibbon (No. 1). En bloc specimen removing from the bony element. **D,E:** The complex relationship among the sympathetic ganglia, cardiac nerves/branches, and surrounding structures in the Müller's gibbon. Viewed from right and left sides, respectively. C2–4, second to fourth cervical nerves; IN, inferior cardiac nerve; LCA, left common carotid artery; LSA, left subclavian artery; MG, middle cervical ganglion; MN, middle cardiac nerve; PB, brachial plexus; Ph, phrenic nerve; RCA, right common carotid artery; RSA, right subclavian artery; SB, superior cardiac branch; SG, superior cervical ganglion; ST, sympathetic trunk; SV, scalenus ventralis muscle; ThC, thyroid cartilage; Tr, trachea; *X*, vagus nerve.

TABLE 3. Appearance of sympathetic cardiac nerves and vagal cardiac branches

			Sympathetic cardiac nerves								Vagal cardiac branches		
		Name	SN		MN				IN	TN			
Species	Case	Side / Origin	SG	ST	aMG	MG	VG	ST	CT	TG	SB	IB	TB
White-handed gibbon (*H. lar*)	No.1	R	(−)	(−)	N	N	(+)	(+)	(+)	(+)	(−)	(+)	(+)
		L	(+)	(+)	N	(+)	(+)	(+)	(+)	(−)	(+)	(+)	(+)
	No.2	R	(−)	(−)	N	(+)	(+)	(−)	(−)	(+)	(+)	(+)	(+)
		L	(+)	(−)	N	(+)	(+)	(−)	(+)	(−)	(+)	(+)	(+)
Agile gibbon (*H. agilis*)	No.3	R	(−)	(−)	N	(−)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
		L	(+)	(−)	(−)	(+)	(+)	(−)	(+)	(+)	(+)	(+)	(+)
	No.4	R	(+)	(+)	N	N	(+)	(+)	(+)	(+)	(+)	(+)	(+)
		L	(+)	(+)	N	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Müller's gibbon (*H. muelleri*)	No.5	R	(+)	(+)	N	N	(+)	(+)	(+)	(−)	(+)	(+)	(+)
		L	(+)	(+)	N	N	(+)	(+)	(+)	(−)	(+)	(+)	(+)
(*H. muelleri funereus*)	No.6	R	(+)	(+)	N	(+)	(+)	(−)	(+)	(+)	(+)	(+)	(+)
		L	(+)	(−)	N	(+)	(+)	(+)	(+)	(−)	(+)	(+)	(+)
Siamang (*S. syndactylus*)	No.7	R	(−)	(−)	N	(+)	(+)	(−)	(+)	(+)	(+)	(+)	(+)
		L	(+)	(+)	(+)	(+)	(+)	(−)	(+)	(−)	(+)	(+)	(+)
	No.8	R	(−)	(+)	N	(+)	(+)	(+)	(−)	(+)	(+)	(+)	(+)
		L	(−)	(−)	N	(+)	(+)	(+)	(+)	(−)	(+)	(+)	(+)
Black crested gibbon (*N. concolor*)	No.9	R	(−)	(−)	(−)	(+)	(+)	(−)	(+)	(+)	(+)	(+)	(+)
		L	(+)	(+)	N	(+)	(+)	(−)	(+)	(+)	(+)	(+)	(+)
	No.10	R	(+)	(+)	N	(+)	(+)	(−)	(−)	(+)	(+)	(+)	(+)
		L	(+)	(−)	N	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Total (20 sides)		Present	13/20	10/20	1/3	15/16	20/20	11/20	17/20	13/20	19/20	20/20	20/20
		Percentage	65.0%	50.0%	33.3%	93.8%	100.0%	55.0%	85.0%	65.0%	95.0%	100.0%	100.0%

Abbreviations: aMG, accessory middle cervical ganglion; CT, cervicothoracic ganglion; IB, inferior cardiac branch; IN, inferior cardiac nerve; MG, middle cervical ganglion; MN, middle cardiac nerve; SB, superior cardiac branch; SG, superior cervical ganglion; SN, superior cardiac nerve; ST, sympathetic trunk; TB, thoracic cardiac branch; TG,thoracic ganglion; TN, thoracic cardiac nerve; VG, vertebral ganglion.
(+) and (−), presence and absence of structures.
*N, ganglion was absent.

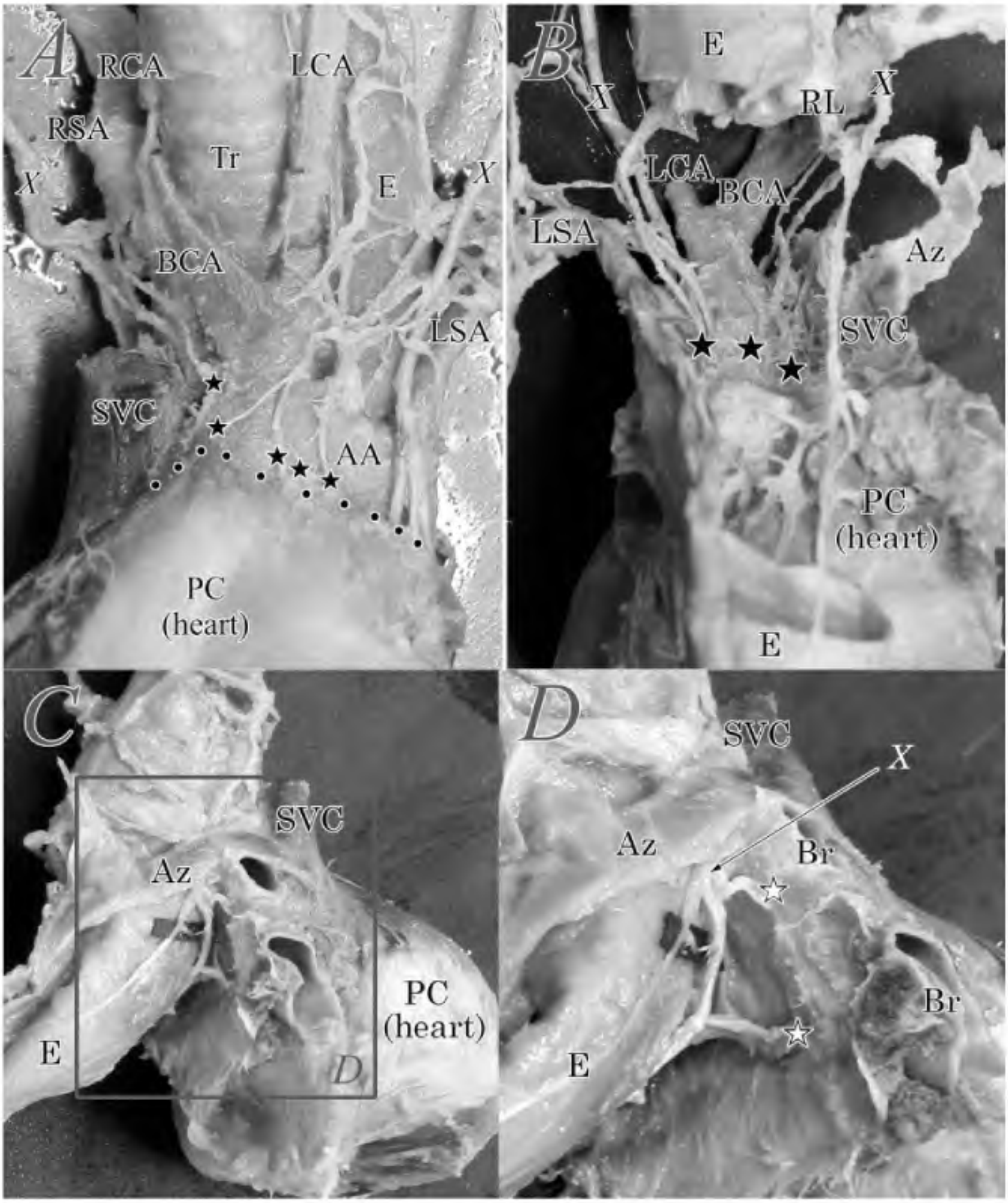

Fig. 7. The relationship between the autonomic cardiac nervous system (ACNS) and pericardium. The black and white stars show the cardiac nerves/branches entering from the arterial and venous portions of the reflecting portion of the pericardium, respectively. **A:** Ventral arterial portion. The dots show the reflecting portion of the pericardium. **B:** Dorsal arterial portion. **C:** Right venous portion. Viewed from right lateral side. **D:** The enlargement of (C). AA, aortic arch; Az, azygos vein; BCA, brachiocephalic artery; Br, bronchus; E, esophagus; LCA, left common carotid artery; LSA, left subclavian artery; PC, pericardium; RCA, right common carotid artery; RL, recurrent laryngeal nerve of vagus nerve; RSA, right subclavian artery; SVC, superior vena cava; Tr, trachea; *X*, vagus nerve.

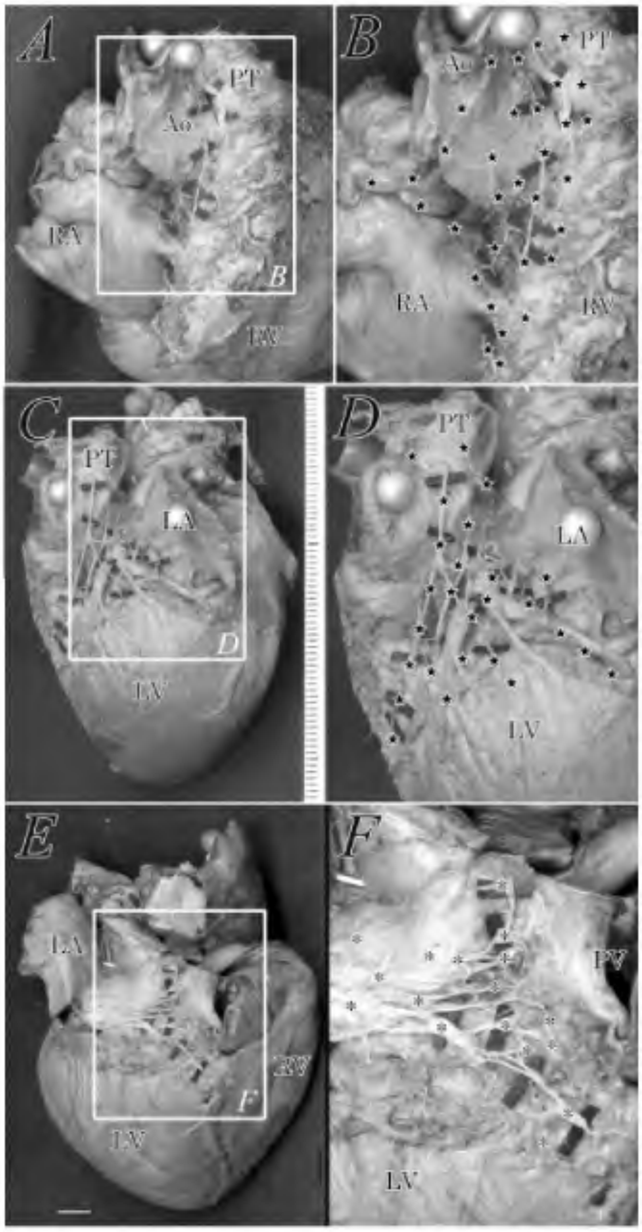

Fig. 8. Intraperipheral cardiac nerovous distribution as shown in black stars. **A,B:** Right coronary plexus entering from the arterial portion. Viewed from the right lateral side. **C,D:** left coronary plexus entering from the arterial portion. Viewed from the left lateral side. **E,F:** Dorsal cardiac plexus and its cardiac ganglia entering from the cardiac hilum and venous portions were indicated by asterisks. Viewed from dorsal aspect. Scale bar = 5 mm. Ao, aorta; LA, left atrium; LV, left ventricle; PT, pulmonary trunk; PV, pulmonary vein; RA, right atrium; RV, right ventricle.

first and second thoracic ganglia and communicated with C6–T2 by means of the vertebral nerve.

In contrast, there are many detailed descriptions and diagrams of the ACNS in Old World monkeys (van den Broek, 1908; Riegele, 1926; Zuckerman, 1938; Sheehan and Pick, 1943; Pick, 1970, Kawashima and Sato, 2000; Kawashima et al., 2005, 2007). Most of these authors stated consistently that the middle cervical ganglion in Old World monkeys had no communicating branches with any cervical nerve, but some variation may exist, since Riegele (1926) stated that the middle cervical ganglion communicated with C4–5 in one rhesus monkey and with C(3)4–5 in some baboons. We conclude that the following anatomical patterns are typical of the Old World monkeys. The superior cervical ganglion communicates with C1–2(3), the middle cervical ganglion does not communicate with any cervical nerves, the cervicothoracic ganglion is composed of the inferior cervical, first thoracic, and second thoracic ganglia and communicates with C8–T2 in addition to the vertebral nerve, and the third to twelfth (thirteenth) thoracic ganglia communicate each with its segmental thoracic nerve.

A few studies have been conducted on the gibbons and great apes (van den Broek (1908), who dissected a white-handed gibbon [*Hylobates lar*) and an orangutan (*Pongo pygmaeus*); Botar (1932), a gorilla (*Gorilla gorilla*); Kolensnikov (1935), a chimpanzee (*Pan sp.*) and an orangutan]. According to van den Broek (1908), the superior cervical ganglion communicated with C1–3, the middle cervical ganglion communicated with C3–4, and the cervicothoracic ganglion was composed of the inferior cervical and the first and second thoracic ganglia and communicated with C5–T2 in the white-handed gibbon. In the orangutan, the superior cervical ganglion communicated with C1–3, two middle cervical ganglia did not communicate with any cervical nerve, the ganglion corresponding to the vertebral ganglion communicated with C7–8, and a single inferior cervical ganglion communicated with C4–6 by means of the vertebral nerve and C7–T1. According to Botar (1932), on the right side of the gorilla, the superior cervical ganglion communicated with C1–3, the middle cervical ganglion did not communicate with any cervical nerve, the vertebral ganglion (inferior cervical) communicated with C5–6, and the cervicothoracic ganglion was composed of the inferior cervical and first thoracic ganglia and communicated with C5–T2, but on the left side the superior cervical ganglion communicated with C1–2, the middle cervical ganglion did not communicate with any cervical nerve, the vertebral ganglion communicated with C4–6, and the cervicothoracic ganglion was composed of the inferior cervical and first thoracic ganglia and communicated with C4–T1.

According to Kolesnikov (1935), on the left side of a chimpanzee, the superior cervical ganglion communicated with C1–3, the middle cervical ganglion communicated with C4–5, and the cervicothoracic ganglion communicated with some unidentified cervical nerves, and on the left side of orangutan, the superior cervical ganglion communicated with C1–3, the middle cervical ganglion communicated with C4, the vertebral ganglion communicated with C6–7, and the cervicothoracic ganglion communicated with some unidentified cervical nerves. So, these authors disagree among themselves on a pattern among the great apes, suggesting variation in the pattern or inaccurate anatomical observations.

Van den Broek's (1908) observations disagree with ours regarding the relationship between the middle cervical ganglion and the cervical nerves for gibbons. His study was based on one specimen of *Hylopetes lar*, whereas our results are based on 20 sides of 10 gibbons including three genera and are consistent. Hence, we summarize the general morphology of the gibbon's sym-

TABLE 4. Comparison of sympathetic ganglia and their communicating branches

Ganglia	Asian Old World monkeys Kawashima et al. (2005) 42 sides	African Old World monkeys Kawashima et al. (2007) 22 sides	Gibbons present study 20 sides	Humans Kawashima (2005) 36 sides
SG	42/42 (100.0%)	22/22 (100.0%)	20/20 (100.0%)	36/36 (100.0%)
⟨communication between SG and spinal nerve⟩				
C1	42/42 (100.0%)	22/22 (100.0%)	20/20 (100.0%)	36/36 (100.0%)
C2	42/42 (100.0%)	22/22 (100.0%)	20/20 (100.0%)	36/36 (100.0%)
C3	16/42 (38.1%)	12/22 (54.5%)	6/20 (30.0%)	26/36 (72.2%)
C4	0/42 (0.0%)	0/22 (0.0%)	0/20 (0.0%)	1/36 (2.8%)
MG	42/42 (100.0%)	22/22 (100.0%)	16/20 (80.0%)	33/36 (91.7%)
⟨Communication between MG and spinal nerve⟩				
C3	0/42 (0.0%)	0/22 (0.0%)	0/16 (0.0%)	11/33 (33.3%)
C4	1/42 (2.4%)	0/22 (0.0%)	0/16 (0.0%)	29/33 (87.9%)
C5	1/42 (2.4%)	0/22 (0.0%)	1/16 (6.2%)	20/33 (60.6%)
C6	0/42 (0.0%)	0/22 (0.0%)	1/16 (6.2%)	5/33 (15.2%)
VN	14/42 (33.3%)	3/22 (13.6%)	0/16 (0.0%)	0/33 (0.0%)
VG	0/42 (0.0%)	1/22 (4.5%)	20/20 (100.0%)	34/36 (94.4%)
⟨Communication between VG and spinal nerve⟩				
C4	N/A	0/1 (0.0%)	0/20 (0.0%)	1/34 (2.9%)
C5	N/A	0/1 (0.0%)	1/20 (5.0%)	2/34 (5.9%)
C6	N/A	0/1 (0.0%)	1/20 (5.0%)	3/34 (8.8%)
C7	N/A	0/1 (0.0%)	0/20 (0.0%)	6/34 (17.6%)
VN	N/A	1/1 (100.0%)	20/20 (100.0%)	26/34 (76.5%)
IG	2/42 (4.8%)	1/22 (4.5%)	0/20 (0.0%)	5/36 (13.9%)
CT	40/42 (95.2%)	21/22 (95.5%)	20/20 (100.0%)	31/36 (86.1%)
(1G+1TG)	(8/42 [19.0%])	(5/22 [22.7%])	(19/20 [95.0%])	(30/36 [83.3%])
(1G+1−2TG)	(29/42 [69.0%])	(16/22 [72.7%])	(1/20 [5.0%])	(1/36 [2.8%])
(1G+1−3TG)	(3/42 [7.1%])	(0/22 [0.0%])	(0/20 [0.0%])	(0/36 [0.0%])
⟨Communication between IG/CT and spinal nerve⟩				
VN	42/42 (100.0%)	22/22 (100.0%)	20/20 (100.0%)	34/36 (94.4%)
C5	0/42 (0.0%)	0/22 (0.0%)	0/20 (0.0%)	2/36 (5.6%)
C6	1/42 (2.4%)	0/22 (0.0%)	0/20 (0.0%)	4/36 (11.1%)
C7	6/42 (14.3%)	3/22 (13.6%)	5/20 (40.0%)	27/36 (75.0%)
C8	41/42 (97.6%)	22/22 (100.0%)	20/20 (100.0%)	36/36 (100.0%)
T1	42/42 (100.0%)	21/22 (95.5%)	20/20 (100.0%)	36/36 (100.0%)
T2	38/42 (90.5%)	18/22 (81.8%)	3/20 (15.0%)	25/36 (69.4%)
T3	3/42 (7.1%)	2/22 (9.1%)	1/20 (5.0%)	1/36 (2.8%)

Abbreviations: CT, cervicothoracic ganglion; IB, inferior cardiac branch; IG, inferior cervical ganglion; IN, inferior cardiac nerve; MG, middle cervical ganglion; MN, middle cardiac nerve; SB, superior cardiac branch; SG, superior cervical ganglion; SN, superior cardiac nerve; ST, sympathetic trunk; TB, thoracic cardiac branch; TG,thoracic ganglion; TN, thoracic cardiac nerve; VG, vertebral ganglion; VN, vertebral nerve.

pathetic ganglia as follows: the superior cervical ganglion communicates with C1–2(3), the (accessory) middle cervical ganglion normally has no communication with any cervical nerve, the vertebral ganglion ramifies into the vertebral nerve which communicates with the lower cervical nerves, the cervicothoracic (stellate) ganglion is composed of the inferior cervical and first thoracic ganglia and communicates with C8–T1(2) in addition to ramifying into the vertebral nerve, and the second to twelfth (thirteenth) thoracic ganglia each communicate with its segmental thoracic nerve.

Therefore, the general morphology of the sympathetic ganglia in gibbons is similar to that in humans rather than to that in the Old World monkeys (Cercopithecidae); although, the middle cervical ganglion in the gibbons differs from that in humans in terms of having no communication with any cervical nerve (Table 4).

When Did the Vertebral Ganglion Appear in Primate Evolution?

The ontogeny and phylogeny of the vertebral ganglion have been discussed in several studies. A major ontogenetic question is whether the vertebral ganglion belongs to or originates from the middle cervical ganglion (Axford, 1927–28; Woodlard and Norrish, 1933; Wrete, 1959) or from the inferior cervical ganglion (the upper part of the cervicothoracic ganglion) as suggested by Lazorthes and Cassan (1939) and Guerrier (1944). To resolve this developmental problem, it will be necessary to observe the ontogeny of the vertebral ganglion in primate embryos, but it will be difficult to obtain the necessary series of primate embryos in differing stages of development. In addition, it is unknown whether the vertebral ganglion develops consistently in nonhuman primates within species, within genera, and within higher taxa. Therefore, we consider the problem of the origin of the vertebral ganglion based on the gross comparative anatomy of nonhuman primates and on normal human development (see details, Kawashima et al., 2007). It has been necessary to conduct additional gross anatomical studies of the vertebral ganglion in various primates because previous research has been fragmentary and has been based on few specimens.

Van den Broek (1908) examined the sympathetic cardiac nervous system using 25 mammalian species

TABLE 5. Comparison of frequencies of cardiac nerves and branches

Cardiac nerve/branch	Origin	Asian old world monkeys Kawashima et al. (2005) 42 sides	African old world monkeys Kawashima et al. (2007) 22 sides	Gibbons present study 20 sides	Humans Kawashima et al. (2007) 52 sides
⟨Sympathetic cardiac nerves⟩					
SN	SG	0/42 (0.0%)	1/22 (4.5%)	13/20 (65.0%)	46/52 (88.5%)
	ST	19/42 (45.2%)	14/22 (63.6%)	10/20 (50.0%)	37/52 (71.2%)
MN	MG	40/42 (95.2%)	22/22 (100.0%)	15/16 (93.8%)	43/49 (87.8%)
	VG	0/0 (0.0%)	0/1 (0.0%)	20/20 (100.0%)	43/50 (86.0%)
	ST	17/42 (40.5%)	11/22 (50.0%)	11/20 (55.0%)	40/52 (76.9%)
IN	IG/CT	19/42 (45.2%)	20/22 (90.9%)	13/20 (65.0%)	43/50 (86.0%)
TN	TG	3/42 (7.1%)	13/22 (59.1%)	13/20 (65.0%)	35/52 (67.3%)
⟨Parasympathetic vagal cardiac branches⟩					
SB	*	38/42 (90.5%)	22/22 (100.0%)	19/20 (95.0%)	52/52 (100.0%)
IB	RL	38/42 (90.5%)	22/22 (100.0%)	20/20 (100.0%)	52/52 (100.0%)
TB	**	37/42 (88.1%)	22/22 (100.0%)	20/20 (100.0%)	43/52 (82.7%)

Abbreviations: CT, cervicothoracic ganglion; IB, inferior cardiac branch; IG, inferior cervical ganglion; IN, inferior cardiac nerve; MG, middle cervical ganglion; MN, middle cardiac nerve; RL, recurrent laryngeal nerve; SB, superior cardiac branch; SG, superior cervical ganglion; SN, superior cardiac nerve; ST, sympathetic trunk; TB, thoracic cardiac branch; TG,thoracic ganglion; TN, thoracic cardiac nerve; VG, vertebral ganglion.
*The vagua nerve in the upper (proximal) portion of the recurrent laryngeal nerve.
**The vagus nerve in the lower (distal) portion of the recurrent laryngeal nerve.

including 7 primates. Although he did not use the term "vertebral ganglion," he seems to have observed it only in one orangutan and not seen it in humans and other primates including a white-handed gibbon. Little is known about the ACNS in the great apes (the orangutan was studied by Sonntag [1924]; the gorilla by Botar [1932]; and the orangutan and chimpanzee by Kolesnikov [1935]). The vertebral ganglion was described only in an orangutan and a chimpanzee by Kolesnikov (1935).

In our previous study of the ACNS in primates (Kawashima and Sato, 2000; Kawashima, 2005; Kawashima et al., 2005, 2007), the vertebral ganglion was present in one Angola colobus (*Colobus angolensis ruwenzori*) out of 64 sides (3.1%) in Old World monkeys and 34 (94.4%) out of 36 sides in humans. In this research, the vertebral ganglion was observed in all sides (100.0%) of the gibbons including three genera. Therefore, according to the phylogeny, it would seem that the vertebral ganglion developed as a normal feature in the common ancestor of gibbons, great apes, and humans.

Segmental Contribution of the Thoracic Ganglia to the Cervicothoracic Ganglion

As described in the results section, there is variation in the composition of the cervicothoracic ganglion. In a variety of Old World monkeys, Zuckerman (1938) described the general morphology of the cervicothoracic ganglion as composed of the inferior cervical, the first thoracic, and the second thoracic ganglia in 16 of 22 sides (72.7%).

In our previous study on Asian macaques (*Macaca: Cercopithecinae*; Kawashima and Sato, 2000; Kawashima et al., 2005), a single inferior cervical ganglion was unfused to any thoracic ganglia in 2 of 42 sides (4.2%), and a cervicothoracic ganglion composed of the inferior cervical and first thoracic ganglia in 8 of 42 sides (19.0%), a cervicothoracic ganglion composed of the inferior cervical, first thoracic, and second thoracic ganglia in 29 sides (69.0%), and a cervicothoracic ganglion composed of the inferior cervical, first thoracic, second thoracic, and third thoracic ganglia in 3 of 42 sides (7.1%). In another study on African Old World monkeys, which included both cercopithecines and colobines (Kawashima et al., 2007), the inferior cervical ganglion was unfused to any thoracic ganglia in 1 of 22 sides (4.5%), and a cervicothoracic ganglion was composed of the inferior cervical and first thoracic ganglia in 5 sides (22.7%), and a cervicothoracic ganglion was composed of the inferior cervical, first thoracic, and second thoracic ganglia in 16 of 22 sides (72.7%). Therefore, the general pattern among extant species and the primitive composition of the cervicothoracic ganglion in Old World monkeys were the inferior cervical, first thoracic, and second thoracic ganglia.

In humans, the contributing thoracic ganglion segmentation to the cervicothoracic ganglion is narrower than that in Old World monkeys (Kawashima, 2005). A single inferior cervical ganglion was observed in 5 sides (13.9%), a cervicothoracic ganglion composed of the inferior cervical and first thoracic ganglia in 31 sides (86.1%), and a cervicothoracic ganglion composed of the inferior cervical, first thoracic, and second thoracic ganglia in one of 36 sides (2.8%).

In the great apes, the normal variation in the contributing thoracic ganglion segmentation to the cervicothoracic ganglion is not detectable. Thus, whether the great ape pattern is more similar to Old World monkeys or humans remains unclear.

In the present study, some variation of the composition of the cervicothoracic ganglion in gibbons was found. It was never a single inferior cervical ganglion; it was a cervicothoracic ganglion composed of the inferior cervical and first thoracic ganglia in 19 sides (95.0%); and it was a cervicothoracic ganglion composed of the inferior cervical, first thoracic, and second thoracic ganglia in one of 20 sides (5.0%).

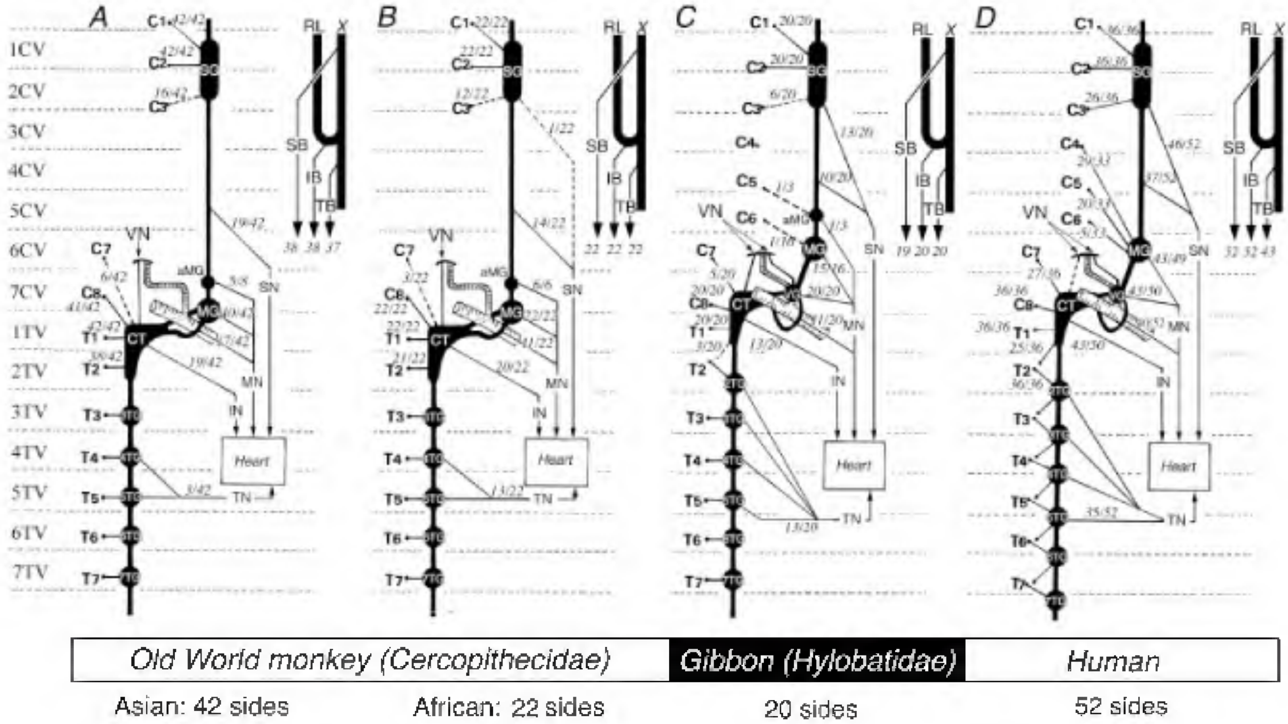

Fig. 9. Schematic representation of comparative and evolutionary anatomical similarities and differences in the autonomic cardiac nervous system. The large left and small right figures show the sympathetic and parasympathetic vagal cardiac systems, respectively. **A:** Asian Old World monkeys (Macaca, Cercopithecidae), 42 sides (Kawashima and Sato, 2000; Kawashima et al., 2005). **B:** African Old World monkeys (Cercopithecidae), 22 sides (Kawashima et al., 2007). **C:** Gibbons (Hylobatidae), 20 sides (present study). **D:** Human, 36 sides (Kawashima, 2005; Kawashima and Sasaki, 2007). Differences in the sympathetic (cardiac) system of Old World monkeys, gibbons, and humans are recognized, despite the similar morphology of the parasympathetic vagal (cardiac) system. These differences include the reduced composition of the cervicothoracic ganglion, the higher positions of the middle cervical and cervicothoracic ganglia, and the expanded origin of the cardiac nerves from Cercopithecidae to humans. aMG, accessory middle cervical ganglion; CT, cervicothoracic (stellate) ganglion; IB, inferior (vagal) cardiac branch; IG, inferior cervical ganglion; IN, inferior cervical cardiac nerve; MG, middle cervical ganglion; MN, middle cardiac nerve; RL, recurrent laryngeal nerve of vagus nerve; SB, superior (vagal) cardiac branch; SG, superior cervical ganglion; SN, superior cardiac nerve; TB, thoracic (vagal) cardiac branch; TN, thoracic cardiac nerve; VG, vertebral ganglion; VN, vertebral nerve; *X*, vagus nerve; 1CV–7TV, first cervical to seventh thoracic vertebrae; 2–7TG, second to seventh thoracic ganglia.

These results suggest that the general composition of the cervicothoracic ganglia in the gibbons is intermediate between those in Old World monkeys and humans and that there is a trend toward a reduction in the number of segments contributing to the ganglion in the primate lineage leading to humans.

General Contribution of the Cardiac Nerves/ Branches in Gibbons

When does the superior cardiac nerve appear in primate evolution? The anatomy of the ACNS has been studied in a variety of primates (van den Broek, 1908; Sonntag, 1922, 1924; Riegele, 1926; Botar, 1932; Kolesnikov, 1935; Zuckerman, 1938; Pick, 1970; Kawashima and Sato, 2000; Kawashima et al., 2005, 2007), but authors used different definitions for parts of the ACNS. Despite this, we were able to compare their results with ours based on their descriptions and figures. The superior, inferior, and thoracic cardiac branches of the parasympathetic vagus nerve were consistently observed in most species, but the sympathetic cardiac nerves tend to have a narrow origin similar to the lack of the superior and thoracic cardiac nerves in the Lemurs and New and Old World monkeys (van den Broek, 1908; Sonntag, 1922; Kawashima and Sato, 2000; Kawashima et al., 2005, 2007).

However, in the great apes and gibbons, descriptions of the ACNS vary among authors (van den Broek, 1908; Sonntag, 1924; Botar, 1932; Kolesnikov, 1935). The descriptions of the origins of the cardiac nerves, particularly the superior cardiac nerve arising from the superior cervical ganglion, differ. Moreover, some authors state that, in the apes the superior cardiac nerve originates from the superior cervical ganglion (gorilla by Botar, 1932; orangutan by Kolesnikov, 1935), whereas other authors oppose this view (white-handed gibbon and orangutan by van den Broek, 1908; orangutan by Sonntag, 1924; chimpanzee, Kolesnikov, 1935). Thus, it is necessary to examine the ACNS in gibbons and great apes to evaluate the previous literature.

When examining the ACNS in a variety of gibbons, we paid special attention to the cardiac nerves and branches, noting how frequently the superior cardiac nerve originated from the superior cervical ganglion and the thoracic cardiac nerve originated from the thoracic ganglia. In our previous studies of the sympathetic cardiac nerves in the Old World monkeys, there were fewer origins than in humans.

In the gibbons, the superior cardiac nerve originated from the superior cervical ganglion and the thoracic cardiac nerves originated from the thoracic ganglion in more than half the sides, and also the other sympathetic cardiac nerves and all the parasympathetic vagal cardiac branches were consistently present (Table 5). However, these two uppermost and lowest cardiac nerves tend to differ between sides. The left superior cardiac and right thoracic cardiac nerves were consistently observed, but the opposite side was rarely observed. This observation agreed with Schumacher (1902) which stated that only the left superior cardiac nerves were present in monkeys. In contrast, the superior and thoracic cardiac nerves are observed bilaterally consistently in humans. In the great apes, some authors state that the superior cardiac nerve originates from the superior cervical ganglion (gorilla by Botar, 1932; orangutan by Kolesnikov, 1935), while other authors oppose this view (orangutan by van den Broek, 1908; orangutan by Sonntag, 1924; chimpanzee by Kolesnikov, 1935). Most authors did not pay attention to the thoracic cardiac nerve. Therefore, it will be necessary to examine the ACNS in great apes to determine whether they have the superior and thoracic cardiac nerves bilaterally or not, and to determine when the bilateral condition of humans evolved. The left superior cardiac nerve would appear to have originated in the common ancestor of gibbons and humans, or earlier if the observations of Schumacher (1902) are correct.

Comparative and Evolutionary Changes of the ACNS in Primates

No systematic morphological description of the primate autonomic cardiac nervous system exists despite a long biomedical history of primate anatomical studies. Only van den Broek (1908) studied the sympathetic cardiac nervous system in a diverse array of mammals, but even he could not provide an evolutionary perspective.

Of course, it is difficult to trace the course of evolution of soft tissues in primates because they have diversified greatly. However, we have examined the ACNS to summarize the common characters in each genus and to surmise the anatomy of their last common ancestors (Kawashima, 2005; Kawashima et al., 2005, 2007).

Each genus has distinctive ACNS characters, differing from those of other primate genera. To clarify the evolution of ACNS morphology, previous and present results are compared in Tables 4 and 5, and Figure 9. We have recognized differences in the sympathetic (cardiac) system, but few differences in the morphology of the parasympathetic (cardiac) system. The differences in the sympathetic system include the composition of the cervicothoracic ganglion, the position of the middle cervical and cervicothoracic ganglia, and the range of origin of the cardiac nerves.

In the course of phylogeny, the composition of the cervicothoracic ganglion exhibits reduced participation of the thoracic ganglia. Associated with this change in composition of the cervicothoracic ganglion, the middle cervical and cervicothoracic ganglia have migrated more cranially in the lineage from our common ancestor with Old World monkeys to *Homo sapiens*. The vertebral ganglion seems to have evolved in the common ancestor of gibbons and humans. In addition, the range of origin of the cardiac nerves tends to expand from our common ancestor with Old World monkeys to humans.

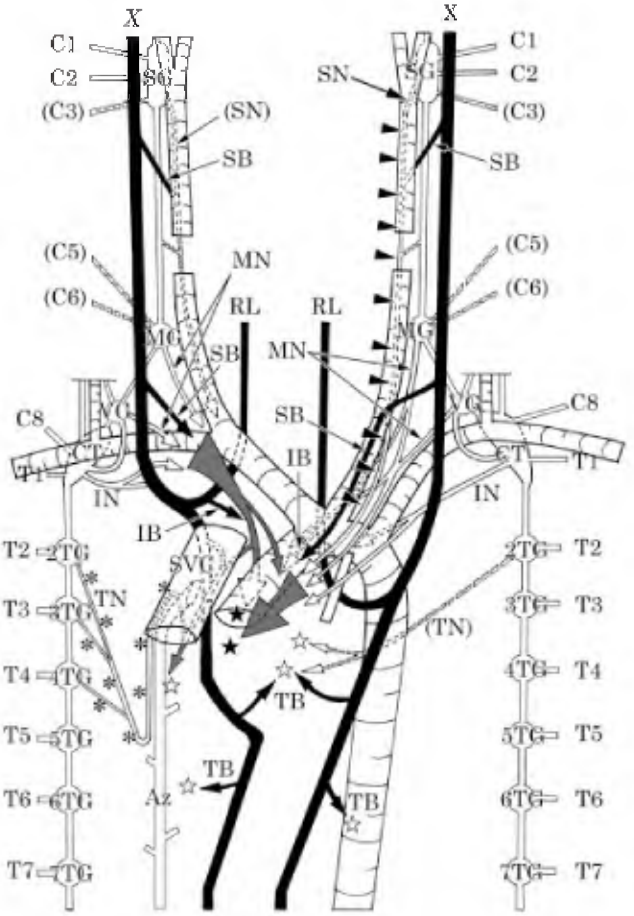

Fig. 10. The general morphology of the autonomic cardiac nervous system in gibbons (Hylobatidae). White, black, and gray nervous systems show the sympathetic, parasympathetic vagal, and combined (mixture) cardiac nervous systems, respectively. The black and white stars show the cardiac nerves/branches entering from the arterial and venous parts of the pericardium reflection, respectively. The left superior cardiac nerve originating from the left superior cervical ganglion as shown in arrowheads and the right thoracic cardiac nerve entering from right venous part of the pericardium reflection by means of azygos vein and arch as shown in asterisks were mostly observed than in the other side. CT, cervicothoracic (stellate) ganglion; IB, inferior (vagal) cardiac branch; IN, inferior cervical cardiac nerve; MG, middle cervical ganglion; MN, middle cardiac nerve; RL, recurrent laryngeal nerve of vagus nerve; SB, superior (vagal) cardiac branch; SG, superior cervical ganglion; SN, superior cardiac nerve; TB, thoracic (vagal) cardiac branch; TN, thoracic cardiac nerve; *X*, vagus nerve; 2–7TG, second to seventh thoracic ganglia.

In conclusion, we propose Figure 10 as a summary of the gibbon ACNS. This morphology of the ACNS is likely to be the anatomy of the last common ancestor of all gibbons, and to be a good approximation of the anatomy of the common ancestor of gibbons, great apes, and humans.

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