On the Musculature of the Sinus Venosus and its Continuation with the So-called Conducting System of the Whale's Heart

By

TEIZO OGAWA

I. Introduction

Since the *Stannius*' ligation experiments of 1852, the fact has ever been confirmed, that in lower vertebrates impulses starting in the sinus venosus control the rhythmic contractions of the whole heart. But the problem, where to seek for the sinus venosus in the mammalian heart, has never been concurrently answered. Mostly among physiologists the opinion prevails, that the sinus venosus is reduced to a high degree, and remains only miserably along the terminal sulcus of the right atrium, making the so-called sinus node. Other scanty remnants are said to exist at the orifices of the inferior cava, of the coronary sinus, and of the pulmonary veins. This theory has its origin without doubt in the famous work of *Keith* and *Flack*, who discovered then the sinus node (1907). Along with the progress of the cardiac physiology, more and more weight has been laid on the significance of the sinus node as "pacemaker," and it has become a usual trend among medical scientists, including sometimes anatomists, to think of the node itself as representing the sinus venosus.

But from the standpoint of anatomy, this way of thinking is rather a difficult one, and has relatively little convincing power. We are more inclined to believe, as we read in *Gray*'s textbook of the human anatomy (24. ed., 1946, p. 499), that the sinus venosus becomes incorporated with and forms a part of the adult atrium, the line of union between it and the auricula being indicated in the interior of the atrium by a vertical crest, the crista terminalis of *His*. Before 1907, such was probably the most common idea. As an example the following sentence is cited from the textbook of *Bardeleben* (1906), "Aus dem Venensinus und der primitiven Vorkammer wird später durch Vereinigung dieser Räume der Vorhof, noch später die beiden Vorhöfe, schliesslich finden wir beim erwachsenen Herzen den Venensinus als Hauptbestandteil der Vorhöfe, während die primitiven Vorhöfe (Vorkammern) zu den Herzohren reduziert sind."

In America *Glomset* (1940) mentioned very sceptically the existence

and significance of the sinus node, studying in detail the hearts of man and some mammals (cattle, horse, dog, pig). According to him, the so-called sinus node is never a part structurally so special as generally believed, because similar structure is found here and there in the walls of both atria, and at the atrio-ventricular groove too. Moreover *Glomset* insisted, that the extirpation experiments performed by previous scientists were not conclusive enough to speak definitely of the pacemaker function of the sinus node.

One chief reason, why the sovereignty of the sinus node is sometimes suspected, is probably the inconsistency between remarks of many researchers upon size, localisation, extension, and histological structure of the node. The far elongation of the sinus node observed recently by *Fukuhara* (1949, 1950) in dog, cat, and rabbit, and also by *Nomura* (1952) in mouse is not a little divergent from the reports of previous workers. Although one can explain this difference to a certain degree from the phylogenetic relation, we should remember at the same time *Takahashi*'s report (1931) on special muscle fibres at the orifice of the inferior cava and also *Thorel*'s paper (1910) on the wide distribution of the "Röhrenfasern." Both of them concerned the human heart; so phylogeny can not be estimated too much here.

In order to treat the problem further, the present author chose as the comparative anatomical means the Cetacean hearts. In the classical work of *Keith* and *Flack* (1907) hearts of two kinds of Delphinidae (porpoise and dolphin) and of the blue whale (Balaenoptera musculus) were studied. Simple as their descriptions concerning the Cetacea are, they must have recognized the sinus node in these animals. *White* and *Kerr* (1917) dissected out the atrioventricular system in the heart of Physeter and published macro- and microscopical photographs. In the same year *Ogata* (1917) made a speech upon the conducting system of whales' hearts (fin and sei whales) at a meeting of Japan Pathological Society. Two years later *Ogata* (1919) published together with *Sassa* their observation on special muscle bundles in the atria of the fin whale (Balaenoptera physalus) again at a meeting of the above mentioned society. Though only a three-page abstract was printed then for publication, it related the following very noteworthy facts.

Just under the epicardium they saw at the orifice of the coronary sinus special-looking muscles, which extend from here to the posterior surfaces of both atria, right and left. The right bundle reaches a place near the middle between superior and inferior cavae, and ends there, while the left one extends obliquely along the *Marshall*'s vein to termi-

nate near the left margin of the ostium of the left pulmonary vein. The bundles in question are lighter colored than the usual atrial muscles, and dispatch in their courses some branches, which are continuous directly with the usual muscles of the atrial wall. *Ogata* and *Sassa* called them "connecting bundles of the sinus venosus."

Dr. *Ogata*, now emeritus professor of our medical school, visited the present author in the University of Tokyo in the autumn of 1948, and encouraged the latter to study this problem, as he, being too busy, had no time to promote the thema by himself.

Since 1919, the attention of very few anatomists has been given to the heart of whales, so far as we consult the literature. In 1934 *Arpino* studied the innervation of the sinus node of Delphinus delphis, and in 1952 *Davies*, *Francis*, and *King* reported their results upon the cardiac nerves of Phocaena communis. Nobody has mentioned yet the special muscle bundles discovered by *Ogata* and *Sassa*.

II. Materials and methods

The hearts studied in the present work are mostly those of Odontoceti, in contrast to the Mystacoceti studied by *Ogata* and *Sassa*. About 10 hearts of the Pacific beaked whale (Berardius bairdii *Stejneger*) make here the most important material; also a few hearts of the sperm whale (Physeter macrocephalus *L.*) were examined. Macroscopical works were performed with knives and pincettes. Microscopical sections were prepared from various places of the hearts, cut sometimes by freezing, but in most cases embedded in paraffin or celloidin, and the sections were stained by hematoxylin-eosine, *van Gieson*'s, or *Bielschowsky*'s method.

III. Observations

A. Special muscle bundles seen in the atrial walls of Berardius bairdii

The hearts of Berardius treated in this work had got more or less lesions at the dissection of the whale bodies, so the observations were usually not completed in one individual, and sometimes it was necessary to fill up the defect in one heart with observations in other ones. Moreover it was perceived soon, the whole system of the special-looking atrial muscles shows not a few individual variations, though there is no essential difference between the cases. In the following, muscular figures of the posterior atrial wall will be described, based chiefly on case I.

Subepicardially, there is a remarkable muscular bundle (A), smoothly outlined, at the base of the coronary sinus. Deeply dissecting, it is easily seen, that it makes a muscular ring around the orifice of this sinus (figs. 1, 2). (In some individuals this ring formation is not complete; the part on the external side of the sinus is wanting or partially

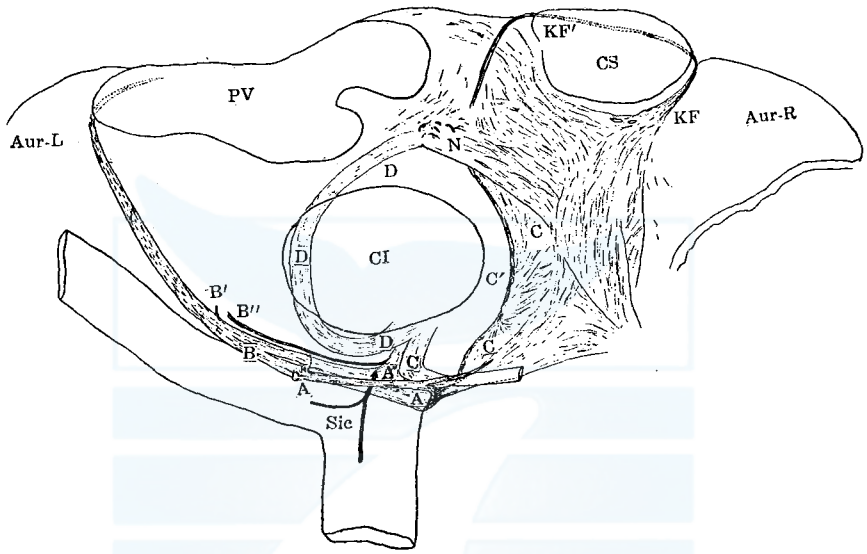

Fig. 1. Muscles of the sinus venosus in the heart of Berardius (case I)
Aur-L: left auricle
Aur-R: right auricle
CS: superior vena cava
CI: inferior vena cava
PV: a large defect in the left atrial wall involving the orifices of the right and left pulmonary veins
SiC: the arrow showing the entrance of the coronary sinus.
As to other letters, see the text or abbreviations of pages 20 and 21

interrupted.) It is darker colored than the usual atrial muscles, and so appears to be of a special nature. From this ring wings stretch out to both sides, right and left, and the right one continues directly to the lowest posterior part of the right atrium, just facing the atrioventricular groove.

The muscular ring dispatches on the external surface of the coronary sinus a remarkable branch (A'), which is directed to right and upwards, becomes soon narrower and terminates not far from the ring, attached to the posterior surface of the lower part of the right atrium (figs. 1, 2). Here no direct continuation to the ordinary atrial muscles is proven.

Minutely examined, the special-looking muscular bundle changes at the terminal to slender tendon-like connective tissue and ends by means of this in contact with the atrial muscles. The terminal sulcus of *His* lies far more laterally; so A and A′ belong to the musculature of the sinus venosus, according to our definition.

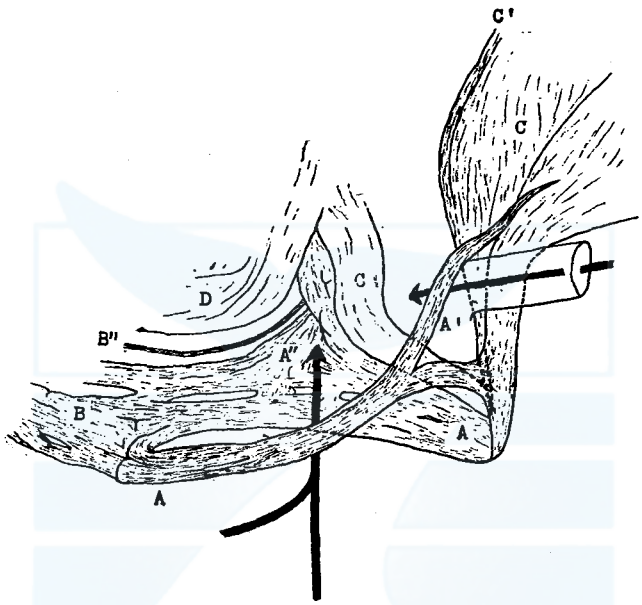

Fig. 2. A portion of fig. 1, near the entrance of the coronary sinus (the arrow from below). The arrow on the right side shows a vein entering the right atrium after passing along the atrioventricular sulcus.

The left wing of the muscular ring is a large assembly of muscular bundles (B) extending obliquely along the *Marshall*'s vein to left and upwards on the posterior surface of the left atrium, and attaining the angle between the left pulmonary vein and the left auricle (figs. 1, 2). During the course it becomes gradually thinner, but as a whole it is very thick and powerful, incomparable to A′. It appears darker red than the usual atrial muscles. Only one small branch (B′) issues from it and ends very soon upon the posterior surface of the left atrium. There is another very thin isolated bundle (B″), which runs parallel and internal to B, restricted only to a distance relatively near the coronary sinus. The bundle B terminates at the lateral margin of the left pulmonary vein; here too we see no direct transition between B and the ordinary atrial musculature.

From the floor (i.e. internal) part of the muscular ring at the orifice of the coronary sinus stretches forwards a triangular broad process (A''), which submerges under C+D later to be mentioned (figs. 1, 2). As the *Tawara*'s node lies just beneath C+D, A'' shows an intimate relation with this node. The relation will be mentioned more precisely in the next chapter.

Special muscular bundles discovered by *Ogata* and *Sassa* in Balaenoptera correspond very probably to A, A', and B, B' of the present paper, though there are some disagreements due at least partially to taxonomic difference. They say the bundles in question are lighter colored than the ordinary atrial muscles, and dispatch many branches directly continuous with the atrial musculature. These remarks are contradictory to the present paper. Only rarely, in one among five specimens, *Ogata* and *Sassa* could see no branching of the bundle. Besides, these authors traced the right bundle to about the middle between superior and inferior cavae, therefore very different from A or A'. But again in one among five hearts studied by them the special bundle did not reach so far. Moreover no ring formation was mentioned in their paper of 1919.

In Berardius anothor well-defined, slender but long muscle bundle (C') is very marked; it runs laterally and below to the entrance of the inferior cava, assuming an arcuate form. It is darker colored than the ordinary atrial muscle, but a little lighter than A and B. C' makes clearly the left marginal portion of a broad, sickle-shaped muscle plate (C), which is the leftmost part of the posterior right atrial wall (fig. 1). When traced mediad and downward, united mass of C' and C is seen on the interior of the atrium, making here a single broad, subendocardial muscular plate (C), which, from a dextrocranial direction, attains the floor of the entrance of the coronary sinus just anterior to A, always a little apart from this. Mixing of muscle fibres does not occur between A and C. As will be related later, C shows the most intimate connection with the *Tawara*'s node.

Upwardly observed, C' reaches between superior and inferior cavae, hides itself there under other atrial musculature, and disappears near a certain place of the right atrium, where many atrial muscles are concentrated (fig. 1). This concentration area of the atrial musculature lies covered by the right pulmonary artery and behind the *Bachmann*'s interauricular bundle; it is very near the anterior upper end of the atrial septum. The present author would call this node-like part of hte right atrial wall with the abbreviation of "N", and takes it for a

portion of the "septal raphe" reported previously by *Papez* (1920).

In case I, "N" shows darker red tone than the ordinary atrial parts, and, being wrapped by thick connective tissue, it was relatively difficult to excise the epicardium here. Besides, the author would lay much stress on the rich innervation of this area, as in the formerly published work (*Ogawa*, 1952) he could trace in Berardius as well as in other Cetacea just under the right pulmonary artery many nerves of vagal and sympathetic components coming from right and left sides. In one Berardius heart (case III), which belonged to a 250 cm long, female foetus, C′ did not reach "N", but ran laterad after it sank from the posterior surface at a place between superior and inferior cavae toward the terminal sulcus. But its connection with the sinus node was not proven.

With "N", i.e. the node-like area, there is continuous a large group of atrial muscles, which run dextrocaudally in a slightly opened fan-like form between superior and inferior cavae to make a broad muscular area limited laterally by the sulcus terminalis (fig. 1). The *Lower*'s torus is caused chiefly by this muscular mass, but the most medial part of the torus is made by the already mentioned C, while the continuance of the *Bachmann*'s bundle, coming partly behind the orifice of superior cava, participates in making the lateral part of this torus.

Moreover a broad, well-defined muscular bundle (D) starting from "N" goes downward into the atrial septum, and forming the posterior margin of the oval fossa attains from sinistrocranial the floor of the right atrium just in front of the coronary sinus (fig. 1). There the fibres of C and D are mixed partly. Just beneath C+D lies the *Tawara*'s node embedded in hard connective tissue. The septal nerve (S), reported in the previous paper (*Ogawa*, 1952), courses together with D.

The presence of the sinus node is in Berardius not always certified. In case I, at the groove between the superior cava and the right auricle a dark red, thin bundle (KF′) is present, runs anteriorly surrounding the entrance of the superior cava, and crosses over the *Bachmann*'s bundle on the left side of this vein and reaches near "N", there disappearing. This special-looking bundle forms at the posterior margin of the superior cava a rounded mass (KF), which corresponds probably to the sinus node (fig. 1). This mass shows direct connection to the left side with the *Bachmann*'s bundle and downward with muscles of the broad area just medial to the terminal sulcus. But no direct intercourse between this probable sinus node and the *Tawara*'s node is seen.

In case II (33 feet long, adult male Berardius) the upper part of the terminal sulcus, where the sinus node according to *Keith* and *Flack*'s paper certainly has to exist, was microscopically examined, but the efforts of finding it were in vain.

B) *Tawara*'s node and its direct continuance with the atrial musculature

In several cases of Berardius the author dissected out the *Tawara*'s node and was in every case much impressed by its direct continuance with C and D of the foregoing chapter, above all on a larger scale with C. Transition from C and D to the node in question occurs completely gradually, without any appreciable boundary. Muscular fibre groups diverge out downward from C and D at the floor of the right atrium

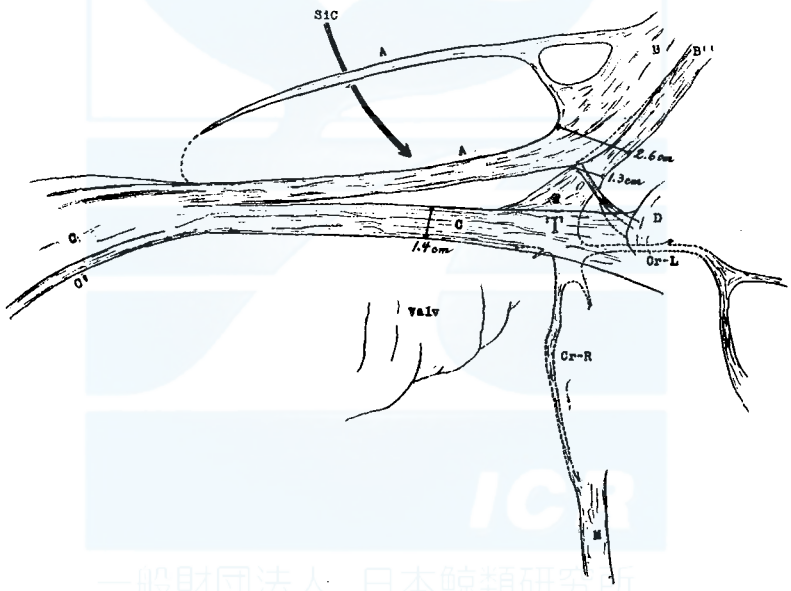

Fig. 3. Macroscopical relations of the *Tawara*'s node (T) of Berardius (case IV), seen from the interior of the heart

SiC: Sinus coronarius
Valv: Valvula tricuspidalis (Cuspis posterior)
M: Moderatorband
Cr-R: right crus of the *His*' bundle
Cr-L: left crus of the *His*' bundle

in front of the coronary sinus, and intermingle with hard connective tissue; muscular fibres run here not straight but more irregularly, are loosely assembled, plexiform with many collagenous fibres between them

(figs. 5, 6). They are cross-striated. In fresh material the node looks macroscopically as diluted red ink infiltrating in white connective tissue. Direct continuation of muscular fibres between the node and the atrial muscles is under microscope very clearly demonstrable in serial sections of this region taken from case IV (figs. 5, 6). In these sections, made as large as possible to include various parts of atrial walls and of the conducting system, one can easily trace the gradual change of the histological structure within the conducting system formed by the union of atrial muscles (figs. 6, α; 6, β), *Tawara*'s node (fig. 6, γ), and *His*' bundle (fig. 6, δ) with its crura (figs. 6, Cr-R; Cr-L).

Not only C and D but also A and B, which are the special-looking muscles surrounding the coronary sinus, and extending along the *Marshall*'s vein, contribute to the formation of the *Tawara*'s node, especially remarkable for A'' and B''.

In case IV the *Tawara*'s node relatively clearly dissected out shows, from cranial seen, a triangular outline, three angles of which are made respectively by B'', C, and D (fig. 3). Even in other cases, when the boundaries of this node are not so clear, one can easily confirm the node by searching at first for the right and left crura of the *His*' bundle. The crus commune is short and macroscopically not discernible from the node itself. Only histologically one can speak substantially about the border, which is but never a sharp one. The discrimination between "Vorhofsabschnitt" and "Ventrikelabschnitt" insisted by *Aschoff* is also not impossible in microscopical preparations.

One thing to be especially noted is, that just under the connective tissue surrounding the *Tawara*'s node the ventricular musculature lies. It tells namely, this node is located not at a place relatively near the interior surface of the right atrium or in the atrial septum, but theoretically on the outer surface of the right atrium. This applies probably to the hearts of man and other mammals too; only in whales the relation is easily recognizable, as both atria are in this animal widely apart posteriorly from each other. *Ogata* (1917) wrote already this fact with great interest in Balaenopteridae.

The *Tawara*'s node of Berardius receives abundant nerve bundles, coming here mostly from the left side through the fossula cordis nervina of *Belowa* as continuation of nerves along the *Marshall*'s vein (F of the former paper) and of the septal nerve (S of the former paper) (cf. *Ogawa*, 1952). In microscopical sections we see here and there in the courses of these nerves groups of ganglion cells chiefly on the left side of and below the node. Some of the nerves go directly into the crura of *His*'

bundle. Until near the end of the crus commune groups of nerve cells are observed (fig. 6, δ).

C. *Tawara*'s node of Physeter

Case VI is the heart of a ca. 35 feet long sperm whale, Physeter macrocephalus, the *Tawara*'s node of which was dissected out solely and was compared with that of Berardius. Many identical relations were proven. Also in Physeter the node in question is largely connected with C-bundle, which comes down from right upper direction to the floor of the right atrium in front of the coronary sinus, and with D-bundle, which descends in the atrial septum down to the same locality. Especially the former shows the nearest topographical and the most intimate relation with the *Tawara*'s node. No sharp boundary exists between C+D, and the node.

Besides, the dark colored, special-looking muscle (A) at the orifice of the coronary sinus, which does not form a ring, differing from case I of Berardius, but continues directly to a large group of the special-looking muscles along the *Marshall*'s vein (B), gives off forward a remarkable process (A''), which submerges beneath C+D, and goes partly directly into the formation of the *Tawara*'s node. This node can with no difficulty be found, firstly by seeking crura of the *His*' bundle and following them to the short crus commune, which shows no macroscopical boundary against the node itself, secondly by rich existence of connective tissue embedding the node, and thirdly by a number of nerve bundles coming to the node from posterior surfaces of both atria.

White and *Kerr* (1917) mentioned the vertical direction of the *Tawara*'s node and of the *His*' bundle in Physeter, which coincides well with the present author's observations not only in the sperm whale, but also in Berardius. But more important is perhaps the position of the *Tawara*'s node, that it lies certainly on the outer surface of the right atrium.

The *Tawara*'s node of Physeter receives several nerve trunks, of which the author calculated six in case VI, from posterior surfaces of both atria, passing more on the right side, less on the left side of the orifice of the coronary sinus, a remarkable contrast to Berardius. In the latter species most of the nerves, as already related, pass on the left side of the coronary sinus. This difference is well to be explained from the deficiency of the septal nerve in Physeter; the homologon of the septal nerve descends in this species on the posterior surface of the right atrium mostly on the right side of the inferior cava.

In the *White* and *Kerr*'s paper we see only one nerve trunk attaining the *Tawara*'s node. This was not the case in all the hearts of Physeter studied in the present paper. These authors' description and photograph on the auriculonodal junction are very interesting, though they did not tell at all, with what part of the atrium this junction occurs.

IV. Comments

a) The sinus venosus in the mammalian heart

From phylo- and ontogenetical viewpoints, it is very difficult to conceive that in the mammalian hearts the sinus venosus remains in so vestigial a state, being restricted to such small areas as the sinus node of *Keith* and *Flack* and to several other places at venous entrances. On the contrary, most anatomists think, that the so-called sinus venarum, which is a large medial portion of the right atrium, bordered laterally by the terminal sulcus or crest and, where the cavae veins and the coronary sinus enter the atrium, corresponds to the sinus venosus of lower vertebrates.

In regard to the extent of the sinus venosus, *Walmsley* wrote in his excellent book (1929) the same opinion as ours, but he added further, "the musculature of the sinus wall, which is never well developed, appears to be replaced by the musculature of the atrium, and there remain, as sinus musculature, only the fibres, or at least some of them, which surround the terminal part of the superior cava and those in the wall of the coronary sinus" (p. 37). The present author cannot be certain about the replacement mentioned by *Walmsley*, whose words sound rather as a compromising hypothesis between divergent ideas of anatomists and physiologists. On the other hand, nobody doubts the large existence of the bulbus arteriosus as a part of the right ventricle making the so-called conus arteriosus. And what is the reason, why we must think of so poor an existence of the sinus venosus musculature in the mammalian heart?

The reason is probably the following. Many authors have clung to the idea, that the parts homologous to the sinus venosus must have the structure similar to the *Tawara*'s node. They searched earnestly for the sinus upon this basis, and found it at the terminal sulcus and some other places. But the present author takes this assumption as not justified, and thinks, that many muscular bundles mentioned in this work, A, A′, A″, B, B′, C, C′, D, KF etc. belong altogether to the sinus

venosus, because all of them are situated more medially than the terminal sulcus.

There is no need to be very anxious about relatively less similarity between the *Tawara*'s node and the muscles in question, though at least it is true that the latter contain rich connective tissue and many nerves, as we realized on the other hand in serial sections of the heart of a Bufo, that muscles of the sinus venosus are more loosely constructed, having more connective tissue between muscle fibres, compared with the auricular and especially with ventricular musculature.

Moreover, the present author has reached the opinion, that the centre of the sinus musculature thus defined lies not in the so-called sinus node of *Keith* and *Flack*, but at a certain place ("N") more sinistral than the entrance of the superior cava, and a little posterior to the *Bachmann*'s bundle. It is near the anterior upper end of the atrial septum. Many of the atrial musculature are concentrated here.

It makes probably a part of the septal raphe described by *Papez* (1920) in human, bovine, and canine hearts, though his "septal raphe" seems to be more deeply located in the atrial wall and generally lower in height than "N" of this work. According to him, the sinus node itself is nothing more than a continuation of the septal raphe, but the special histological structure of the nodal tissue is not seen in the septal raphe. *Papez* traced many branches from the right vagosympathicus to this locality, so the question arose to him, whether this might have the pacemaker function for all the left atrium and for the deeper layer of the right atrium. But without mentioning the reason, he seemed to have abandoned this idea, because we read at another place in his paper the septal raphe has only the meaning of mechanical support for the atrial musculature.

The present author deems, the physiological meaning of "N" should be considered more seriously, for as reported formerly (*Ogawa*, 1952), vagal and sysmpathetic nerves not only from the right side, as *Papez* said, but also from the left side attain this place in a large number and so "N" makes apparently a more special locus, than the sinus node, where relatively few nerves starting only from the right side are traceable.

Recently *Uchiyama* and his collaborators have endeavoured to determine in the anuren hearts the centre of automatism within the whole extent of the sinus venosus, "node of venous sinus, Venensinusknoten". This way of thinking is very important in the cardiac physiology, and "N" of us seems to have an intimate relation with *Uchiyama*'s "node

of the venous sinus". Physiological experiments upon "N" must be done hereafter, though they may be relatively difficult to perform, as it lies concealed under the right pulmonary artery.

b) On the so-called sinus node

As to the problem, whether the sinus node of *Keith* and *Flack* be the most important portion of the sinus venosus in the mammalian hearts, the present author cannot stand on the affirmative side. In Berardius he observed occasionally at the groove between the superior cava and the right auricle dark colored muscle bundles, which correspond almost certainly to the so-called sinus node. They showed however in form and extension much individual variations, and in some cases they are not found at all. *Glomset*'s scepticism upon the existence and meaning of this node was already introduced at the beginning of this paper. The present author would say accordantly with him, that the so-called nodal tissue is not confined to such small areas as the sinus node and to orifices of other veins entering the atria, but shows a much wider distribution in the atrial walls.

Richness of nerves is never a characteristic for the so-called sinus node, though this attribute is quite naturally expected for the pacemaker of the cardiac actions. Together with *Papez*, the present author would indicate much more abundant nerves attaining the septal raphe, than reaching the sinus node.

Since *Lewis*' electrocardiographic works the pacemaker function of the sinus node has been insisted by a great many authors, but according to *Glomset*'s criticism "most experiments on ablation of the sinuatrial node fail to show convincingly that the node is the pacemaker of the heart"; he introduced then the works of *Flack*, *Jaeger*, *Magnus-Alsleben*, *Moorhouse*, *Brandenburg* and *Hoffmann*, *Eyster* and *Meek*, and *Borman*, and added further that "there is no unanimity of opinion as to location, size, and structure of the node".

c) On the connecting bundles of the sinus venosus discovered by *Ogata* and *Sassa*

Ogata and *Sassa* supposed as the functional meaning of the "connecting bundles of the sinus venosus" (A and B of this paper), that as the venous entrances must have been closed before the contraction of both atria begins, the bundles in question might convey impulses for the contraction to the venous entrances, and that though their morphological studies had not yet revealed the direction, they assumed basing on general structure, that the bundles might have the function

to conduct impulses arising at the coronary sinus to the venous entrances of both atria.

The present author cannot altogether agree about this assumption, because in Berardius no direct relation with the venous orifices, except with the coronary sinus, is ascertained, and too many individual differences are seen in the course, extension, and size of the bundles in question, to permit thinking of such important function. But they make surely a part of the sinus venosus, and must have intimate relation embryologically with the left horn of the sinus venosus (fig. 8), while

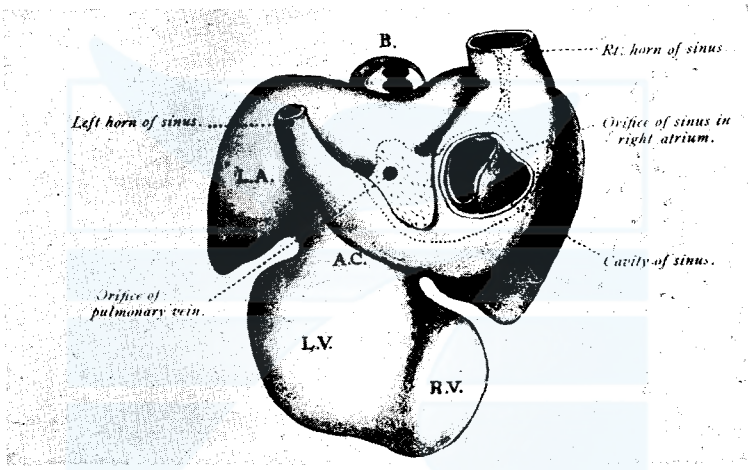

Fig. 8. The heart of a human embryo, from behind. (*Walmsley* 1929, drawn after the model of *His*) B., bulbus cordis; A.C., atrial canal; L.A., R.A., left and right atria; L.V., R.V., left and right ventricles.

the above mentioned C and D together with KF seem to belong to the embryologically better developed right horn and to the middle part of the sinus venosus. Moreover, if we read the detailed descriptions of *Papez* (1920) on the musculature of the coronary sinus, we know that the presence of A and B can not be taken as a characteristic for Cetacea, as he wrote "in the bovine heart the sinus is a continuation of the left common cardinal system and is surrounded by musculature for a distance of several inches" (p. 271).

d) Upon the direct continuity between the muscles of the sinus venosus and the *Tawara*'s node

In the heart of Berardius a broad muscular band (C+C'), which arising near "N" and passing dextral to and below the orifice of the

inferior cava, reaches in front of the floor of the coronary sinus, and another broad muscular band (D), which starting also from "N" descends through the atrial septum, and meets with C in front of the floor of the coronary sinus, show very clearly direct transition into the *Tawara*'s node. This node is situated embedded in thick connective tissue just under the two muscular bands meeting together. Besides,

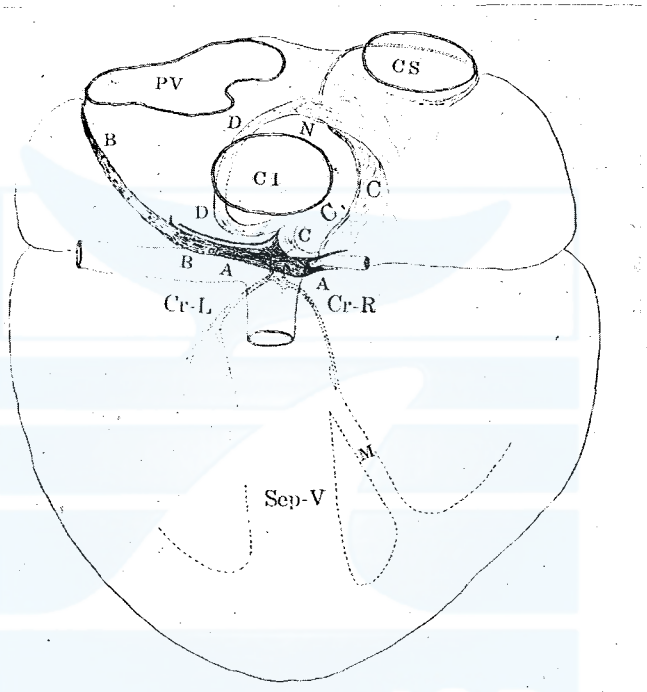

Fig. 9. Schema showing the whole musculature of the sinus venosus continuing directly to the so-called conducting system

A and B show also direct continuity with the *Tawara*'s node, by means of A'' and B''. Between A'' and B'' a compensatory relation seems to exist, as when A'' is largely developed B'' is small, and vice versa. So we can reckon three sources of muscular fibres streaming into the *Tawara*'s node, A+B, C, and D; this means the node in question receives its muscle fibres from all parts of the sinus venosus, not only from the right horn but also from the left one. In the sperm whale, too, nearly the same relations are proven.

Similar facts have already been reported by *Curran* (1909) in the calves' and sheep's hearts. He said that three large bands "radiate" out from the *Tawara*'s node: 1) "a branch to the interauricular septum

and proceeding almost as far as the superior cava where it is lost in the auricular musculature". This branch may correspond to our D, though according to *Curran*'s figure (Anat. Rec. Vol. 3, 1909, pl. I, fig. 1) most of the fibres in question are passing in front of the oval fossa. And also in Berardius some fibres pass probably anterior to this fossa. 2) "a branch, which can be traced to the pericardial surface of the right auricle, blending with the auricular muscle as it proceeds on its way to the pectinate muscles of the right auricular appendix". This resembles our C, though there is a difference, that C does not extend so far dextral as the pectinate muscles. 3) "a similar branch going to the left auricle—it gives some branches to the coronary sinus". This is perhaps A+B of this work. According to *Curran*, moreover numerous smaller branches radiate from the *Tawara*'s node to adjacent auricular muscle. The present author wishes to oppose *Curran*'s using of the word "radiate", because the muscle fibres seem to concentrate from the sinus venosus to the node in question.

Though *Curran* observed in the human hearts only fine threads, but no large branches of muscle radiating from the node to the atrial musculature, *Holl* (1912) wrote, when he studied macroscopically hearts of man, and some mammals (calf, sheep, pig, horse, dog) that "das (atrioventrikulare) Bündel nimmt mit einem Faserwerk in der Wandung des Sinus coronarius und wahrscheinlich auch in den benachbarten Wandungsstellen des rechten (und linken?) Vorhofes seinen Anfang; diese Fasermassen bilden ein Netzwerk *Tawara*'scher Knoten)". This remark of *Holl* is altogether adopted by *Rauber-Kopsch* in their famous textbook of anatomy (16. Aufl., Bd. 2, 1941, S. 384); so students must know this very commonly. Only the origin or course of the atrial muscle fibres connecting with the *Tawara*'s node has not yet been determined. Ambiguity of the origin or course is bluntly expressed in *Spalteholz*'s textbook (13. Aufl., 1933, S. 451). "Es beginnt ...., meistens mit einer Verdickung (*Tawara*'scher Knoten), in welche aus der Vorhofsmuskulatur (namentlich von der Gegend unter der Mündung des Sinus coronarius) Züge unsicherer Herkunft einstrahlen".

Chiefly from the observations in Berardius, the present author believes to have known the "Herkunft" of the atrial muscles connecting with the *Tawara*'s node in the Odontoceti.

e) On the *Tawara*'s node and the *His*' bundle

There are many anatomical data to assume the functional importance of the *Tawara*'s node. But this node never makes the upper end

of the so-called conducting system, never begins abruptly in the right atrium or in the atrial septum. It is continued directly from both horns and middle part of the sinus. Just in front of the floor of the coronary sinus, where embryologically the spina vestibuli is to seek, a certain portion of the sinus venosus muscles becomes loose downwards, and is surrounded by and interwoven with a large amount of hard connective tissue. Here we see a remarkable reticulum of muscular fibre groups embedded in the connective tissue. Nerve bundles reach this node, and show intimate relation with the reticular muscle fibres, as seen by the *Bielschowsky*'s method. Groups of nerve cells were observed here and there near the node, but few between the reticular muscular fibre groups.

Transition from this node to the *His*' bundle takes place again quite gradually. Within the atrioventricular bundle, muscle fibres, swollen like those of the bovine heart, ran parallel to each other, being embedded in a large mass of connective tissue. Many nerve fibres are seen following the *His*' bundle, and groups of nerve cells exist only as far as the end of the crus commune, but not after its bifurcation.

The moderator band of the right ventricle and the left crus a little below the semilunar valve in the left ventricle, were examined histologically, with the results, that the chief constituent of the crura of the *His*' bundle is the dense connective tissue containing collagenous fibres in a large quantity. The swollen muscular fibres and more or less large groups of nerve fibres are contained within the rich connective tissue. Compared with the neighbouring ventricular myocardium, sparseness of muscle fibres and richness of nerve fibres must be taken as characteristic of the *His*' bundle.

Abundance of nerve fibres in the *His*' bundle of the Cetacea was recently reported by *Davies*, *Francis*, and *King* (1552) in the common porpoise (Phocaena). They met with similar relations only in ungulates, but not in many other sorts of mammals. In the latter cases the authors saw many nerves only as far as *Tawara*'s node. This great difference between animals mentioned by them requires detailed reexamination, because *Nomura* in the same year (1952) demonstrated by photographs (plate 8, figs. 40–42) a rich content of nerve fibers in the *His*' bundle of the mouse. It may be an interesting problem to determine, whether so remarkable diversity really exists between the hearts of mouse and rat, two members of the genus Mus, just as the gall bladder exists in the former, but not in the latter.

V. Summary

1. Observed in the hearts of Berardius, the "connecting bundles of the sinus venosus" described by *Ogata* and *Sassa*, are a special portion of the sinus venosus musculature, belonging to the coronary sinus and to the *Marshall*'s vein, in other words, nothing more than the musculature pertaining to the left horn of the sinus venosus.

2. The middle part and the right horn of the sinus venosus are by far better developed, occupying a wide field of the right atrium bordered laterally by the terminal sulcus, never so vestigial as many authors have thought since the *Keith* and *Flack*'s discovery of the sinus node.

3. Within the thus-defined sinus venosus, there is a centre of the musculature "N", where many atrial muscles are concentrated, in the posterior upper part of the right atrium, left to the entrance of the superior cava, and behind the *Bachmann*'s interauricular bundle, covered above by the right pulmonary artery. This centre is probably a portion of the "septal raphe" reported by *Papez*. Here reach, as mentioned in the former paper (*Ogawa*, 1952), a large number of cardiac nerves, vagal as well as sympathetic branches, not only from the right but also from the left side. Anatomically it may be possible to postulate, that the so-called pacemaker is located at this place.

4. The presence of the sinus node of *Keith* and *Flack* is not always proven in Berardius, and even in cases of being present, it shows too much individual variation in size, form, etc. to have attributed to it such a great functional significance. Sometimes this node is continuous directly to "N" by a thin muscular bundle, surrounding anteriorly the orifice of the superior cava.

5. Connecting directly "N" and the *Tawara's* node, there are two large groups of atrial muscles belonging both to the sinus venosus, one group (C) in an arcuate form on the right side of the orifice of the inferior cava, the other (D) descending within the atrial septum along the posterior margin of the oval fossa. Both of them meet together in front of the floor of the coronary sinus. And just under this meeting place the *Tawara*'s node lies, embedded in dense connective tissue and receiving a large number of nerve bundles, which come here in Berardius chiefly from the left side, continued partly from the septal nerve, partly from the nerves along the *Marshall*'s vein.

6. The muscular reticulum of the *Tawara*'s node is directly con-

tinuous with the muscle fibres of C and D; the relation is clearly demonstrable not only by naked eye but also under microscope. The "connecting bundles of the sinus venosus" of *Ogata* and *Sassa* (A+B of this work) show also partly direct muscular continuation with the *Tawara*'s node. So the presence of three muscular bands "radiating" from the reticulum to the atrial walls insisted by *Curran* in his work upon calves' and sheep's hearts were also proven in the Odontoceti.

7. The *Tawara*'s node of Berardius and Physeter, vertically placed, lies theoretically on the posterior surface of the right atrium just above the ventricular musculature, and is so to speak the middle part of an extensive cardiac muscular system (fig. 9), which begins above, embracing widely the sinus venosus, and continues downward directly to the *His*' bundle, to its right and left crura, and at last to the *Purkinje*'s fibres. Direct continuation and gradual histological change of muscle fibres in this whole system are seen clearly in the hearts of whales treated in this work.

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Abbreviations for figs. 1–9.

A, A′, A″: Musculature at the entrance of the coronary sinus
Aur-L: Left auricle
Aur-R: Right auricle
B, B′, B″: Musculature along the *Marshall*'s vein
C, C′: Muscular bundle descending on the right side of the inferior cava to the floor of the right atrium in front of the coronary sinus
D: Muscular bundle descending through the atrial septum to the floor of the right atrium in front of the coronary sinus
C+D: Meeting place of C and D, in front of the coronary sinus
CI: Inferior vena cava
Cr-C: Truncus of the *His*' bundle
Cr-L: Left crus of the *His*' bundle
Cr-R: Right crus of the *His*' bundle

CS: Superior vena cava
KF, KF′: Sinus node of *Keith* and *Flack* (very probably) and its continuance
M: Moderatorband=Trabecula septomarginalis
N: Node-like portion of the right atrium, where many muscles belonging to the sinus venosus are concentrated
PV: Orifices of the right and left pulmonary veins and vestibule of the left atrium
SiC: Sinus coronarius
T: *Tawara*'s node
Valv: Valvula tricuspidalis

From the Department of Anatomy,
Medical Faculty, University of Tokyo.
Hongo, Tokyo.

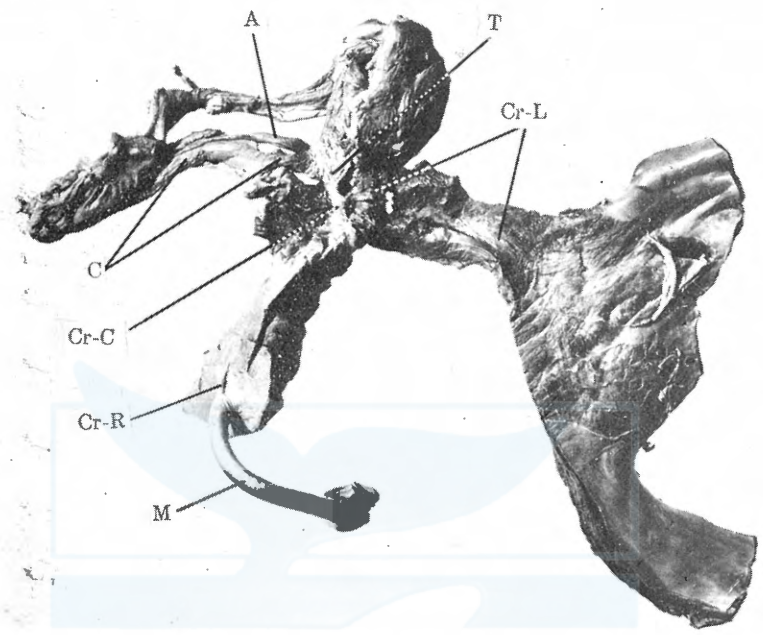

Fig. 4. (a) Macroscopic specimen showing the whole of the conducting system (Berardius, case IV).

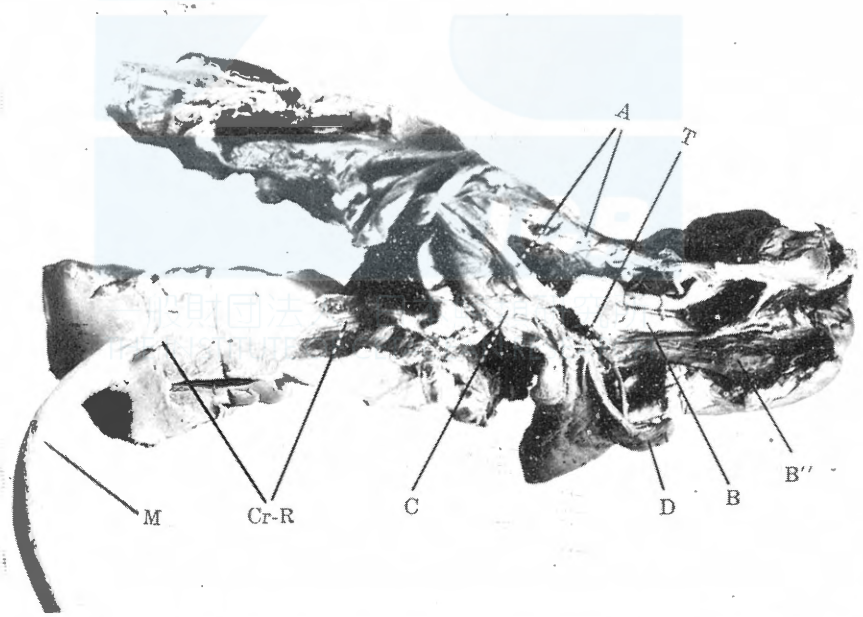

Fig. 4. (b) The *Tawara*'s node and the right crus of the *His*' bundle, seen from above (Berardius, case IV).

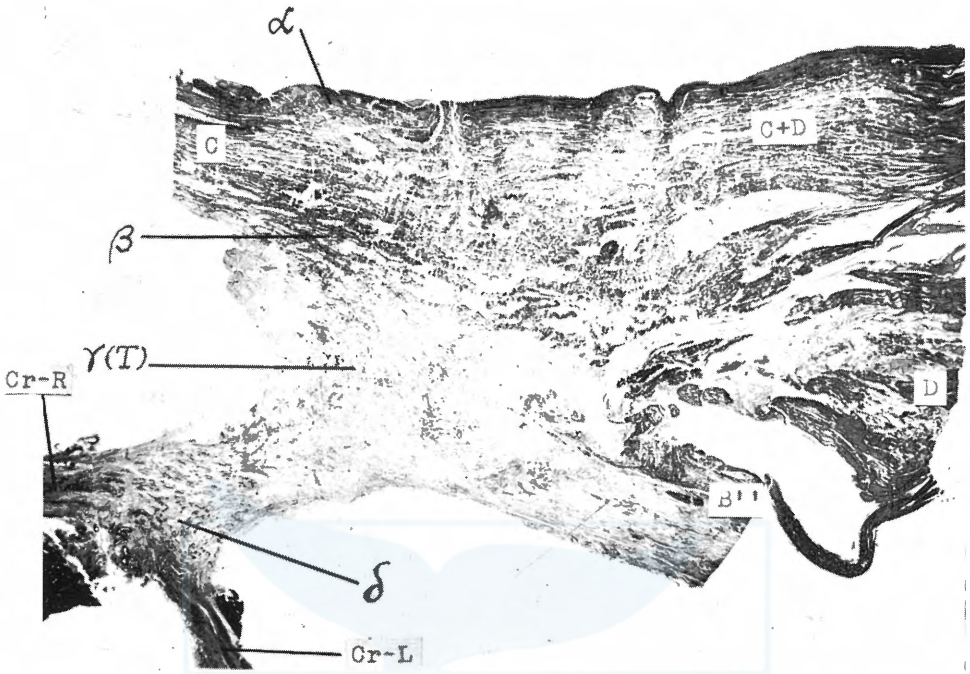

Fig. 5. (a) A microscopical section from the heart of Berardius (case IV) showing the *Tawara*'s node (T) and its neighbourhood. Note the direct continuance of muscular fibre groups of C into the node, and further into the *His*' bundle. α, β, γ, δ, Cr-R, Cr-L mean that the photographs of fig. 6 were taken about from these localities.

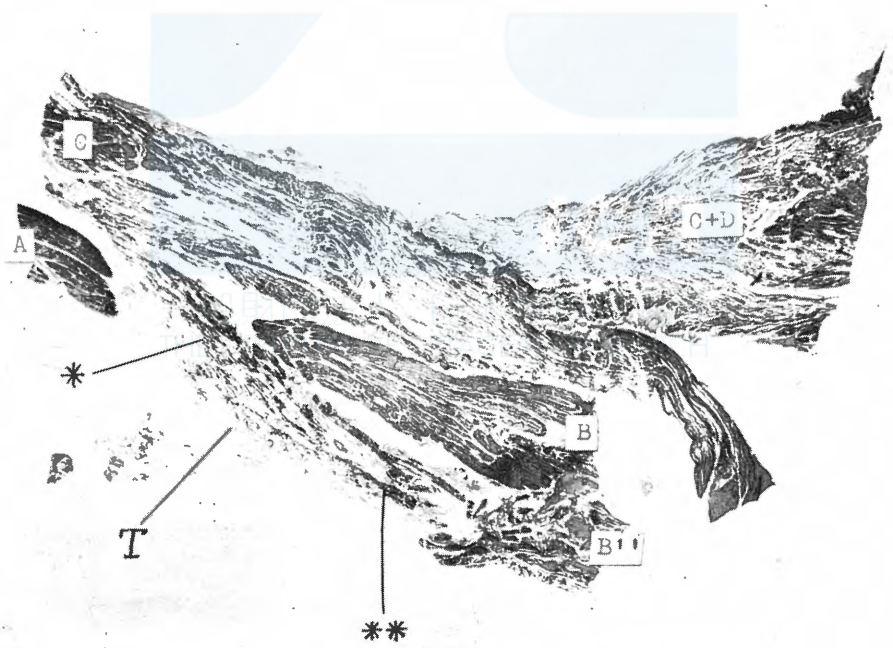

Fig. 5. (b) Another section belonging to the same series as (a).
T: *Tawara*'s node
*: transition between C and the node
**: transition between B'' and the node

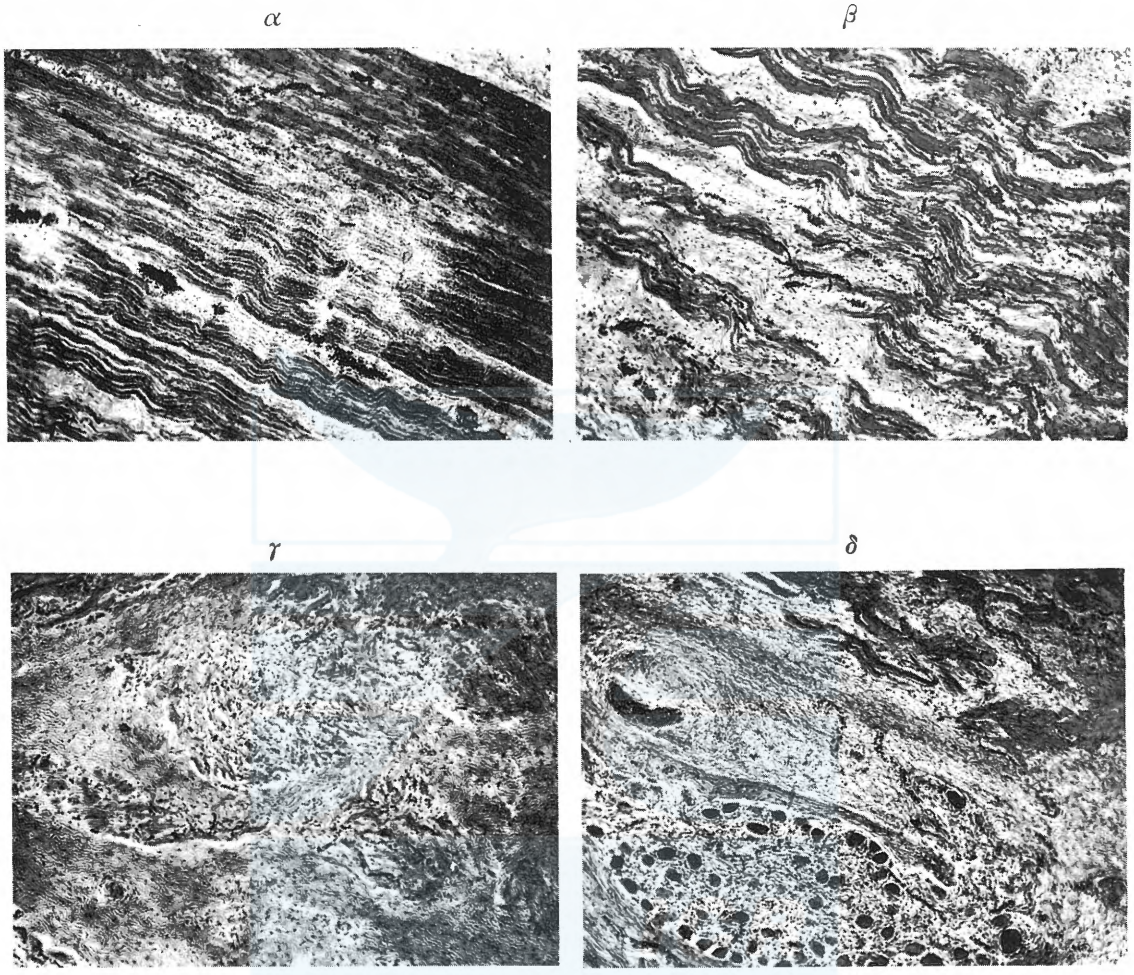

Fig. 6. Photographs taken from several places of fig. 5, magnified.

α: Superficial layer of the C-bundle. Note the relatively straight and parallel course of muscle fibre groups and pauvity of the connective tissue.

β: Deep layer of the C-bundle continuing directly into the *Tawara*'s node. Wavy course of muscle fibre groups and increase of the connective tissue.

γ: A portion of the *Tawara*'s node. Reticular muscle fibre groups between very rich connective tissue.

δ: At the bifurcation of the *His*' bundle. Swollen muscle fibres (upper right) and a group of ganglion cells (below) are seen.

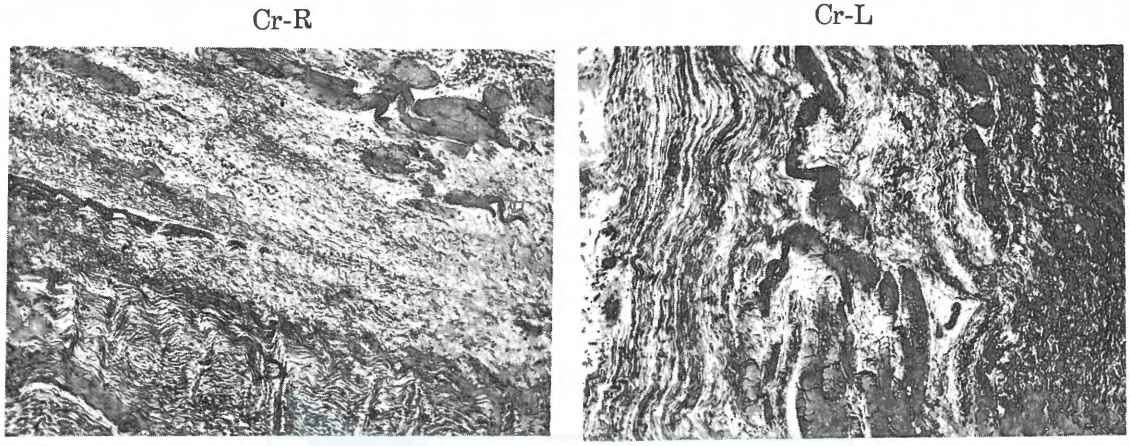

Fig. 6. Photographs taken from several places of fig. 5, magnified.

Cr-R: Right crus of the *His*' bundle, near the bifurcation. Swollen muscle fibres (upper) and a nerve bundle (left below, half hidden); between them very rich connective tissue.

Cr-L: Left crus of the *His*' bundle, near the bifurcation. Swollen muscle fibres (in the middle) and abundant collagenous fibres.

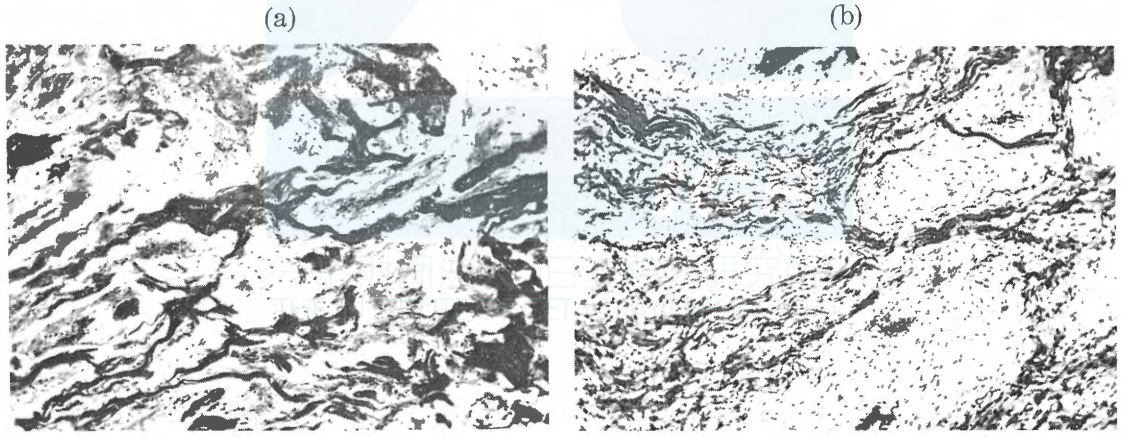

Fig. 7. The *Tawara*'s node of Berardius (case V), showing reticular arrangement of muscle fibres.

(a) Stained by hematoxylin-eosine.

(b) *Bielschowsky*'s method.