Branches of the vagus nerve destined for the heart and the adjoining great vessels in the house shrew, suncus murinus, with reference to the terminology of the vagal cardiac branches

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Branches of the Vagus Nerve Destined for the Heart and the Adjoining Great Vessels in the House Shrew, *Suncus murinus*, with Reference to the Terminology of the Vagal Cardiac Branches

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Abstract: In order to help to organize the understanding of the bewildering complexities of the innervation of the mammalian heart by the vagus nerve and to clear up of confusions as regards the vagus cardiac branches, we scrutinized these branches in the adult house shrew, *Suncus murinus*, under a stereomicroscope. A number of branches were given off from the vagus nerve not only to the heart, but also to the adjoining great vessels, both outflowing and inflowing. When compared from the developmental viewpoint, the basic conformations of these branches on two sides were found not to differ from each other, but rather presented a symmetrical configuration, the feature which has been ascertained also in mammalian embryos. Relying on developmental criteria, we classified them into the arterial porta-related and the venous porta-related groups, formulating a new terminology by naming them on the basis of their destination. This version of terminology allowed us to define the vagus cardiac branches of the house shrew more accurately than the current terminology (e.g., Nomina Anatomica), and seems to provid us a clue for clearing up confusions concerning the terminology of the vagus cardiac branches in mammals.

Key words: vagus nerve, cardiac branches, great vessels, house shrews, gross anatomy

INTRODUCTION

A great deal of work has been carried out on the innervation of the heart in mammals including humans. The studies conducted by Gómez (1958), King and Coakley (1958), Yamauchi (1973) and Pardini et al. (1987), has greatly furthered our knowledge of the structure and function of the heart (for further details refer to Yamauchi, 1973). In these studies, however, greater attention has been paid to the fine structure of the cardiac nerve branches and ganglia at the level of the light or electron microscopy, while there are markedly fewer reports dealing with the gross morphology of the cardiac innervation (Perman, 1924; Wolhynski, 1928; Hausmann, 1956; Fukuyama, 1982).

As regards the definition and naming of the vagal cardiac branches, two methods, at least, have been used: One is that based on the level of origin, and includes categories such as 'superior cervical' and 'inferior cervical' (Paturet, 1964), 'superior cervical', 'middle cervical' and 'inferior cervical' (Kopfsch, 1952; Hausmann, 1956), 'superior cervical', 'inferior cervical', 'thoracic' (Nomina Anatomica, 1989), and 'cervical', 'cervicothoracic' and 'thoracic' (Mizeres, 1963; Fukuyama, 1982). The other method is that made from the developemental viewpoint, with more importance being attached to the relationship of the vagus cardiac branches with the arterial and venous portae (His, Jr., 1891; Licata, 1954). Neither of these two methods, however, can be said to be practically satisfactory. By the former method, it is difficult to formulate satisfactory criteria because of the marked differences in the height of origin of the vagal cardiac branches between different species, different individuals of the same species and even between different sides of the same individual. By the latter method, on the other hand, one cannot define the level of origin of these branches. This troublesome problem itself is the cause of the profusion of variable interpretations and descriptions with respect to these

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branches, which sometimes have led us to confusion or misunderstanding. To settle this problem it is requested to elucidate the overall morphology of the vagus cardiac branches in animals where the heart and the great, outflowing and inflowing, vessels still retain characteristics in common with the embryos, and to evaluate this morphology from the developmental viewpoint. For this purpose we chose the house shrew, *Suncus murinus* as the materials, since the great vessels in this animal still reveal a remarkable bilateral symmetry, a configuration which can be observed at early stages of vertebrates in general. The authors believe that the present study will provide us with a clue for clearing up confusions concerning the terminology of the mammalian vagus cardiac branches, paving thus the way for more precise studies on these branches from the comparative as well as ontogenetical point of view.

MATERIALS AND METHODS

The laboratory house shrew, *Suncus murinus*, a species of the family Soricidae, Insectivora, was studied. The adult house shrews used in this study were obtained from a closed colony bred in our laboratories. The mother colony, Jic: CR, is maintained at the Central Institute for Experimental Animals, Kawasaki, Japan. Adult animals (4 females and 6 males, weighing 30–45 gm) were first anesthetized with ether, and then intraperitoneally injected with a solution of urethane (sodium ethylcarbamate, 900 mg/kg). After the shrew was completely anesthetized, the abdominal cavity was opened, and a catheter was inserted retrogradely into the abdominal aorta at the level immediately below the origin of the renal artery. Perfusion was commenced with 50 ml of normal saline containing heparin (10 IU/ml). The outflow of perfusate was via the cut inferior caval vein below the diaphragm. When the outflow was quite free of blood, the shrew was perfused with 50–100 ml of 2.5% glutaraldehyde or 4% formaldehyde in 0.1 M phosphate buffer solution and then postfixed in the same fixative for about 2–3 days. Thereafter, in order to remove fat from the materials and simultaneously to stain the peripheral nerves and ganglia en bloc, they were preserved for 5–7 days in 95–99% ethanol containing 0.001% alizarin red (sodium alizarin sulfonate, Wako, Japan). The heart and the adjacent great vessels were dissected using iridectomy scissors and fine forceps while observing under a stereomicroscope (Nikon SMZ–10) equipped with photographic attachments (Nikon UFX–2) at a magnification of 4 to 10 times.

Terminology 1

In this study 'anterior' and 'ventral', 'posterior' and 'dorsal', 'cranial' and 'superior', 'caudal' and 'inferior' will be interchangeably.

Terminology 2

In an attempt to compensate the limitation of definition and naming the vagal cardiac branches inherent to the current terminology, we combined two methods adopted by Shaner (1953) and Mizeres (1963). Our way of formulating terminology is based on two definitions, a principal and a supplementary.

Principal definition

We first classified the vagal cardiac branches primarily according to their entrance ('the arterial porta-' or 'the venous porta-related group'). They were then named according to their destination in the heart and the great vessels (Fig. 1). According to Kuratani and Tanaka (1990), the following destinations are important for the principal definition of the branches from the developmental viewpoint:

Arterial site of the heart

a) the common carotid arteries which have been reported to be derived from the ventral aortic root between aortic arches 3 and 4; b) the brachiocephalic artery derived from the paired portion of the ventral aortic root between aortic arches 4 and 6; c) the aortic arch which is composed of: i) a portion of the aorticopulmonary trunk; ii) the portion equivalent to the brachiocephalic artery, i.e., the ventral aortic root between the aortic arches 4 and 6; iii) aortic arch 4; and iv) the dorsal aortic root (refer to Barry, 1951); d) the pulmonary trunk and the arteriosum ligament derived from the aorticopulmonary trunk and aortic arch 6; e) the aorticopulmonary septum—a connective tissue septum intercalating the aorta and pulmonary trunk (Beal, 1990; Rosenquist et al. 1990; Steding et al. 1990).

Venous site of the heart

a) the caval veins derived from the common cardinal vein; b) the pulmonary veins near their opening into the pulmonary venous sinus (see just below); c) the coronary sinus; d) the caval venous sinus (sinus venarum cavarum, Nomina Anatomica) into which the superior and inferior caval veins open; e) the pulmonary venous sinus into which the pulmonary veins of both sides unite immediately before their opening into the left atrium (Auër, 1948); and f) the fossula (cordis) nervia which is bordered on the right by the caudal portion of the caval venous sinus, on the left by the pulmonary venous sinus, and caudally by the terminal portion of the coronary sinus (Belowa, 1928) (Figs. 2, 3), thus being the more limited site in the cmx of the heart.

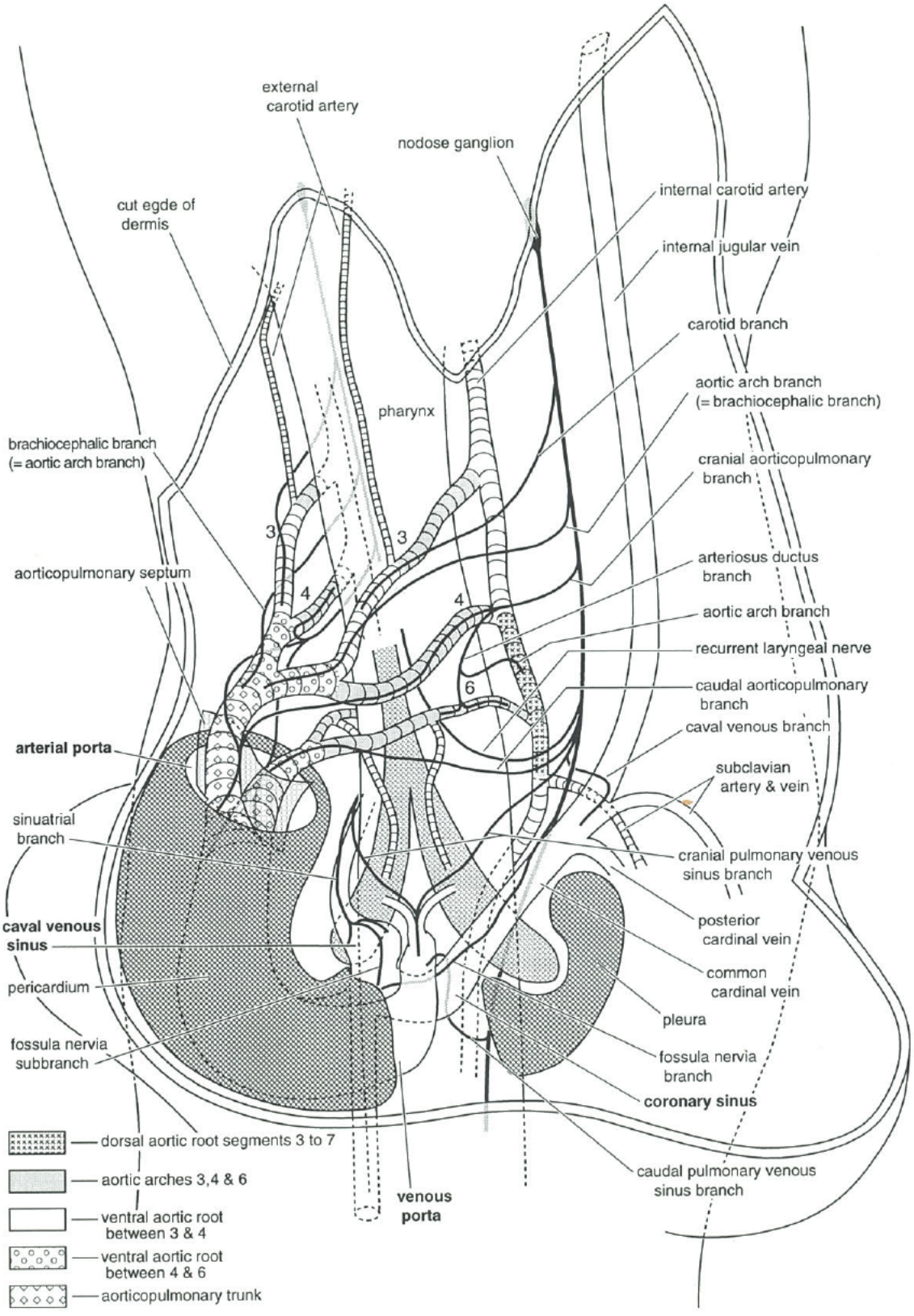

Fig. 1. A sinistro-ventral view of the vagal cardiac branches which are distributed to the heart and the adjoining great vessels, both outflowing and inflowing, at the fetal stage. This figure was conjectured to consider the bilateral equivalence of the vagal cardiac branches on two sides on the basis of the homology of the destination of these branches. The developmentally homologous portions of the aortic arches and the ventral and dorsal aortic roots between these arches are marked.

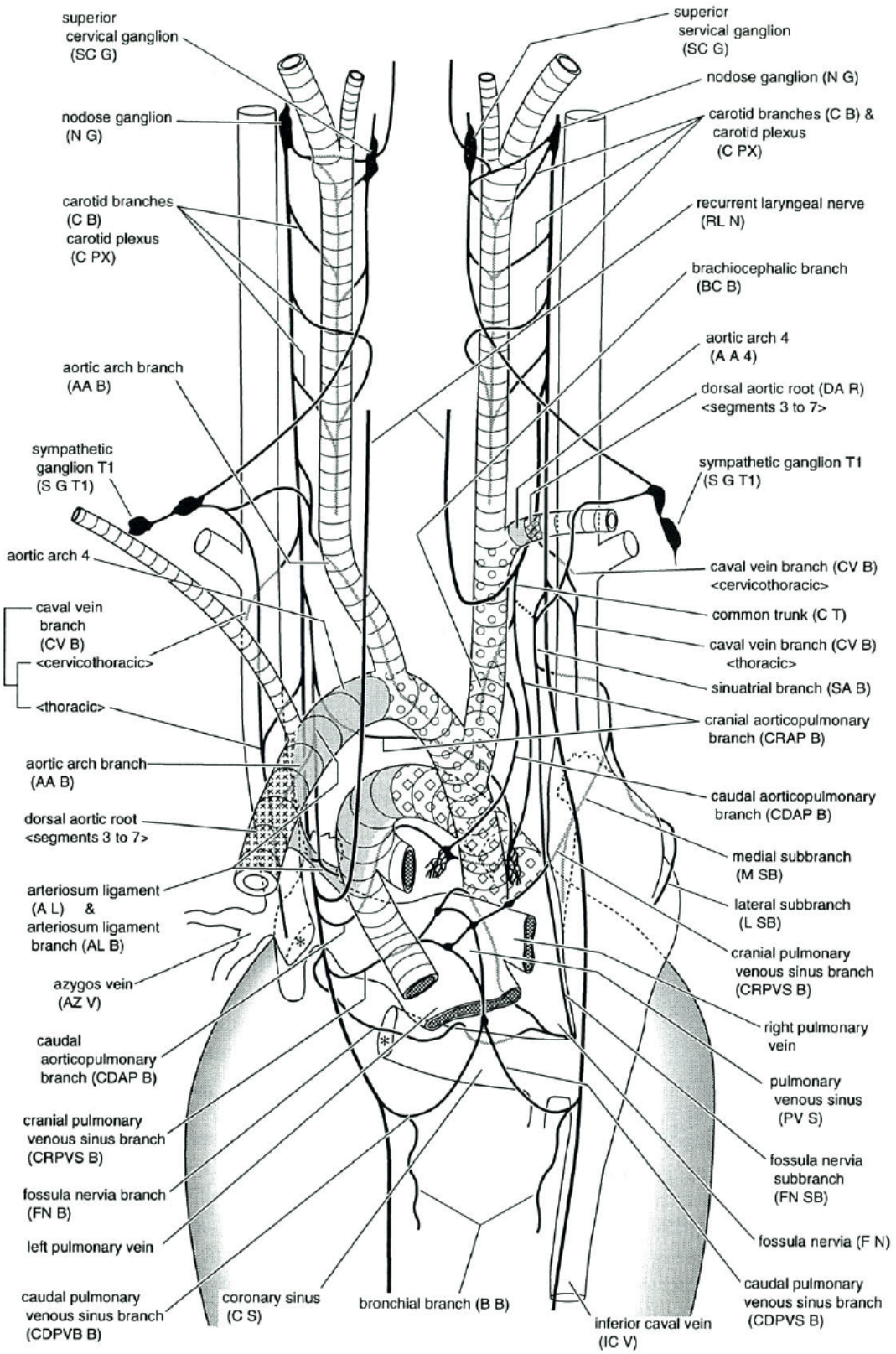

Fig. 2. A diagrammatic representation of the vagal cardiac branches of the house shrew, *Suncus murinus*, which were found in this study, viewed from dorsally. Abbreviations used in another figures are indicated. The developmentally homologous portions of the aortic arches and the ventral and dorsal aortic roots between these arches are indicated with the same marks as in Figure 1. In order to reveal the contour of the left atrium, the boundary region between the left superior caval vein and coronary vein has been resected (asterisks).

Supplementary definition

The principal definition was supplemented with additional descriptions of their relative height of origin from the vagus nerve trunk to the vertebrae, as follows: 'cervical' (C1–5 V), 'cervicothoracic' (C6-T1 V, refer to Mizeres 1963), 'thoracic' (T2-T12 V); 'juxta-cervicothoracic (C4–5 V)' (see Fig. 4), and with description of their relative height of origin to that of the recurrent laryngeal nerve such as 'suprarecurrent(ly)', 'recurrent (ly)', 'infrarecurrent(ly)' and 'juxta-recurrent(ly)'.

RESULTS

General morphology of the vagus nerve and its anatomical relationship to the trachea, bronchus and to the esophagus

In the house shrew, the vagus nerve was observed to take a caudalward course along the lateral aspect of the common carotid artery toward the inlet of the thorax (Figs. 2, 3). The tracheal bifurcation was considerably shifted from the midline to the right, being located immediately dorsal to the boundary between the caval venous sinus and the pulmonary venous sinus (Fig. 3). The right vagus nerve traversed toward the esophageal hiatus of the diaphragm by crossing dorsal to the tracheal bifurcation, while the left vagus nerve coursed at good distance away from this bifurcation. Despite these topographical relations of the bilateral asymmetry of the heart and of the great vessels (the aortic arch, the right and left superior caval veins, and the inferior caval vein), the fundamental symmetry of the branches from the vagus nerve to these structures was not vanished in this species (Fig. 2). Further description proceeds with respect to the branches arising from the vagus nerve on the right side.

Right side

The vagus nerve in the cervical, cervicothoracic and thoracic regions

In most (7 of 10) house shrews, the right vagus nerve gave off the recurrent laryngeal nerve in its caudalward course in the cervical or cervicothoracic regions, and both nerves coursed caudalward alongside the common carotid artery in the cervicothoracic regions toward the superior thoracic aperture (Figs. 2, 5). After passing this inlet, the vagus nerve crossed ventral to the subclavian artery immediately medial to the right superior caval vein (Figs. 2, 3). Here it wrapped caudally this artery from ventral to dorsalwards and turning medially, and coursed caudalward alongside the esophagus, being located dorsomedial to the right superior caval vein. While continuing its further caudalward course, the right vagus nerve, as described above, crossed dorsal to the tracheal bifurcation and the right pulmonary vein and continued its course toward the esophageal hiatus in the diaphragm (Fig. 3).

The right vagus nerve and the recurrent laryngeal nerve were found to emit the arterial and venous porta-related branches to the heart and the great vessels, as follows:

Arterial porta-related group—carotid branches, brachiocephalic branch, cranial aorticopulmonary branch, caudal aorticopulmonary branch;

Venous porta-related group—caval vein branches, sinuatrial branch and its three subdivisions (lateral subbranch, medial subbranch with a cranial pulmonary venous sinus branch, and fossula nervia subbranch), and caudal pulmonary venous sinus branches.

Arterial porta-related group on the right side

In its caudalward course along the common carotid artery, the right vagus nerve gave off serially fine filamentous *carotid branches* which were joined consecutively with each other and also with filaments from the sympathetic trunk, thus forming a loose meshwork of nerve filaments around the common carotid artery, the *carotid plexus* (Fig. 2; refer to Riegele, 1926). The *brachiocephalic branch* (Figs. 2–4) arose in common with the cranial and caudal aorticopulmonary branches and, sometimes, with the sinuatrial branch described below as well. The common trunk for these branches was found to arise from the recurrent laryngeal nerve approximately at the level of the body of the 6th cervical vertebra which is characterized by its great anterior (or ventral: see Terminology 1) tubercle of the transverse process (Fig. 4), that is, near the cranial limit of the cervicothoracic region. As its name implies, the brachiocephalic branch was distributed to the artery of the same name, a portion which is reported to have developmentally derived derived from the ventral aortic root between the 3rd and 4th aortic arches (refer to Barry, 1951). The *cranial aorticopulmonary branch* (Figs. 2, 4) arose with the common trunk described above from the recurrent laryngeal nerve, coursed caudalward along the brachiocephalic artery on its lateral side, and ran down along the cranial aspect of the aortic arch adjacent to the origin of the brachiocephalic artery, reaching the arterial porta. The branch traversed thereafter the ventral aspect of the aorticopulmonary septum (Fig. 3; see also Fig. 1) where it communicated with the fellow branch of the left side (Figs. 3, 4, 6). After further caudalward coursing in this septum and spiraling clockwise along the upstream circulation, the joined aorticopulmonary branch extended as far as the root of these two great arteries. Here it further communicated with the branches of the

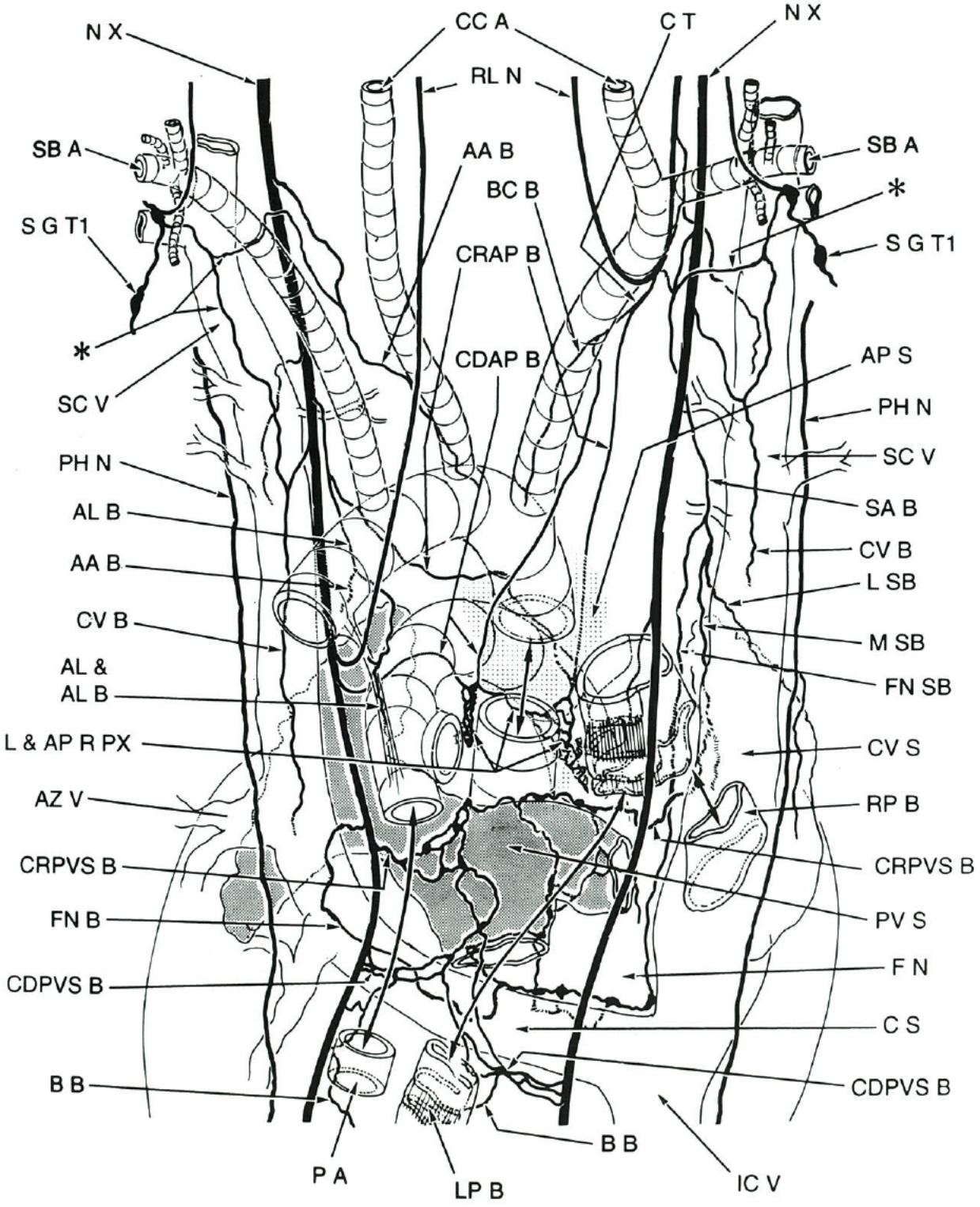
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Fig. 3

caudal aorticopulmonary branch (described in the following paragraph), thus forming a component of the aorticopulmonary root plexus (Fig. 3) which corresponds to the truncoconal plexus (Licata, 1954) or the "Bulbusgeflecht" of His, Jr. (1891). Careful observation under the stereomicroscope allowed us to trace the nerve filaments from this aorticopulmonary root plexus through the plexus around the left and right coronary arteries (=the plexus cardiaci anteriores sinister et dexter of Ssinelnikow, 1928) as far distally as the ventral and dorsal ventricular sulci, respectively (not depicted). The *caudal aorticopulmonary branch* (Figs. 2–4), soon after its arising from the common trunk described above, traversed the lateral aspect of the brachiocephalic artery, then entering the arterial porta. It then took an oblique and caudalward course from right to left around the lateral and caudal aspect of the root of the aorta, reaching the dorsal aspect of the aorticopulmonary septum (Fig. 3), where this caudal aorticopulmonary branch is joined by the fellow branch of the left side. The now 'joined caudal aorticopulmonary branch' coursed in this septum and communicated with the joined cranial aorticopulmonary branch, thus forming a connecting loop of nerve branch spanning between these two joined branches. While its traverse of the aorticopulmonary septum, the caudal aorticopulmonary branch emitted numerous fine branches which were connected with each other, thus forming the aorticopulmonary root plexus. This caudal aorticopulmonary branch was also found to communicate with the ganglion cardiacum of Wrisberg (refer to Hausmann, 1956) located between the concavity of the aortic arch and the ventral aspect of the right pulmonary artery.

Venous porta-related group on the right side

The *caval vein branches* comprised of the cervicothoracic and thoracic ones (Figs. 2–4), the former issuing from the recurrent laryngeal nerve not far from its origin from the vagus nerve and distributed the ventral aspect of the superior caval vein, and the latter arising from the vagus nerve immediately above the sinuatrial branch (described below), receiving a contribution from the inferior cervical ganglion of the sympathetic trunk, and distributed to the dorsal aspect of this vein.

The *sinuatrial branch* (Figs. 2–5) was a solid branch which, as aforementioned, arose infrarecurrently from the vagus nerve, or, sometimes, recurrently in conjunction with the common trunk of the brachiocephalic branch and the cranial and caudal aorticopulmonary branches (Figs. 2, 4; dotted line). Soon after entering the thorax, this sinuatrial branch received a contribution from the sympathetic ganglion in the cervicothoracic region (the inferior cervical ganglion of human beings), and coursed caudally now in close vicinity with the medial aspect of the superior caval vein. When arriving at a point slightly cranial to the sinuatrial boundary, the branch divided into three—medial and lateral subbranches, and the fossula nervia subbranch. The *medial* and *lateral subbranches* took their course toward the terminal sulcus which demarcated the boundary between the caval venous sinus and the right atrium. Just below this sulcus, the parietal layer of the pericardium folded internally upon itself, continuing into the visceral layer, thus forming the venous porta. The medial and lateral subbranches now traversed in the medial and lateral limbs of the terminal sulcus, respectively, thus forming together a horse-shoe-shaped loop of nerve branch wrapping the sinuatrial boundary from cranialward (Figs. 2–4). From the medial subbranch of the sinu-

Fig. 3. A diagram showing the vagal cardiac branches entering the arterial and venous porta, viewed from dorsally. The pulmonary venous sinus plexus with minute ganglia is seen on the wall of the same-named sinus. The initial portion of the aortic arch has been removed so as the vagal cardiac branches entering the arterial and venous porta to be more clearly observed. The right and pulmonary arteries, the greatest portion of the trachea and the initial portion of the principal bronchus have been removed so as the pulmonary venous sinus with ganglia, the caval venous sinus and the coronary sinus to be clearly observed. The contribution from the sympathetic trunk is indicated with asterisks.

Abbreviations: AA B, aortic arch branch; AC A, ascending cervical artery; A L, arteriosum ligament; AL B, arteriosum ligament branch; AP R PX, aorticopulmonary root plexus; AP S, aorticopulmonary septum; AZ V, azygos vein; B B, bronchial branch; BC B, brachiocephalic branch; C B, carotid branch; CC A, common carotid artery; CDAP B, caudal aorticopulmonary branch; CDPVS B, caudal pulmonary venous sinus branch; CRAP B, cranial aorticopulmonary branch; CRPVS B, cranial pulmonary venous sinus branch; C S, coronary sinus; C T, common trunk; CV B, caval vein branch; CV S, caval venous sinus; C6 S N, 6th cervical spinal nerve; C4–7 V, 4th to 7th cervical vertebrae; E, esophagus; F N, fossula nervia; FN B, fossula nervia branch; FN SB, fossula nervia subbranch of sinuatrial branch; GA T, great anterior tubercle of 6th cervical vertebra; IC V, inferior caval vein; L, connecting loop between cranial and caudal aorticopulmonary branches; L SB, lateral subbranch of sinuatrial branch; LSC V, left superior caval vein; LP B, left principal bronchus; LX, larynx; M SB, medial subbranch of sinuatrial branch; NG, nodose ganglion; N X, vagus nerve; P A, pulmonary artery; P B, preventricular branch of right coronary artery; PH N, phrenic nerve; PV S, pulmonary venous sinus; RL N, recurrent laryngeal nerve; RP B, right principal bronchus; RSC V, right superior caval vein; SA B, sinuatrial branch; SB A, subclavian artery; SC G, superior cervical ganglion; SC V, superior caval vein; S G 1, sympathetic ganglion at the level of Th1; S T, sympathetic trunk; T, trachea; T1 V, first thoracic vertebra; 3, 4, 6, 3rd, 4th, and 6th aortic arches.

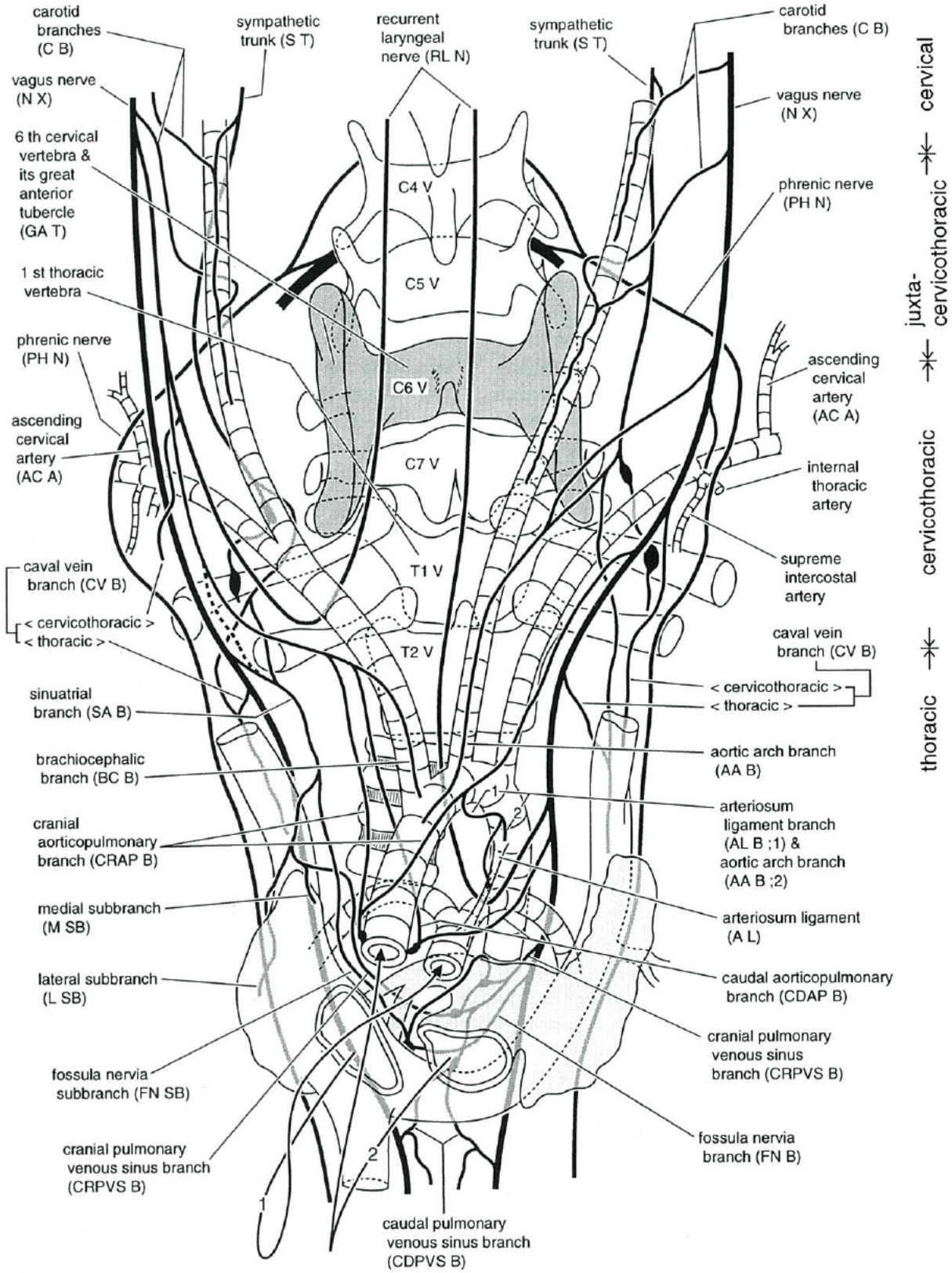


Fig. 4. Diagram showing the vagus nerve and its branches in the cervical, cervicothoracic and thoracic regions of the house shrews, viewed from ventrally. Abbreviations are also indicated. The right and left ventricles, the initial portion of the aorta and pulmonary trunk been removed so as the vagal cardiac branches entering the arterial and venous porta to be more clearly observed. The directions of the blood flow in the right and left ventricles are shown by line 1 and 2, respectively.

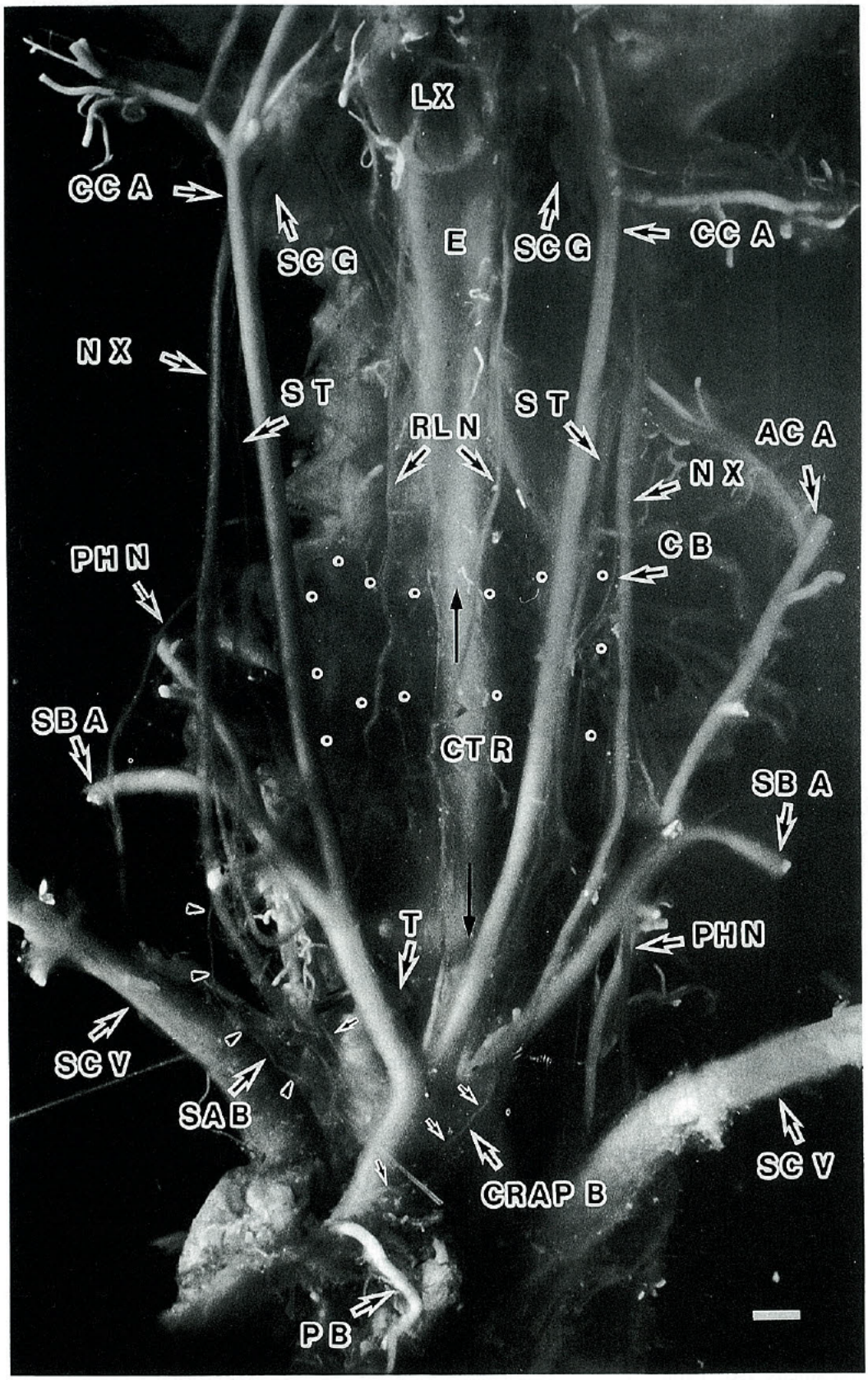


Fig. 5. A photograph showing the general features of the vagus nerves of the house shrew, *Suncus murinus*. Most of the trachea has been removed. The contour of the 6th cervical vertebra is dotted. Long arrows indicate the cranial and caudal boundaries of the cervicothoracic region. The course of the cranial aorticopulmonary branches and the sinuatrial branches are indicated by small arrows and arrow heads, respectively (see also Fig. 3). Scale bar = 1 mm.

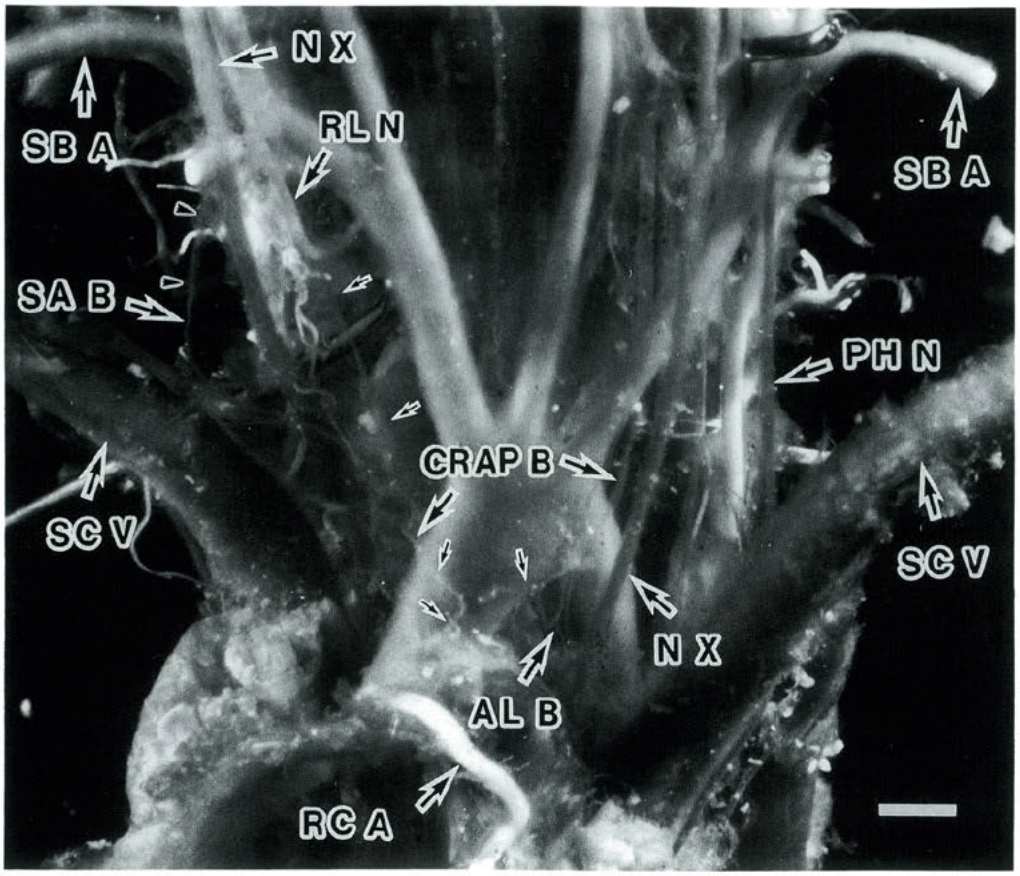


Fig. 6. A regional enlargement of the Figure 2. The cranial aorticopulmonary branches of both sides are more noticeable. Scale bar = 1 mm.

atrial branches concerned, arose a solid branch—the *cranial pulmonary venous sinus branch*, which crossed dorsally to the interatrial sulcus (see Licata, 1954), arriving at the cranial aspect of the right pulmonary vein near its opening into the pulmonary venous sinus. As its name implies, this branch participated in the formation of the cranial pulmonary venous sinus plexus or 'plexus atriorum anterior' of Ssinelnikow (1928). The *fossula nervia subbranch* (Figs. 2–4), still a solid branch, arose from the sinuatrial branch described above, and pushed its way caudalward in the interatrial sulcus. After crossing the tracheal bifurcation ventrally, this branch arrived at the fossula nervia described above. Here, the branch formed a component of the plexus of the fossula nervia in which ganglia were located. The corresponding branch has previously, though not termed as such, being described as well in the calf embryos by Shaner (1930) as branch 'X' and in the human embryo in the 9th week by Licata (1954) as 'a branch of the sinal (sinuatrial, in this study) nerve to the ganglion in the interatrial sulcus' (see Table 2).

In its further caudalward course but before crossing dorsal to the pulmonary radix, the vagus nerve, being located slightly dorsal to the superior caval vein, issued branches to the dorsal and ventral aspect of the tracheal bifurcation and the principal bronchus (not depicted). Having crossed dorsal to the tracheal bifurcation, the vagus nerve entered the interval space between the principal bronchi of both sides, and here gave rise to the *caudal pulmonary sinus branches* (Figs. 2, 3) which, after issuing the branches to the bronchus, coursed medially and cranially to the dorso-caudal wall of the pulmonary sinus, forming, together with the fellow branches of the left side, the caudal pulmonary venous sinus plexus, which seemingly corresponds to the plexus atriorum posterior of Ssinelnikow (1928).

Left side

The vagus nerve in the cervical, cervicothoracic and thoracic region

In the cervical and cervicothoracic regions, the left vagus nerve descended along the lateral aspect of the common carotid artery to the inlet of the thorax (Figs. 2–5). After entering the thorax, the vagus nerve coursed caudally in close relationship with, or even adhering to, the medial aspect of the left superior caval vein, crossing ventral to the aortic arch and thereafter the arteriosum ligament (Fig. 2). Just caudal to this arteriosum ligament, the vagus nerve emitted the recurrent laryngeal nerve. Thereafter, the nerve crossed

dorsal to the coronary sinus, coursing caudally, reached the dorsal aspect of the left pulmonary radix; in this place the nerve was located dorso-lateral to the pulmonary artery, dorsal to the left principal bronchus and the left pulmonary vein (Fig. 3), and ventral to the esophagus. The vagus nerve took its further caudalward course now along the side wall of the esophagus, entering finally the esophageal hiatus and then the abdominal cavity (not depicted).

Along this course, the vagus nerve gave rise to the arterial and venous porta-related branches to the heart and the great vessels adjacent to the heart. Importantly, the greatest majority of them were comparable with those of the right side. They are as follows:
Arterial porta-related group—carotid branches, aortic arch branches, cranial aorticopulmonary branch and its subdivisions (arteriosum ligament branch with the aortic arch branch), caudal aorticopulmonary branch;
Venous porta-related group—caval vein branches, fossula nervia branch, cranial and caudal pulmonary sinus branches.

Arterial porta-related group on the left side

The *carotid branches*, like their equivalent on the right side, joined consecutively with each other and formed component of the carotid plexus around the common carotid artery (Fig. 2). This plexus received also with filaments from the sympathetic trunk. At the cervicothoracic level, the left vagus nerve consistently emitted a solid branch—the *aortic arch branch* (Figs. 2–4), which, receiving a contribution from the sympathetic ganglion in the cervicothoracic region (the inferior cervical ganglion of human beings), coursed down along the left common carotid artery on its ventral aspect, reaching the aorta adjacent to the origin of this carotid artery. This portion of the aorta is reported to be derived developmentally derived from the ventral aortic root between the 3rd and 4th aortic arches (Barry, 1951), and thus homologous with the brachiocephalic artery of the right side (confer to Fig. 1). The *cranial aorticopulmonary branch* (Figs. 2–4) arose from the vagus nerve at the cervicothoracic level and ran down along the left common carotid artery and the aortic arch on their ventral aspect. After giving off the arteriosum ligament branch (described later), the branch changed its course from caudal to medial and crossed ventral aspect of the aortic arch as far as the ventral aspect of the aorticopulmonary septum (Fig. 3; see also Fig. 1). Descending in this septum, it turned in a clockwise direction along the upstream circulation and then communicated with the fellow branch of the right side, forming in a part of the aorticopulmonary root plexus and extending its innervation along the right coronary artery as far as the ventricle (not depicted). The cranial aorticopulmonary branch gave off a ramus, the *arteriosum ligament branch* (Figs. 2, 3, 6) which coursed between the wide opened interval between the aortic arch and the pulmonary trunk, reaching the same-named ligament and the nearby portion of the aorta. The arteriosum ligament branch gave off a minute branch, the *aortic arch branch* (Figs. 2, 3, 6) to the aortic arch.

The *caudal aorticopulmonary branch* (Figs. 2, 6, 7) arose from the vagus nerve immediately caudal to the origin of the recurrent laryngeal nerve. Coursing in the upstream direction along with the left pulmonary artery and then the pulmonary trunk, it passed the arterial porta, reaching the dorsal aspect of the aorticopulmonary septum where it communicated with the ipsilateral caudal aorticopulmonary branch; traversing further in this septum and turning in a clockwise direction along the upstream circulation. The now joined caudal aorticopulmonary branch took in part of the formation of the aorticopulmonary root plexus and the connecting loop (see Right side) and extended its innervation along the left coronary artery as far as the ventricle (not depicted).

Venous porta-related group on the left side

The left vagus nerve issued *caval vein branches* at the cervicothoracic and thoracic levels. They arose suprarecurrently and were distributed to the ventral or dorsal wall of this vein (Figs. 2–4). The caval vein branch arising at the thoracic level received a contribution from the sympathetic ganglion in the cervicothoracic region (the inferior cervical ganglion of human beings). Approximately at the level of (or more strictly just caudal to) the opening of the azygos vein, the vagus nerve issued the *fossula nervia branch* (Figs. 2–4) which traversed dorsal wall of this sinus, and then in the coronary sulcus toward the right side to enter the fossula nervia. In this fossula, the branch communicated with the fossula nervia subbranch on the right side. This left fossula nervia branch is comparable in every way to the 'left sinal branch' of the human embryo described by Licata (1954) and Navaratnam (1965).

Immediately caudal to the origin of the left recurrent laryngeal nerve, the *cranial pulmonary sinus branch* (Figs. 2–4, 7) arose. This branch passed medially across the roof of the pulmonary venous sinus, communicating with the branch of the same name arising from the medial subbranch of the sinuatrial branch on the right side, thus forming the cranial pulmonary venous sinus plexus on the roof of the left atrium.

The *caudal pulmonary sinus branches* (Figs. 2–4, 7) arose from the left vagus nerve, where this nerve trunk, having crossed dorsal to the coronary sinus, reached the

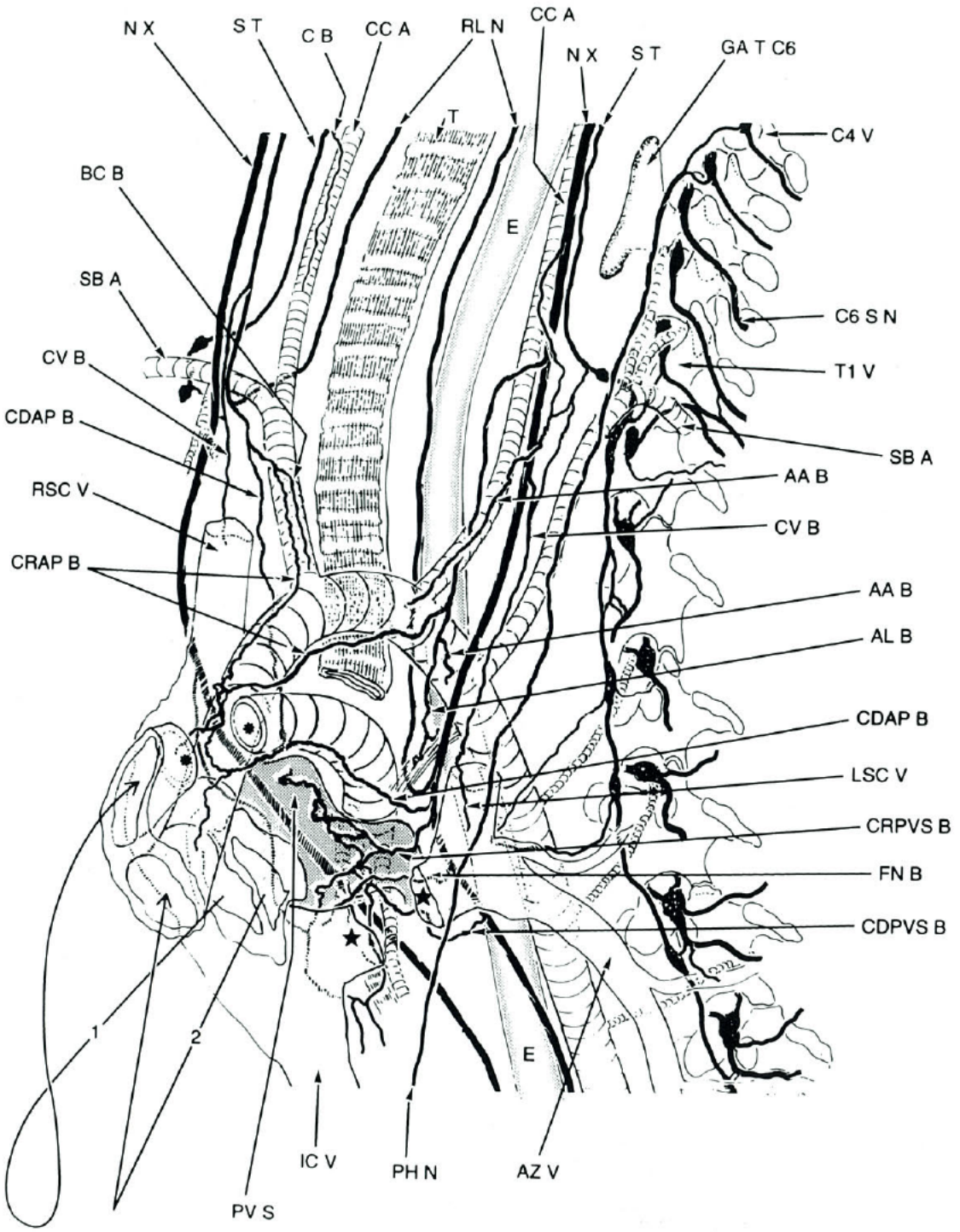


Fig. 7. A diagrammatic representation showing the vagal cardiac branches of the vagus nerves, viewed from sinistroventrally. The left and right ventricles, the initial portion of the pulmonary trunk and a portion of the coronary sinus have been removed so as the vagal cardiac branches entering the arterial and venous porta to be more clearly observed. The direction of the blood flow in the right and left ventricles are indicated by line 1 and 2, respectively.

interval between the principal bronchi of the bilateral sides. These branches, after giving off branches to the bronchus, coursed medially across the dorsal aspect of the left pulmonary vein. Running ventral to the left pulmonary artery and to the left principal bronchus, the caudal pulmonary sinus branches communicated with their fellows of the right side, thus forming the caudal pulmonary venous sinus plexus (Fig. 3).

DISCUSSION

Bilateral symmetry of the vagal cardiac branches in the house shrew—a key figure

We compared the vagal cardiac branches on the two sides from the developmental viewpoint, and classified them on the basis of the homology of their destination. We found that the fundamental features of the vagal cardiac branches do not different on the two sides and that each pair of branches is rather remarkably symmetrical in appearance. This finding is in a good accordance with the description of Shaner (1953), who, in his Figures 1 and 2 illustrating 40 and 79 mm calf embryos, respectively, demonstrated that the vagal cardiac branches at the early stages of development show a remarkable degree of bilateral symmetry.

The method of formulating terminology used in this study

In an attempt to circumvent the limitation of definition and naming currently used, we formulated in this study a new terminology, abandoning the current concept of the 'superior', 'inferior' and 'thoracic' vagus cardiac branches of the Nomina Anatomica. Comparison of this of terminology with the current terminology is shown in Table 1. The principal advantages of our classification and naming are that the vagal cardiac branches of the house shrew can be much more accurately defined as compared with the descriptions given in previous work; furthermore, to us very fortunately, the cardiac branches in this species can be easily compared with those in other mammals including human beings, and they can be more easily discussed from the standpoint of development. The vagal cardiac branches, their way of branching and the corresponding cardiac plexuses in the house shrew are summarized and compared with the branches of the Nomina Anatomica in Table 1.

Validity of our terminology in developmental studies

As shown in Table 2, our terminology is in very good agreement with that of Shaner (1953) who elaborated a detailed description of the vagal cardiac branches of calf embryos, attaching great importance to their relationship not only with the heart itself, but also with the great vessels, both outflowing and inflowing. This table shows furthermore that the branching of the vagus cardiac branches of the house shrew (dotted lines) is well compatible with the description by Shaner (1953) in calf embryos (gothicized lines). The Table 2 also demonstrates that our terminology is quite comparable with that of the vagal cardiac branches of humans which was adopted by Perman (1924). This fact seems to substantiate the validity of our terminology and to give us a foothold for re-examination of the current terminology of the vagus cardiac branches of humans.

Re-examination of the current terminology of the Nomina Anatomica

As regards the superior vagus cardiac branches of humans, Hausmann (1956), for example, described in his very detailed report that the left superior cardiac branches arose on the level with the middle portion of the thyroid gland, coursing ventral to the aortic arch and connecting with the ganglion cardiacum of Wrisberg in the aorticopulmonary root plexus. The right superior vagal cardiac branch, on the other hand, crossed dorsal (and not ventral as is the case for the branch on the left) to the aortic arch and joined with the inferior vagal cardiac branches, forming thus the paratracheal portion of the deep cardiac plexus. From the results of our study, however, it can be seen that the left vagal cardiac branch described by Hausmann obviously corresponds to the cranial aorticopulmonary branch in our study, while the right vagal cardiac branch corresponds to the caudal aorticopulmonary branch. This means that these two branches given the same name by Hausmann ('rami cardiaci craniales' in his terminology) are, according to our terminology, of different nature. From the developmental standpoint, it can be also mentioned that the cranial aorticopulmonary branch is located cranial to the ventral aortic root between the aortic arch 4 and 6, while the caudal aorticopulmonary branch is situated caudal to this ventral aortic root (see Fig. 1). Our opinion in this respect is thus that the current term 'superior vagal cardiac branches' has been applied to different branches on different sides, and is in need of a clearer definition from the developmental point of view as was performed in this study.

Of much more of complexity and obscurity is the current definition of the 'inferior vagal cardiac branches'. Our investigation of the literature including Perman (1924), Hausmann (1956), and Mizeres (1963) revealed that quite variable interpretations and descriptions have been made with respect to these branches, especially as to their relationship to the recurrent laryngeal nerve. In an attempt to prevent confusion, Hausmann (1956) applied the modifier 'medius' to vagal cardiac branches arising recurrently, and 'caudalis (=inferior)' to those arising infrarecurrently. According to the Nomina Anatomica (6th ed), the vagal cardiac branches are divided into the superior cervical cardiac branch, the inferior cervical and the thoracic cardiac branches. It must, however, be stressed that this terminology system still imposes restrictions upon the accurate definition of each cardiac branch. In fact, as we

Table 1. Classification of arterial and venous porta-related cardiac branches of the vagus nerve in the house shrew, and comparison with current terminology of the Nomina Anatomica. Asterisk indicates the level of origin of these branches according to the vertebral level. They are defined as follows: superior cervical (C1-C5), cervicothoracic (C6-T1), thoracic (T2-T12), and juxtacervicothoracic (C4-C5). Dagger indicates their levels of origin in relation to that of the recurrent laryngeal nerve.

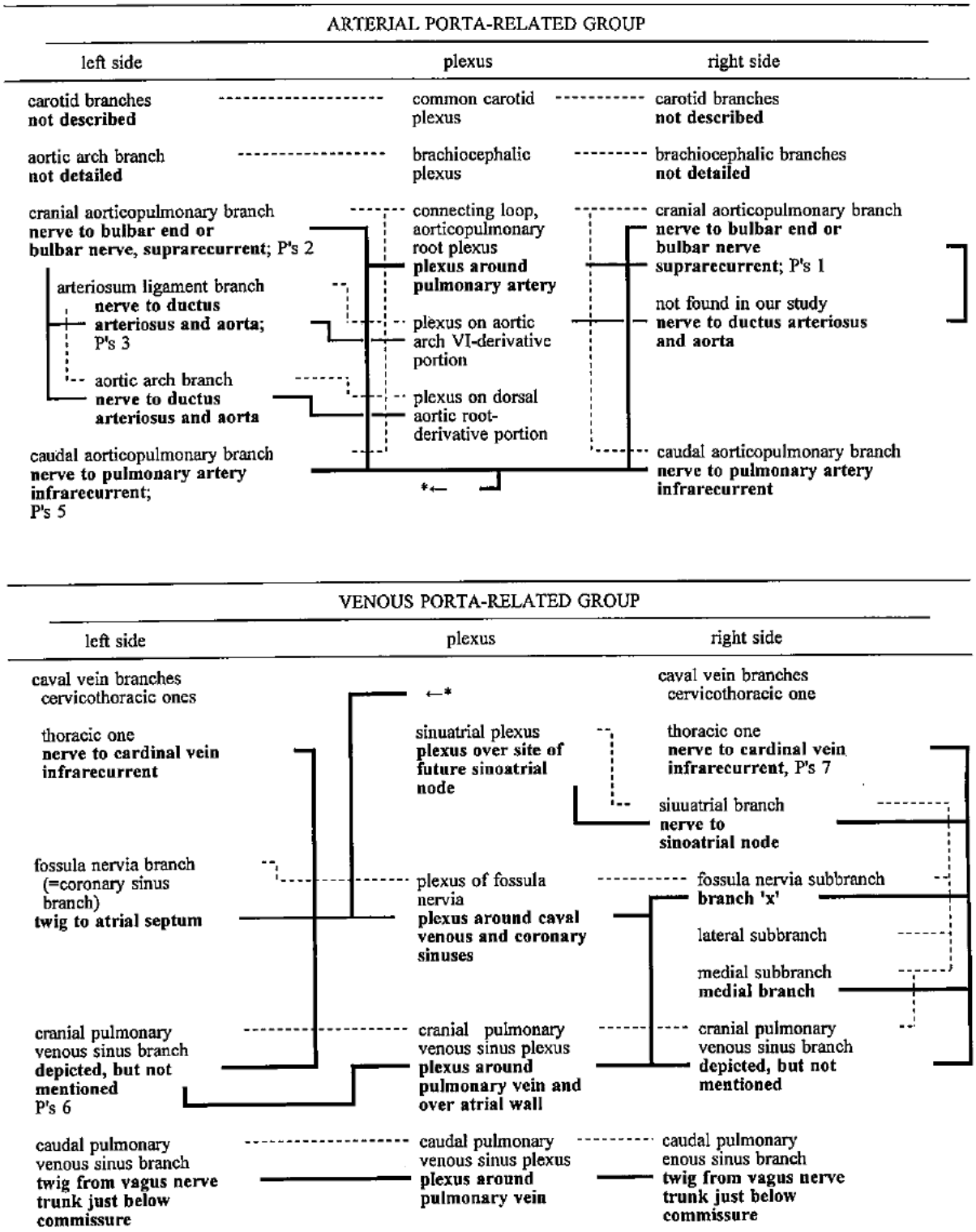
current terminology of Nomina Anatomica	ARTERIAL PORTA-RELATED GROUP		
	left side	plexus	right side
superior cervical cardiac branches of left side ↓	**carotid branches** cervical * suprarecurrent †	**common carotid plexus**	**carotid branches** cervical suprarecurrent
	aortic arch branch cervicothoracic suprarecurrent to: derivative of ventral aortic root between arches 4 & 6	**brachiocephalic plexus**	**brachiocephalic branch** juxtacervicothoracic recurrent to: derivative of ventral aortic root of aortic arches 4 & 6
↑ inferior (on left side) and superior (on right side) cervical cardiac branches ↓	**cranial aorticopulmonary branch** cervicothoracic suprarecurrent	**connecting loop, aorticopulmonary root plexus**	**cranial aorticopulmonary branch** juxtacervicothoracic recurrent or infrarecurrent
	arteriosum ligament branch	**plexus on aortic arch VI-derivative portion**	
	aortic arch branch	**plexus on dorsal aortic root-derivative portion**	
↑ inferior cervical cardiac branches of right side	**caudal aorticopulmonary branch** thoracic infrarecurrent		**caudal aorticopulmonary branch** juxtacervicothoracic, recurrent or infrarecurrent

current terminology of Nomina Anatomica	VENOUS PORTA-RELATED GROUP		
	left side	plexus	right side
	caval vein branches **cervicothoracic one** suprarecurrent		**caval vein branches** **cervicothoracic one** recurrent
	thoracic one suprarecurrent		**thoracic one** infrarecurrent
		sinuatrial plexus	**sinuatrial branch** juxtacervicothoracic recurrent or infrarecurrent
↑ thoracic cardiac branches (not clearly defined) ↓	**fossula nervia branch** (=coronary sinus branch) thoracic infra(but juxta)recurrent	**plexus of fossula nervia** (or around orifice of coronary sinus)	**fossula nervia subbranch** **lateral subbranch** **medial subbranch**
	cranial pulmonary venous sinus branch thoracic infra(but juxta)recurrent located ventrocranial to bronchus	**cranial pulmonary venous sinus plexus**	**cranial pulmonary venous sinus branch** located ventrocranial to bronchus
	caudal pulmonary venous sinus branch thoracic infrarecurrent located dorsocaudal to bronchus	**caudal pulmonary venous sinus plexus**	**caudal pulmonary venous sinus branch** thoracic infrarecurrent located dorsocaudal to bronchus

found in this study of house shrew, these terms can not define all the vagal cardiac branches, which pass the arterial or, especially, the venous porta to be distributed to a number of topographically and ontogenetically important portions of the heart and the adjacent great vessels (see Table 1). The conclusion derived from this study are thus as follows:

1. The present terminology and description of the vagal cardiac branches (superior and inferior; or superior, middle and inferior; or cervical, cervicothoracic and

Table 2. Arterial and venous porta-related branches of the vagus nerve in the house shrew, and comparison with those of Shaner (1953) and Perman (1924). Solid lines indicate the formation of the cardiac plexus by the branches of Shaner, while broken lines indicating that by branches of our study. Gothicized branches are vagal cardiac branches of calf embryos described by Shaner (1953). Perman (1924)'s branches are indicated as P's 1, 2, 3 and 5; P's 4 was not found in our study. Asterisk shows the connection between the plexus of the arterial porta-related group and that of the venous porta-related group.



thoracic) requires re-examination from the developmental view point.

2. In formulating more practical terminology to describe the vagal cardiac branches, it is important for us to select criteria for nomenclature from the developmental standpoint, with primary importance being laid on the final distributions of the branch in the heart and the adjacent great vessels and, especially, on its relationship with the arterial and the venous porta.

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