# On the Cardiac Nerves of Some Cetacea, with Special Reference to Those of *Berardius Bairdii Stejneger*

By
Teizo Ogawa

(Received June 10, 1952)

The innervation of the mammalian hearts has very often become the subject of profound and extensive studies in the anatomy as well as in the physiology, and among a great many anatomists, who have devoted themselves to this problem, especially *His jr.* (1891), *Schumacher* (1902), *Perman* (1924), and *Worobiew* (1928) are noted for their very fruitful researches. The detailed works of the last mentioned author and his collaborators, *Anufriew*, *Belowa*, *Schurawlew*, *Wolhynski*, etc., seemed to have left nothing important in the gross anatomy of the cardiac nerves. Later, *Nonidez* (1939) made still a remarkable progress, as he reported the possibility of discerning stain-technically between sympathetic and parasympathetic fibers in the dog's heart, and quite recently *Nomura* by his microscopical works (1951, 1952) on the cardiac nerves of the mouse contributed much upon the problem. *Nomura* as well as *Glomset* (1940) insisted upon the abundance of nerve fibers in or near the so-called conduction system of *His jr.* and *Tawara*.

The aim of the present paper lies mainly in mentioning my own observations on the cardiac nerves in a fetus of the Pacific beaked whale, *Berardius bairdii Stejneger*, for they contain some very different points from the remarks of previous investigators, and though the materials here treated are yet scanty, the results have, I guess, a greater meaning than they at first look. Afterwards the cardiac nerves in two other sorts of the Cetacea, *Balaenoptera borealis Lesson* and *Prodelphinus caeruleoalbus Meyen*, will be described, comparing with *Berardius*, as the cardiac innervation of the Cetacea has attracted till today seemingly very few attention of the anatomists.

## Material and Method

The cetologically very interesting species, *Berardius bairdii Stejneger* (Japanese name: *Tuchi-kujira*), haunts our sea near Awa, the southern province of Chiba Prefecture from June to September, mostly in summer. The adult whales attain usually the body length of 10 m. Two fishery companies are erected to perform works for catch and utilization of

this beaked whale. The research materials were given us from these companies.

The Sei whale (Japanese name: *Iwashi-kujira*) treated in this paper was caught near the Bonin Islands, and so it may belong to the *Bryde*'s whale, *Balaenoptera brydei*, rather than to *Balaenoptera borealis* (*H. Omura* et al, 1952). But as this problem of identification is not yet fully settled, the more common nomination will be adopted here.

The dolphin, *Prodelphinus caeruleoalbus Meyen* (Japanese name: *Suji-iruka*), is very abundantly seen and caught at Izu Peninsula in winter (*Ogawa*, 1937). The villages Kawana and Arari are famous for the dolphin fishery, and we got the materials there.

In the present work nearly always fetal hearts of them were dissected with naked eye and without any staining. Only sometimes the adult hearts were examined and a few microscopical preparations stained with hematoxylin-eosin or by *van Gieson*'s method or by the *Bielschowsky*'s method were also employed.

The fetal hearts are very appropriate for the observation of the nerves, for these are relatively well developed, and clearly visible owing to scantiness of the adipose tissue and poor existence of the connective tissue. Besides, the size is fitted for our treatment, the adult hearts of *Balaenoptera* and *Berardius* being too bulky to handle for studying.

## Observations

*Berardius bairdii Stejneger* (Figs. 1, 2, and 3)

One fetal heart, which is ca. 13,5 cm long measured straight from basis to apex cordis, and ca. 14,0 cm wide in the transverse direction at the height of the coronary sulcus, was examined. The heart had been taken out by another person from a fetus of *Berardius*, the body length of which was about 1.8 m, and consulting the size it must be in the later period of pregnancy.

Nearly the whole heart is undamaged, showing only a little wound limited to the base of the left pulmonary vein. The cut out material includes, besides the heart itself, the aortic arch, the *Botallo*'s duct, the pulmonary artery with its right and left rami, the lower portion of the trachea with bilateral bronchi, a portion of oesophagus with vagi attached to its wall, and some parts of thymus remaining near the heart. The stem of the pulmonary artery is ca. 3,5 cm wide, while the ascending aorta is ca. 5,5 cm in its greatest transverse diameter.

The left vagus, which is a large trunk of ca. 5 mm thickness, while descending on the ventral surface of the aortic arch, dispatches at the height a little above the upper end of the *Botallo*'s duct a remarkable branch (A) mediocaudally (figs. 1 and 2). This branch seems to consist mostly of vagal fibers, but partly to contain sympathetic ones, as the vagus trunk shows anastomosis with the left sympathetic near the origin of this branch and in addition the branch (A) itself receives a few twigs from the left sympathetic.

The further course and distribution of A are noteworthy, for it

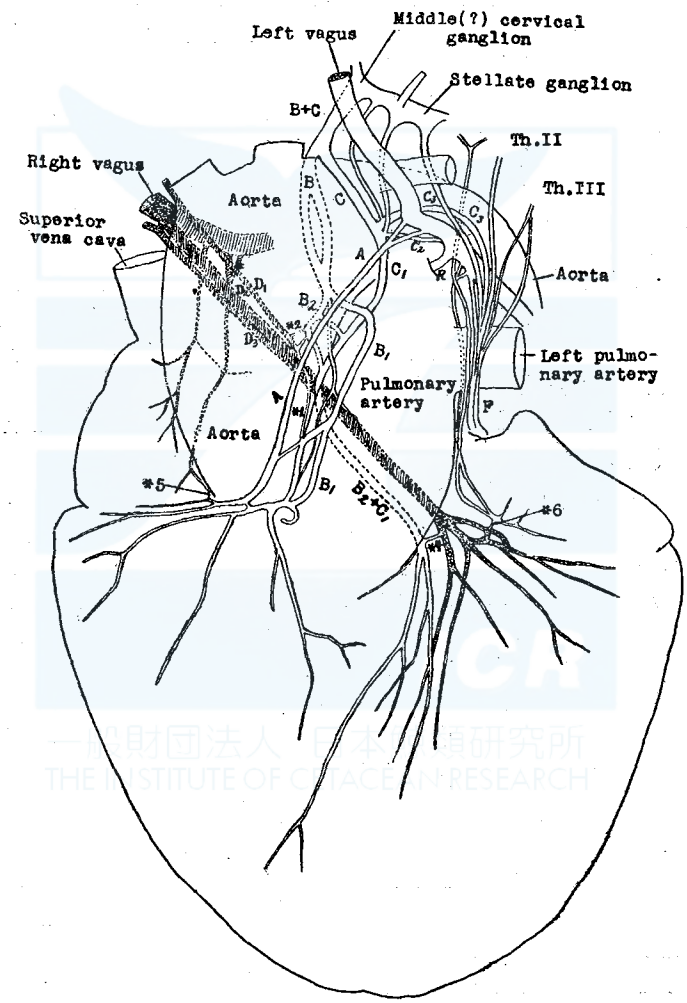


Fig. 1. Cardiac nerves of *Berardius bairdii* (anterior view)
Dark···Right vagosympathetic

runs down and to the right side always attached to the ventral surface of the ascending aorta, until it reaches above the beginning part of the right coronary artery. On the way it shows two small connections with sympathetic twigs coming from B, which will be related later. The branch (A) is distributed, after dividing into many small rami, to the upper lateral portion of the ventral wall of the right ventricle. Anastomosis occurs very few between this branch and the nerves existing on the ventral surface of the right atrium (fig. 1, *5). It is important, that this A, departing from the left vagus and receiving twigs from the left sympathetic nerve, undergoes during its whole course no large connection with the right nerves, definitely innervates a certain part of the right ventricle.

Next the stout sympathetic branches (B and C) will be described (figs. 1 and 2). Both start, at first being united in a common trunk, downwards from the middle cervical ganglion of the left side. This trunk bifurcates at the height of the upper margin of the aorta into two thick branches, anterior (C) and posterior (B).

The branch (B) descends behind the aorta in contact with the left ventrolateral surface of the trachea and reaches the right side of the *Botallo*'s duct, after passing in front of the right pulmonary artery. Behind the aorta it is divided temporarily into two portions, both of which unite together again. Then it ramifies into two branches, right ($B_2$) and left ($B_1$).

$B_1$ crosses over the later to be mentioned $C_1$, where very few fibers seem to be exchanged between $B_1$ and $C_1$ at the crossing, and then proceeds forwards and to the right side on the right upper surface of the pulmonary artery. Precisely persuing the rami and ramuli of $B_1$, we know that this nerve reaches solely the conus arteriosus of the right ventricle, running there subepicardially in downward direction. On the way it receives a small twig (*1) apparently coming from the right nerves. But as the right nerves show just at the origin of this twig two small anastomoses (*2, *3) with the left sympathetic nerve ($B_2$), it is not decided, whether the twig in question conveys fibers originating from the right or from the left nerve.

$B_2$ sends off at first a small ramus, which crosses over $C_1$ dextral to $B_1$, where no exchange of fibers is found between them, and then goes down and forwards on the right upper surface of the pulmonary artery. It then courses forwards under $B_1$ and disappears as fine ramuli from sight at the basis of the pulmonary artery.

The stem of $B_2$ is strongly bent to the right side, and after

dispatching a branch forwards to unite with $C_1$, shows two small anastomoses with $D_1$ coming from the right side. These two anastomoses (*2, *3) are worthy of special attention, for in this fetal heart direct communication between the nerves of both sides reaching in front of the transverse sinus of the pericardium occurs only at these places, at any rate in a very small amount. The stem of $B_2$ goes then to the left caudal direction and makes with $C_1$ a large trunk ($B_2+C_1$), which

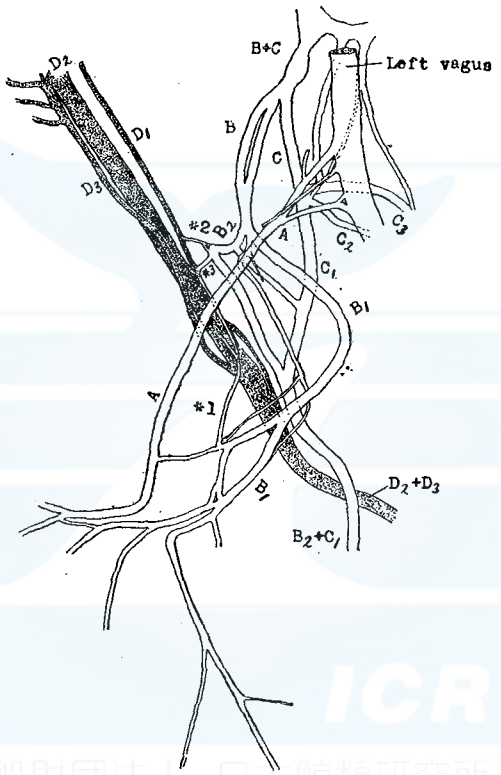


Fig. 2. Plexus cardiacus superficialis of *Berardius bairdii*
Dark...Right vagosympathetic

courses behind the pulmonary artery obliquely from right upper to left lower and reaches the uppermost portion of the interventricular groove. During its course posterior to the pulmonary artery no direct connection exists between this trunk ($B_2+C_1$) and the later to be mentioned $D_2+D_3$. Branches of the trunk ($B_2+C_1$) are followed to the medial part of the ventral wall of the right ventricle adjacent to the interventricular groove, in other words, to a part of the conus arteriosus, running in

apical direction from the left upper region (fig. 1).

The other thick branch (C) descends anterior to the aortic arch and ramifies into three ($C_1$, $C_2$, $C_3$). One of them ($C_2$), comparatively the smallest, goes into the stem of the left vagus at a level between the origin of A and the recurrens (fig. 1, R). Another branch ($C_3$), larger than $C_2$, turns to sinistral and reaches together with other left sympathetic nerves and with a branch from the left vagus, after descending anterior to the left pulmonary artery, the wall of the left atrium to continue into F, which will be related afterwards.

The thickest branch ($C_1$) makes the stem of C, attains the right side of the *Botallo*'s duct and then the right upper surface of the pulmonary artery. Here it is crossed over at first by $B_1$, later by a branch of $B_2$, while it courses to the right lower direction. Then it is fused with the stem and a branch of $B_2$, building so a large trunk ($B_2+C_1$), the course and destination of which were mentioned already.

In short, the conus arteriosus of the right ventricle is innervated mostly, if not all, by rostrally originating sympathetic fibers of the left side. These fibers descend partly in front of, partly behind the aorta and reach the destination passing dextral, and partially sinistral to the basal portion of the pulmonary artery.

On the other hand, we see directly behind the aorta three nerves ($D_1$, $D_2$, $D_3$) of various sizes, all coming from the right side, at first almost parallel to each other, in an oblique direction on the right ventrolateral surface of the trachea (figs. 1 and 2···dark drawn). Though owing to incompleteness of the material, their origins from the vagus and from the sympathetic trunk are not definitely determined, the largest and middle placed $D_2$ contains quite certainly both vagal and sympathetic fibers, while the much smaller $D_1$ and $D_3$ consist nearly exclusively of sympathetic fibers.

$D_1$ lies a little upper than $D_2$ and shows at the level of the lower margin of the aortic arch two small anastomoses, proximal (*2) and distal (*3), with $B_2$, as these were already mentioned in relation to $B_2$. At the distal anastomosis $D_1$ unites with $D_2$ and just from the place of this fusion a thin nerve extends down and forwards, on the way receiving a small branch from $D_2$, and runs through the narrow space between the aorta and the pulmonary artery to reach further a branch of $B_1$. This thin nerve (*1) was accounted for already in the description of $B_1$. It is the only nerve, which apparently belongs to the right nerves ($D_1$, $D_2$), and is distributed further together with the left nerves ($B_1$). But it is difficult at present to decide, whether its fibers originally

belong to the right or to the left nerves, when one considers the small anastomoses between $B_2$ and $D_1$.

$D_2$ is a stout, cylindrical nerve trunk and unites with the slightly lower running $D_3$ in front of the right pulmonary artery. The large trunk ($D_2+D_3$), to which $D_1$ also might be mixed ($D_2+D_3+D_1$?), proceeds behind the pulmonary artery obliquely downwards and to the left side and reaches above the left coronary artery, where it is divided into three. It is quite remarkable, as pointed out above, that behind the pulmonary artery no direct connection takes place between $D_2+D_3$ and $B_2+C_1$.

Branches of $D_2+D_3$, after repeated ramifications, go partly into the interventricular groove, partly proceed into the medial part of the left coronary sulcus, and innervate the ventral wall of the left ventricle. One can see many of them run subepicardially either from the interventricular groove or from the medial portion of the coronary sulcus, generally to the left caudal direction. They never follow the branchings of the coronary artery, as the independency between nerves and vessels is easily proven also in all other parts of the heart.

With enthusiasm I looked for anastomosis between $D_2+D_3$ and $B_2+C_1$ in this region, but found only a small one at the upper end of the interventricular groove (*4). Besides, a twig deviates from the main trunk of $D_2+D_3(+D_1?)$ to attain the lower part of the ventral surface of the left atrium, but it sinks for the most part into the depth of the coronary sulcus to be delivered with other branches of $D_2+D_3$ to the lateral marginal part of the left ventricle. Only a tiny anastomosis was seen between this portion and the nerves on the ventral surface of the left atrium (*6).

Observing as the next step the heart from behind (fig. 3), the right and left relations of the cardiac nerves are quite unlike to those of the anterior view. Along the superior vena cava there are two middle sized nerves coming from the right side and consisting probably for the most part of the sympathetic fibers ($D_4$ and $D_5$). One of them ($D_4$) descends behind this vein and after ramification partly unites with $D_5$, partly attain the terminal sulcus. The sinus node, if this be existent, must receive this branch, though I could not ascertain the presence of the sinus node in *Berardius*.

$D_5$ descends along the left side of the superior vena cava, and some of its branches reach the ventral surface of the right atrium, making here plexus with a portion of branches arisen from $D_6$. This plexus sends twigs to the right auricula and to the terminal sulcus. The

sinus node may receive these twigs too.

On the dorsocranial surface of the right atrium, more sinistral than the orifice of the superior vena cava a remarkable nerve plexus (*7) exists directly ventrocaudally to the right pulmonary artery. It is made chiefly by branches of $D_5$ and $D_6$. One finds just in its neighbourhood a concentration area of the atrial musculature, corresponding probably to the septal raphe reported by *Papez* (1920). $D_6$ comes out

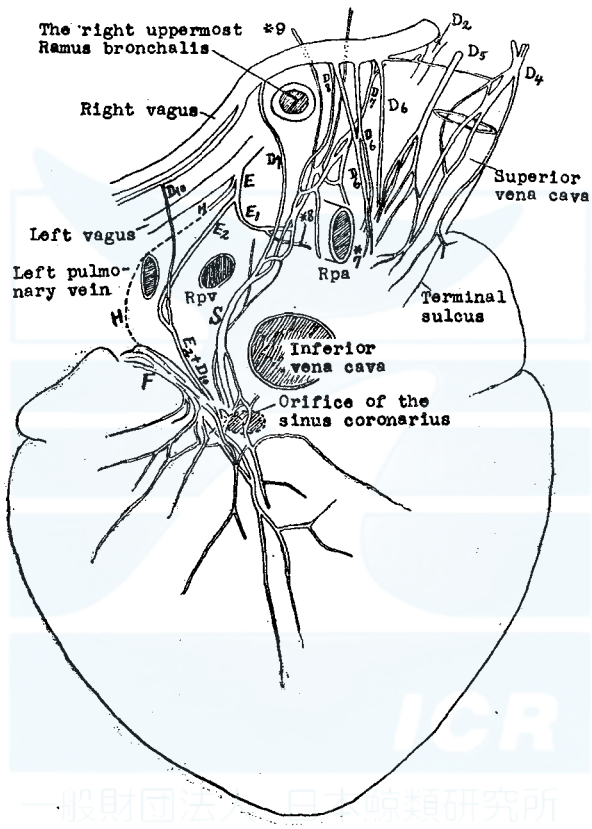


Fig. 3. Cardiac nerves of *Berardius bairdii* (posterior view)
Rpa···Right pulmonary artery
Rpv···Right pulmonary vein

more caudally than $D_2$ from the right vagus as three separated nerves, goes down partly to the ventral surface of the right atrium, partly to the plexus on the dorsocranial surface of the right atrium (*7).

Two other branches ($D_7$ and $D_8$) start also from the right vagus nearly at the same level as $D_6$, but more medially than this. $D_7$ shows

at the origin an anastomosis with the sympathetic nerve. $D_7$ and $D_8$ descend posterior to the right pulmonary artery, except a small portion of $D_7$, which goes to the ventral surface of the atrium. They make behind this artery a remarkable nerve plexus (*8), to which besides them the left vagus and the left sympathetic send also branches very clearly. For the problem of the cardiac innervation this part surrounding the right pulmonary artery from before and behind, where the vagal and the sympathetic fibers coming from both sides meet together, seems to be the most important. The concentration area of the atrial musculature lies just beneath the plexus in question. One branch from the left sympathetic can be traced a long distance (*9) from the dorsal surface of the aorta to this plexus. Another branch belonging to the left vagus ($E_1$) is issued from E, which will be mentioned below. Within this plexus (*8) the nerve bundles look here and there ganglionated, and the plexus sends to the hinder and lower direction a well developed septal nerve (S), which descends through the interatrial septum to the fossula nervina of *Worobiew*.

$D_9$ is a branch from the right vagus, issued more caudally than $D_8$. It descends at first behind the uppermost ramus bronchalis and reaches further down the lower part of the remarkable nerve plexus, but it continues more distinctly to the septal nerve, apparently making its main constituent. Fibers of the septal nerve are distributed partly to the dorsal walls of the ventricles, but partly disappear from sight, sinking deeply at the left side of the orifice of the coronary sinus. In the heart of an adult *Berardius* I could prove the intimate connection of this deeply going nerve with the atrioventricular node of *Tawara*. The septal nerve shows also anastomosis with F, viz. branches from the left vagus and left sympathetic.

The left vagus sends off a fairly large branch (E) at the height a little below the recurrens. After it runs to the right lower direction for a short distance, it bifurcates, and the one branch ($E_1$) turning sharply to the right side enters the large plexus behind the right pulmonary artery, while the other ($E_2$) courses for a long distance on the surface of the left atrium, and descends to the fossula nervina a little sinistral to the septal nerve, nearly parallel to this. It anastomoses on the way with a small nerve ($D_{10}$) started very distally from the right vagus. At the fossula nervina the nerve ($E_2+D_{10}$) lies more superficially and more sinistral than the septal nerve, but further distribution of its fibers seems to be the same as that of the septal nerve.

On the dorsal surface of the left atrium a large assembly of nerve bundles (F) run obliquely along the *Marshall*'s vein. About one half of them comes down from the left stellate ganglion and from the second and third thoracic ganglia of the left side (fig. 1), while about the other half makes the continuation of $C_3$ and of a branch (H) of the left vagus, dispatched from this at the same level as E. All of the sympathetic and vagal nerves descend in front of the aorta, then of the left pulmonary artery, and reach the angle between the left auricula and the left pulmonary vein. Here they are contained in the plica nervina of *Worobiew*, and then proceed to the coronary sinus, on the way they give off small branches to the dorsal wall of the left atrium. From the coronary sinus branches of F after making anastomoses with the septal nerve and with $E_2+D_{10}$ are delivered widely over the dorsal surfaces of the right and left ventricles. Some fibers seem to attain the *Tawara*'s node through the anastomosis with the septal nerve. Nerves on the ventral surface of the left atrium show also an intimate relation with the proximal part of F. Besides, a small nerve can be traced downwards from the sympathetic between the stellate and the second thoracic ganglia at first behind the aorta, then just before the left pulmonary artery to the ventral surface of the left atrium (fig. 1, not signed in the picture).

To summarize, the cardiac branches both of the vagus and the sympathetic going in front of the transverse sinus to the ventral walls of both ventricles are crossed, at least for the greatest part. They constitute the so-called superficial cardiac plexus, but in this plexus of *Berardius* anastomosis occurs in a very small amount between the nerves of both sides. On the other hand, the branches distributed to both atria and to the dorsal walls of the ventricles passing posterior to the transverse sinus, do not cross, or at least the crossing is never clearly seen. These belong to the so-called deep cardiac plexus, and in this plexus anastomosis takes place very frequently between the nerves coming from both sides. Moreover it is worthy of notice, that the conus arteriosus of the right ventricle receives chiefly sympathetic fibers coming from the left side.

In addition one can definitely say that the nerves going to the ventral walls of the ventricles depart from the stems of vagus and sympathetic at levels generally higher than those innervating the atria and the dorsal walls of the ventricles. The nervous supplies to the sinus node of *Keith* and *Flack* and to the atrioventricular node of *Tawara* will be discussed afterwards.

*Balaenoptera borealis Lesson* (Figs. 4 and 5)

The heart was taken out from a 120 cm long fetus of the Sei whale. It is 9,8 cm long from basis to apex cordis and 9,2 cm wide measured at the coronary sulcus. The left vagus, a 3,4 mm thick bundle descending down the neck, sends off, while it runs in front of the aortic arch a remarkable branch (A) mediocaudally. This branch makes its course to the right side always attached to the ventral surface of the aorta and reaches above the beginning part of the right coronary artery, where it communicates with a thick nerve (G) coming from the superficial cardiac plexus through the narrow space between the ascending aorta and the pulmonary artery. This plexus is built by the left sympathetic branches (B + C) and by the right vagosympathetic nerve (D). These nerves have reached here from both sides passing almost all behind the aorta. From the confluent nerve bundle (A + G) many branches are given to the ventral surface of the right ventricle inclusive of the conus arteriosus, all of them running downwards directly under the epicardium. From the complicated form of the plexus it is in this heart difficult to know, how much G conveys fibers from the right or from the left side.

The left sympathetic nerve, B and C, start from the trunk at a very high level, probably from the superior cervical ganglion and descend for the greatest part behind the aorta. Only a very small portion runs anterior to this vessel. Therefore, in comparison with *Berardius*, one might conceive almost all of them as belonging to B. B and C are divided into several branches in front of the right pulmonary artery dextral to the *Botallo*'s duct, some of them making ansae with each other, and most of them being united to the right nerves (D). One small branch of B and C shows a very noteworthy course (b). It passes at first in front of D to the right side, reaches the left concave surface of the ascending aorta and goes then further down passing behind D to the lower part of the anterior surface of the left atrium, where it unites with the most sinistral branch of D (fig. 4 a, b). It is probable that fibers of this small branch are distributed to the lateral marginal part of the left ventricle.

D lies behind the aorta as a very thick nerve arising from the right side. It is made by union of $D_1$ and $D_2$. $D_1$ comes out from the lower end of the right superior cervical ganglion, so is sympathetic in nature, while $D_2$, certainly vagosympathetic, is much larger and starts from the right vagus at the same level as the recurrens, but separately

from this. Just after confluence of $D_1$ and $D_2$ a remarkable branch is given off from the dorsal part of D to the anterior surface of the right atrium (*1). This branch seems to bring the fibers corresponding to the anterior branches of $D_5$ and $D_6$ of *Berardius*, considering the destination of the fibers.

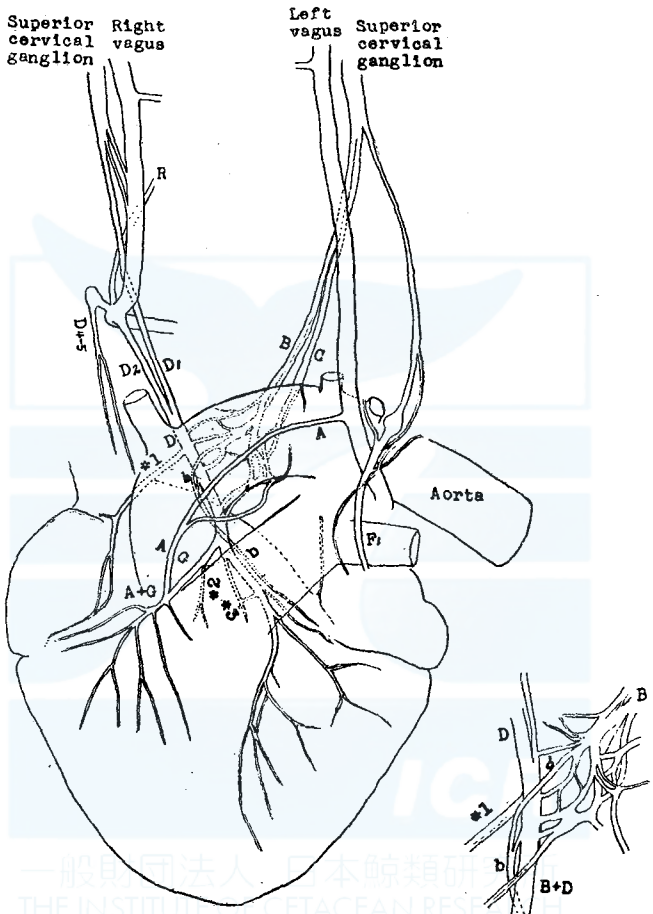


Fig. 4. Cardiac nerves of *Balaenoptera borealis* (anterior view)




Fig. 4 a. The nerve plexus just behind the aorta, in details

Behind the aorta the thick nerve D receives B and C from the left side, but as C is minimal in this case, one can call hereafter the resulted large trunk "B+D". From this B+D a thick branch (G) deviates to the right side, and connects with A, as already described.

It may be possible, though not fully proven, that G makes chiefly the continuance of B, as one can guess comparing the relation in this region between *Berardius* and *Balaenoptera*.

Small ramuli are given off from G and from B+D to the hinder circumference of the pulmonary ostium (fig. 4, *2, *3), to end probably in a part of the conus arteriosus. B and D, or simply D if the analogy with *Berardius* holds true, descend obliquely behind the stem of the pulmonary artery to the left side and reach after ramification partly the anterior interventricular groove and partly the coronary sulcus. The fibers are followed to the ventral wall of the left ventricle. It seems that none of them goes from here to the right ventricle, but many fine anastomoses are seen between nerves of the right and left ventricles on the ventral surface.

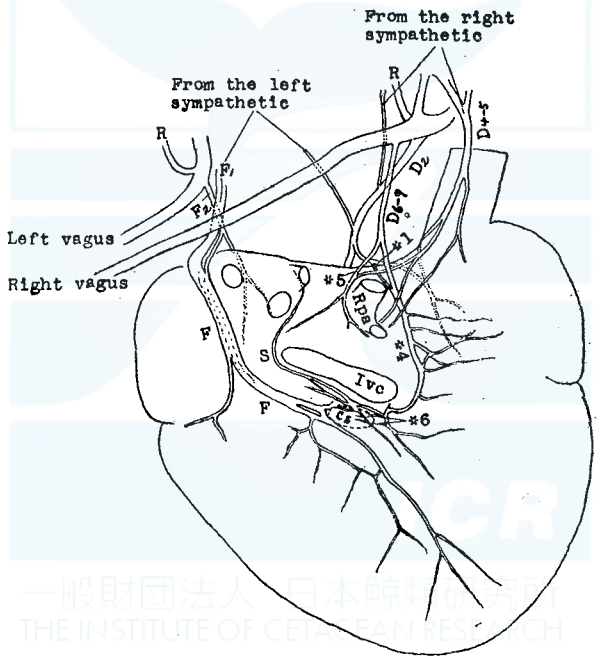


Fig. 5. Cardiac nerves of *Balaenoptera borealis* (posterior view)
Rpa···Right pulmonary artery
Ivc···Inferior vena cava
Cs····Sinus coronarius

Corresponding to $D_4$, $D_5$, $D_6$, $D_7$, $D_8$, $D_9$ of *Berardius*, the fetal heart of *Balaenoptera* has only two nerves, or better to say three, if one adds the branch of D going to the anterior surface of the right atrium. The two nerves might be called here $D_{4-5}$ and $D_{6-9}$. $D_{4-5}$, sympathetic

in nature, descends along the posterior and left surface of the superior vena cava, and is distributed mostly to the atrial wall sinistral to this vein, a few of its branches extending further into the right lung.

$D_{6-9}$ arises from the right vagus a little below the recurrens and goes down the lateral surface of the right bronchus. Above the right pulmonary artery it is divided into two, one of which (fig. 5, *4) descends in front of this vessel, becomes attached to the surface of the atrial musculature, gives off many branches horizontally to this, and runs subepicardially on the right side of the inferior vena cava, reaching at last the medial part of the coronary sulcus, caudally to this vein. On the way it receives a small branch, which is issued from the branch of D going to the anterior surface of the right atrium (*1), and comes posteriorly after penetrating through the *Bachmann*'s bundle. The other branch (fig. 5, *5) of $D_{6-9}$ descends behind the right pulmonary artery, undergoes an anastomosis with a branch of $D_{4-5}$ and continues downwards in the atrial septum, partially reaching the left side of the inferior vena cava. The bundle, which corresponds topographically to the septal nerve of *Berardius*, is very poorly developed in *Balaenoptera* (S); also the nerve plexus is relatively better developed anterior than posterior to the right pulmonary artery. As to the septal nerve a great defference is perceived between *Berardius* and *Balaenoptera*.

The presence of a large assembly of nerve bundles (F) along the *Marshall*'s vein is common to both whales in question. These bundles come in *Balaenoptera* too from the left vagus and the left sympathetic. The sympathetic nerves ($F_1$) start from the stellate ganglion and from the 2. and 3. thoracic ganglia. They descend, making a large trunk, in front of the vagus stem and of the aorta, then anterior to the left pulmonary artery and reach the angle between the left pulmonary vein and the left auricula, giving rise here to the plica nervina of *Worobiew*.

One branch is sent off from the left vagus at the level of the recurrens, to take part in the formation of F after passing behind the pulmonary artery. The bundles of F reach mostly the coronary sinus, after giving some ramuli to the dorsal wall of the left atrium and to the marginal part of the left ventricle, and then innervate after repeated ramifications the greater part of the dorsal walls of the right and left ventricles. A portion of them sinks deeply at the left side of the orifice of the coronary sinus, to enter probably into connection with the atrioventricular node. The septal nerve (S), lying sinistral to the inferior vena cava, is small and seems to come mostly from the left vagus. It shows anastomosis with the long branch of $D_{6-9}$ (*4), which

attains here dextral to the inferior vena cava. The connection between the nerves originating from the right side and the atrioventricular node is less marked than in *Berardius*, though two small twigs (fig. 5, *6) from the long branch of $D_{6-9}$ are tracable, sinking deeply at the right side of the coronary sinus, to the direction of the *Tawara*'s node.

*Prodelphinus caeruleoalbus Meyen* (Figs. 6 and 7)

The left vagus sends off mediocaudally a remarkable branch (A) at a level slightly above the aortic arch. It descends along the ventral surface of the aorta and then unites with the left sympathetic nerves (B), which have reached here behind the aorta. These sympathetic nerves are grouped into two ($B_1$ and $B_2$), both starting from the middle cervical ganglion of the left side. A joins at first with the more lateral coursing $B_1$, and then with the more medial running $B_2$.

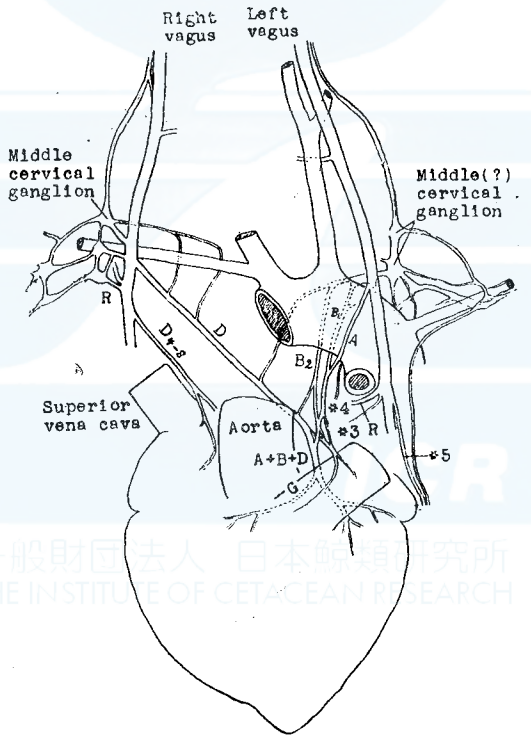


Fig. 6. Cardiac nerves of *Prodelphinus caeruleoalbus* (anterior view)

The thus formed nerve (A+B) unites then with a large trunk (D) coming posterior to the aorta from the right side. D starts from the right vagus a little above the recurrens. It must contain both vagal

and sympathetic components. On its way D receives small sympathetic ramuli not only from the right but also from the left side.

The large trunk (A+B+D) gives off a branch (G), which goes through the narrow space between the ascending aorta and the pulmonary artery to the base of the right coronary artery. The larger remaining portion of A+B+D descends obliquely behind the pulmonary artery to reach partly the interventricular groove and partly the coronary sulcus, and the fibers are distributed chiefly to the ventral surface of the left ventricle. Only a very small portion attains the lower part of the ventral surface of the left atrium.

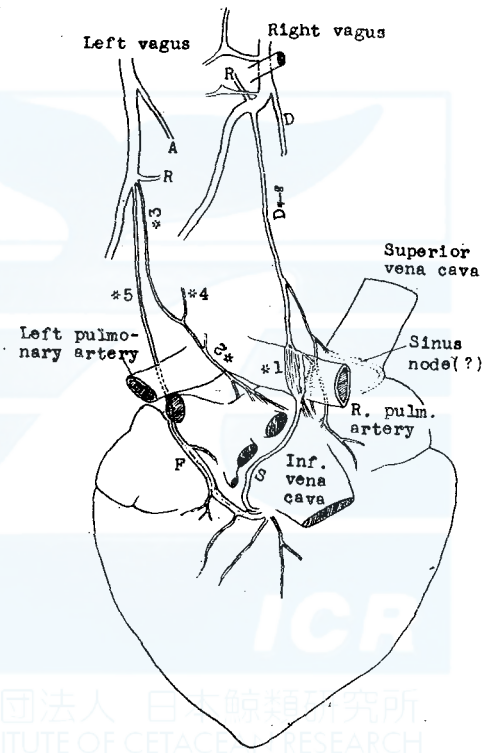


Fig. 7. Cardiac nerves of *Prodelphinus caeruleoalbus* (posterior view)

At the space between the aorta and the pulmonary artery each of $B_1$, $B_2$, and D dispatches a thin branch, in all three rami, which unite together into a single trunk, proceeding forwards on the right side of the *Botallo*'s duct to the dextrocranial surface of the pulmonary artery. This innervates probably the conus arteriosus of the right ventricle. Some small branches issued forth from the left sympathetic descend behind the aorta and innervate the ventral surface of the left atrium.

From the right vagus another remarkable branch, corresponding to $D_{4-8}$ of *Berardius*, starts a little below the recurrens. It is about half so thick as D, and is divided while descending into two, anterior and posterior. They go partly to the ventral surface of the right atrium, partly behind the *Bachmann*'s bundle just in front of the right pulmonary artery to the septal raphe of *Papez*, but for the greater part behind the right pulmonary artery, making here a thin but broad sheet of nerve fibers closely attached to the dorsal surface of this vessel (fig. 7, *1); thence the fibers reach partly the septal raphe, partly the atrial septum to continue further down into a remarkable septal nerve (S). Just above the septal raphe, where many of the atrial musculature show the tendency to concentrate, we see well developed nerve plexuses. To these the right vagal and sympathetic fibers are brought in by $D_{4-8}$, while the left vagal and sympathetic fibers are conveyed by a nerve bundle (*2), which descends obliquely from upper left to lower right directly behind the bifurcatio of the right and left pulmonary arteries, and whose origins each from the left vagus and from the left sympathetic are determined clearly. The vagal component (*3) comes from the base of the recurrens; the sympathetic one (*4) belongs to the most sinistral bundles of B.

F is a large group of nerve bundles, running along the *Marshall*'s vein. It consists of the vagal and sympathetic fibers coming from the left side. The vagal branch (*5) begins nearly at the same level as the recurrens. Fibers of F are distributed partly to the dorsal wall of the left atrium, but for the greater part to the dorsal walls of the right and left ventricles. At the fossula nervina of *Worobiew* a part of F together with a portion of the septal nerve sinks deeply to the direction of the *Tawara*'s node.

Speaking in short, the cardiac nerves of *Balaenoptera* and *Prodelphinus* are considerably different from those in *Berardius*. In them the crossing of the nerves going to the ventral walls of the ventricles is not so clearly seen, except as to the branch A in *Balaenoptera*, which starts from the left vagus and innervates definitely a portion of the ventral wall of the right ventricle. In *Prodelphinus* even the vagal branch corresponding to A is lost in the superficial cardiac plexus, so its further course, whether to the right or to the left ventricle, is very difficult to ascertain. But the possibility, that also here the same relation as in *Berardius* exists, should not soon be excluded. No definite proof could be obtained against this assumption. I thought at first to have met such a proof in a small branch (b) of *Balaenoptera*,

which belongs to the left sympathetic nerve and goes after a complicated detour to the left ventricle. But as its destination is certainly the transitional part between the ventral and dorsal walls of the left ventricle, this observation too never disproves the thesis.

The second problem, that the nerves ending in the atria and the dorsal walls of the ventricles start from the stems generally more caudally than the nerves going to the ventral walls of the ventricles, and moreover they are probably not crossing, holds also in *Balaenoptera* and *Prodelphinus*, though in these Cetacea the cardiac nerves especially on the right side, which descend posterior to the transverse sinus, are gathered into a small number of trunks, 2 or 3, while in *Berardius* the corresponding number is so large amounting to 10, that one can in this whale more easily determine the height of origin for each branch innervating various parts of the heart.

The third problem is relative to the nerve plexus lying near the right pulmonary artery just above the concentration area of the atrial musculature and to the septal nerve descending through the atrial septum. Concerning them there is a great difference between the toothed whales, *Berardius* and *Prodelphinus*, and the baleen whale, *Balaenoptera*. In the former the nerve plexus in question is very well developed and branches from the vagus and sympathetic of both sides are clearly traced to this plexus and an imposing septal nerve descends passing sinistral to the inferior vena cava toward the fossula nervina. Contrarily, the nerve plexus surrounding the right pulmonary artery as well as the septal nerve is meagre in *Balaenoptera*. Instead of the septal nerve, the Sei whale has a large nerve, which departs from the right vagus and descends on the dorsal surface of the right atrium passing dextral to the inferior vena cava.

To the *Tawara*'s node the left nerves go mostly through the nerve bundles running along the *Marshall*'s vein and the right nerves chiefly through the septal nerve. These relations are seen well in the toothed Cetacea, while in the Sei whale the nerve descending right to the inferior vena cava seems to substitute for the septal nerve, as to the innervation of the atrioventricular node.

## Comment

It was a much impressive observation in the fetal heart of *Berardius*, that the cardiac nerves leaving the vagus and the sympathetic at relatively high levels to innervate the ventral walls of the ventricles decussate for the greatest part, and the present author does not take

this fact for a mere variation or a characteristic feature restricted only to this species. It seems to have more important significance.

Up to the present time the crossing of the cardiac nerves has been very few spoken of. *Kazem-Beck* saw in 1888 in the rabbit branches of the superficial cardiac plexus, especially those coming from the left cardiac ramus, go between the aorta and the pulmonary artery to the surface of the right ventricle. Moreover, in some rabbits *Kazem-Beck* found that the left cardiac ramus, before it undergoes connection with the right nerves, sends off a twig, which goes along the pulmonary artery to the surface of the ventricle. By this "ventricle" he must have meant the right one, as we can estimate from his figure and explanation (fig. 1 d of his paper). Also in the dog's heart *Kazem-Beck* traced a portion of fibers, which belong mostly to the right cardiac rami, from the plexus to the surface of the left ventricle. Perhaps he was of the opinion, that not a small amount of the cardiac nerves are crossed in these animals, though he did not emphasize at all upon the decussation.

On the contrary, *Schumacher* (1902) concluded in his extensive studies on many mammalian hearts, that the right nerves innervate in general the right atrium and the right ventricle, including a part of the left ventricle adjacent to the anterior interventricular groove, while the left nerves are distributed solely to the left ventricle and the left atrium. The remarks of *Schumacher* seem to have found relatively much agreement in the successors. Meanwhile *Perman* (1924) proposed partial correction of *Schumacher*'s conclusion, though he acknowledged also the ipsilateral relation for the most of the cardiac nerves. In several mammals *Perman* could trace one or two nerves coming from the left side and passing anterior to the aortic arch, to the right ventricle.

My own acquisition in *Berardius* looks quite extraordinary in this respect. But to my mind the more general occurrence of the contralateral relation for the cardiac nerves is never inconceivable, if one considers that in most mammals through the inextricable maze of the superficial cardiac plexus each nerve bundle can never be persued with confidence. The difficulty of tracing them confidently through the plexus was great also in *Balaenoptera* and *Prodelphinus*, and thereupon the unique finding in *Berardius*, in which only minimal anastomosis takes place between the nerves of both sides, seems to mean much.

The decussation of the cardiac nerves above referred to was caused in my opinion by the torsion of this part of the ventricular canal, which must have occurred in the early embryo in the region of the porta

arteriosa. *Braus* wrote in his famous textbook, "eine Torsion des Herzschlauches in der Nähe der Porta arteriosa mit dem Uhrzeiger (von der Arterie stromaufwärts gesehen)—auch an Einrichtungen des menschlichen Herzens erkennbar." (*H. Braus:* Anatomie des Menschen. Bd. 2, 1924, S. 626) Our finding tells probably, that the musculature of the ventral wall of the right ventricle was given rise at first on the left side, and that of the ventral wall of the left ventricle on the right side, the nerves retaining their original relation honestly till the adult stage.

A natural deduction from this is my rather bold assumption, that the neuromuscular connection must have begun in the heart very early, though since *His jr.* (1891) the late innervation of the heart has often been reported. In the fowls' heart *His jr.* saw the first nerves appear on the 6. day of incubation, and *Perman* (1924) observed them in the embryo of 4 days and 2 hours. As to mammals, *Hall* (1951) met with nerve fibers in the sinus venosus and atria only of the rat embryos older than 14,5 day stage, a remark which sounds not a little contradictory to the earlier work of *Shaner* (1930), who proved the presence of all nerves going to the heart of a 20 mm long calf embryo already. Anyway, the relatively late development of the cardiac nerves has furnished, as well known, the most powerful basis for the myogenic theory of the conduction or automatism in the cardiac function.

My hypothesis upon the early innervation of the heart finds, however, another support in the fact, that the nerves entering the superficial cardiac plexus, which corresponds undoubtedly to the "Bulbusgeflecht" of *His jr.*, start from the vagus and sympathetic at levels generally higher than the nerves descending posterior to the transverse sinus to both atria and to the dorsal walls of both ventricles. The nervous connection of the heart seems to have been established in a very young embryo, when the porta arteriosa was situated more rostrally than the porta venosa. Otherwise, the above mentioned difference of the levels, where the cardiac nerves leave the vagus and sympathetic trunk, might be difficult to explain.

Another finding, that in *Berardius* the conus arteriosus of the right ventricle receives a special innervation, viz. chiefly the most rostral sympathetic fibers coming from the left side, deserves also much attention from the embryological viewpoint, as this part is generally looked upon as nothing than the bulbus arteriosus of the early embryo.

As to the problem of the cardiac nerves the sinus node discovered by *Keith* and *Flack* seems to be in the Cetacea no special locality, as

only a few small branches of the right nerves reach there. Contrarily a remarkable nerve plexus, especially well developed in the toothed whales, is attached to the atrial wall just dextral to the interatrial septum and directly under the right pulmonary artery. *Papez* named this portion "septal raphe" and called attention to the richness of nerves coming there from the right vagosympathetic. I myself could observe in addition branches from the left vagus and from the left sympathetic reaching distinctly the nerve plexus in question.

## Summary

The cardiac nerves were studied with naked eye in the fetuses of *Berardius bairdii*, *Balaenoptera borealis* and *Prodelphinus caeruleoalbus*. In *Berardius* the vagal and sympathetic nerves originating from the right and left side and attaining the ventral walls of the ventricles decussate at least for the most part, the left nerves going to the right, the right ones to the left ventricle. In *Balaenoptera* and *Prodelphinus* the decussation of these nerves is not definitely determined, though its possibility can also never be denied. They start from the vagus and sympathetic trunk always more rostrally than the other nerves, which descend posterior to the transverse sinus to both atria and to the dorsal walls of the ventricles. For the latter the ipsilateral innervation, the right to right and the left to left, probably prevails.

We may explain these findings the most easily from the complicated morphogenesis of the mammalian heart, but at the same time we have to assume the very early innervation of the heart musculature, a fact, which does not coincide well with the data reported by previous authors.

Innervations of the sinus node, of the *Tawara*'s node and of the septal raphe of *Papez* were also studied, special attention being paid to the septal nerve, which descends through the atrial septum, and to the thick nerve bundles, which run together with the *Marshall*'s vein. A great difference was recognized as to the development of the septal nerve between the toothed whales and the Sei whale.

## Literature

1) W.N. Anufriew: Die Herznerven der Katze. Zeit. f. Anat. u. Entw. Bd. 86 (1928) 639-654.
2) G. Arpino: Die Innervation des Sinusknotens bei Delphinus delphis L. Anat. Anz. Bd. 77 (1934) 241-252.
3) G. Bachmann: The Intraauricular Time Intervall. Amer. J. of Physiol. Vol. 41 (1916) 309-320.

4) M. Belowa: Fossula cordis nervina. Zeit. f. Anat. u. Entw. Bd. 86 (1928) 517-531.
5) H. Braus: Anatomie des Menschen, Bd. 2. Eingeweide. 1924, Berlin.
6) E.J. Glomset and A.T.A. Glomset: Morphologic Study of the Cardiac Conduction System in Ungulates, Dog, and Man. I, Sinoatrial Node; II, Purkinje System. Amer. Heart Journal. Vol. 20 (1940) 389-398; 677-701.
7) E.K. Hall: Intrinsic Contractility in the Embryonic Rat Heart. Anat. Rec. Vol. 111, No. 3 (1951) 381-399.
8) W. His jr.: Die Entwickelung des Herznervensystems bei Wirbelthieren. Abhandl. d. mathem.-physischen Classe d. Königl. Sächs. Gesell. d. Wiss. Leipzig. Bd. 18, No. 1 (1891) 1-64.
9) Kazem-Beck: Beitrag zur Innervation des Herzens. Arch. f. Anat. u. Physiol., anat. Abt. (1888) 325-352.
10) A. Keith and M. Flack: The Form and Nature of the Muscular Connections between the Primary Divisions of the Vertebrate Heart. J. of Anat. and Physiol. Vol. 41 (1907) 172-189.
11) S. Nomura: On the Cardiac Nerves and Ganglia of the Mouse. Cytol. and Neurol. Studies (edited by S. Saguchi). No. 9 (1951) 15-40.
12) ———: On the Structure, Distribution and Innervation of the Special Heart Muscle System of the Mouse. Idem. No. 10 (1952) 211-256.
13) J.F. Nonidez: Studies on the Innervation of the Heart. I, Distribution of the Cardiac Nerves, etc. Amer. J. Anat. Vol. 65 (1939) 361-413.
14) T. Ogawa: List of the Odontoceti in Japan. Annual Report of the Work, Saito Ho-on Kai. Sendai, Japan. No. 12 (1937) 63-65.
15) H. Omura, S. Nishimoto and K. Fujino: Sei Whales (Balaenoptera borealis) in the Adjacent Waters of Japan. Japan Whaling Association, Tokyo. May, 1952.
16) J.W. Papez: Heart Musculature of the Atria. Amer. J. Anat. Vol. 27 (1920) 255-285.
17) E, Perman: Anatomische Untersuchungen über die Herznerven bei den höheren Säugetieren und beim Menschen. Zeit. f. Anat. u. Entw. Bd. 71 (1924) 382-457.
18) S. v. Schumacher: Die Herznerven der Säugetiere und des Menschen. Sitz.-ber. d. kaiserl. Akad. d. Wiss., mathem.-naturwiss. Cl. Wien. Bd. 111, Abt. 3 (1902) 133-235.
19) A.N. Schurawlew: Die Herznerven des Hundes. Zeit. f. Anat. u. Entw. Bd. 86 (1928) 655-697,
20) R.F. Shaner: On the Development of the Nerves to the Mammalian Heart. Anat. Rec. Vol. 46, No. 1 (1930) 23-39.
21) J. Tandler: Anatomie des Herzens. Bardelebens Handb. d. Anat. d. Menschen. Bd. 3, Abt. 1 (1913), Jena.
22) T. Walmsley: The Heart. Quain's Elements of Anatomy. Vol. 4, Part 3 (1929), London.
23) F.A. Wolhynski: Die Herznerven des Kalbes. Zeit. f. Anat. u. Entw. Bd. 86 (1928) 579-607.
24) W. Worobiew: Plica nervina atrii sinistri. Idem. Bd. 86 (1928) 509-516.
25) ———: Methodik der Untersuchungen von Nervenelementen des makro- und makro-mikroskopischen Gebietes. 1925, Berlin.

---

From the Department of Anatomy (Prof. Dr. T. Ogawa)
Medical Faculty, University of Tokyo