The Development of the Interventricular Septum of the Human Heart; Correlative Morphogenetic Study

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For the understanding of the developmental significance of various parts of the normal ventricular septum, 54 normal human embryos and 154 mature heart specimens showing different types of VSD's and AV canal malformation were studied. The pars interventricularis of the septum membranaceum is derived primarily from the right superior and inferior tubercles of the AV cushions. The pars atrioventricularis is formed by the closure of the bulboauricular canal. The posterior smooth septum is a result of the balanced growth of the margins of the interventricular foramen. The posterior trabeculated septum develops as a result of the expansion of the two ventricles on both its sides. The anterior portion of the crista, the conoventricular septum, is derived from the anterior portion of the conoventricular flange. The midportion of the crista represents the conus septum and it is derived from conus ridges 1 and 3. The parietal portion of the crista is derived from conus ridge 3.

The developmental significance of various parts of the normal ventricular septum and of defects in this structure has been a subject of difference of opinion. In order to obtain first-hand information on this subject, a study was done on a series of normal human embryos, with particular emphasis upon development of the ventricular septum and on gross specimens of hearts with ventricular septal defect.

The primary purpose of this study was to determine the developmental basis for the various components of the ventricular septum in the normal heart.

Certain hearts with ventricular septal defect were selected as portraying arrest in development in one or another component of the ventricular septum.

Material and Methods

The study of embryos was done in the Department of Embryology, The Carnegie Institution of Washington. Existing serial sections of the following embryos were studied under the microscope:

**Horizon IX**: Embryo IX 5080+1 somite
**Horizon X**: Embryos X 3709+4 somites, X 8244 6 somites, X 5074+10 somites, X 3707+12 somites
**Horizon XI**: Embryos XI 6344+13 somites, XI 6784 17 somites, XI 8116 17 somites, XI 7665 19 somites, XI 2053+20 somites
**Horizon XII**: Embryos XII 8944 22 somites, XII 8943 22 somites, XII 8505B 25 somites, XII 7852 25 somites

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**The term horizon was introduced by Streeter to indicate developmental morphologic age. The serial number of each horizon is marked by Roman numeral and each horizon equals approximately two days of age.**

†Reconstruction models of these embryos were available in the Carnegie collection for this study.
wax models, together with the solid cavity models of the Carnegie collection, they were helpful in clarifying embryologic processes.

Various structures related to the developing ventricular septum were measured (Table 1). These measurements were performed directly on the microsections in planes that offered the best projection for the particular measurement. Thus, for example, the vertical diameter of the interventricular foramen (IVF) was measured on frontal sections.

The pathologic information presented here is based on a morphologic study of two basic septal anomalies; the atrio-ventricular canal malformation and ventricular septal defect (VSD). A part of the study of AV canal malformation, which included 36 heart specimens, previously was reported.7 Seventeen additional specimens were studied and the various components of the ventricular septum were measured. The information about the VSD is based on a recent study of 101 specimens demonstrating 112 VSD’s. A part of the study on VSD which included 70 heart specimens was previously reported.8

**Definition of Terms**

As the observations in embryos will be related to parts of the ventricular septum in the mature heart, the components of the mature ventricular septum need definition. From the left ventricular aspect, the ventricular septum may be divided into four parts as defined below (Fig 1):

1. The membranous septum (septum membranaceum) is a fibrous membrane occupying a portion of the basal part of the septum and its anterior end

### Table 1—Measurements of Various Components in Developing Heart

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<th>Diameter AV canal</th>
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Age indicated by horizon.
Som: somite; F: frontal section; S: sagittal section; T: transverse sections. Measurements in microns.
is levelled below the midportion of the right aortic cusp.

2. The anterior septum is the small portion of the septum which lies between the septum membranaceum and the anterior wall of the left ventricle.

3. The posterior smooth septum (smooth septum) represents about the superior one-third to one-half of the muscular part of the septum. Characteristically, its surface is smooth and devoid of individual trabeculations. Anteriorly, it is bordered by the anterior septum. Posterosuperiorly, it extends to the posteromedial commissure of the mitral valve. Postero-inferiorly, it is separated from the diaphragmatic wall of the left ventricle by a spur of the fourth portion of the ventricular septum, the posterior trabeculated septum.

4. The posterior trabeculated septum forms the septal wall of the apical one-half to two-thirds of the ventricle. As the name implies, it has an irregular trabeculated character. Its anterior boundary is the anterior wall of the left ventricle. Posteriorly lies the diaphragmatic wall of the left ventricle. Posterosuperiorly, a spur of this portion of the septum intervenes between the posterior smooth septum and the diaphragmatic wall of the left ventricle.

Collectively, the posterior smooth and posterior trabeculated septa (septums) may be termed, "the posterior septum."

From the right ventricular aspect of the ventricular septum, certain structures are apparent (Fig. 1).

1. Part of the membranous septum lies overhung by the septal leaflet of the tricuspid valve. This portion may be termed the "interventricular portion of the membranous septum (pars interventricularis)." The remainder of the membranous septum lies just superior to the septal leaflet of the tricuspid valve and forms part of the floor of the right atrium. This portion of the membranous septum, termed "pars atrioventricularis," separates the left ventricle from the right atrium.

2. The papillary muscle of the conus is a specialized portion of the basal part of the septal wall which receives chordae from the adjacent portions of the anterior and septal tricuspid leaflets. It is located on the border between the right ventricle and the infundibulum.

3. The right ventricular infundibulum (conus) is that part of the right ventricle which lies between the pulmonary valve, above, and an imaginary line through the papillary muscle of the conus and the upper edge of the membranous septum, below. This line is termed the "infundibuloventricular line."

4. Arching upward along the anterior wall of the right ventricle from the tricuspid ring to the ventricular septum just below the pulmonary valve is a muscle bundle. This may be called the "parietal band." Forming a pointed structure with parietal band is a muscle bundle which extends inferiorly...
along the septum from the pulmonary valve. The latter bundle is termed the "septal band." In some normal hearts, the septal band is ill-defined. A depression between the abutment of the parietal and septal bands is termed the "bulbar raphé." The raphé lies immediately inferior to the left pulmonary cusp.

The parietal and septal bands together include some elements of the crista supraventricularis. In this communication, the term "crista supraventricularis" will refer to the muscular septum intervening between the pulmonary valve and the septum membranaceum. This also includes adjacent portions of the parietal and septal bands, as defined above, as well as a small part of the ventricular septum, which is anterior to the septal band. Thus, the crista supraventricularis is bounded by the right and left pulmonary cusps, superiorly. Inferiorly, it is bounded by the infundibuloventricular line. Posteriorly the crista blends indistinguishably with the right ventricular parietal wall. Anteriorly, the crista is bounded by the anterior wall of the right ventricular infundibulum. In essence, the term crista supraventricularis, as used here, refers to the septal wall, as well as to a small portion of the parietal wall of the right ventricular infundibulum or conus.

The parietal portion of the crista supraventricularis extends superiorly beyond the level of the ventricular septum as seen from the left side, while the most anterior part of the crista corresponds to the anterior septum as seen from the left ventricle. In the right view the crista is divided into the anterior septum and parietal portion by an imaginary line extending between the septum membranaceum and the commissure between the right and left pulmonary cusps. This imaginary demarcation line is termed the conus septum fusion line (Fig 1). The most anterior portion of the crista intervenes between the subpulmonary infundibulum and the left ventricle and it may thus be termed the "conoven- tricular septum." The central portion of the crista intervenes between the pulmonary and aortic outflows and it represents the embryonic conus septum. It extends approximately between the midportions

![Diagram](http://journal.publications.chestnet.org/pdfaccess.ashx?url=/data/journals/chest/21503/)

**Figure 2.** Diagrammatic illustrations of various stages in the development of the bulboventricular loop. A) the segments of the primitive endocardial tube; B) expansion of the greater curvature of the proximal bend and of the AV canal. Arrows indicate the orifice between the expanding left ventricle and the primary heart tube. The x-line indicates the future plane of the inflow orifice of the left ventricle, and of IVF; C) the shape of the heart following the expansion of the AV canal and the lengthening of the diaphragmatic wall, and the transformation of IVF to IVF. Notice the position of the conoventricular flange; D) same as C except that the anterior wall of the right ventricle and conus, as well as the conoventricular flange have been removed to show the relationship of the conoventricular flange.
of the left and right pulmonary cusps. The posterior end of the crista intervenes between the right ventricular infundibulum and the exterior of the heart.

5. The moderator band is a muscle bundle or collection of bundles which extends forward from the inferior aspect of the septal band. After crossing the right ventricular cavity, it inserts into the anterior wall of the right ventricle.

6. The posterior septum, as seen from the left ventricle, is represented on the right side by that part of the muscular septum which walls the right ventricle inferior to the infundibulum. Although the entire surface of this portion is trabeculated, it corresponds, in part, to the smooth and, in part, to trabeculated components of the left ventricular aspect of the ventricular septum. Corresponding to the smooth septum is that part which lies posterior to the septal band. The apical part of the right ventricular aspect of the septum, the septal band and the septal tissue anterior to the latter correspond to the trabeculated part of the posterior septum, as seen from the left, representing thus the posterior trabeculated septum.

The orientation of the diaphragmatic wall of the embryonic heart is considered horizontal and the plane of the atrioventricular orifices is considered vertical. The terms caudal, cephalic, dorsal and ventral apply to orientation of the embryonic heart. The terms posterior and anterior, whenever used, apply to orientation of the heart in the fully developed individual. The terms proximal and distal are referred to structures along the blood stream; the proximal end of the heart being the atria, and its distal end being the great vessels.

The Embryology of the Ventricular Septum

The Developmental Changes of the Interventricular Foramen (IVF)

As the name implies the interventricular foramen...
(IVF) is the communicating space between the developing ventricles. During its development the IVF is constantly remodeled showing three anatomic versions destined as IVF₁, IVF₂, and IVF₃ consecutively. In each of these patterns the IVF maintains a constant diameter of approximately 300 microns (Table 1).

The Interventricular Foramen I (IVF₁)

Using the basic scheme offered by DeVries and Saunders, with additions, one can identify in the endocardial tube of the bulboventricular loop the following segments. The most proximal one is the AV canal and it is oriented approximately in a ventrodorsal direction (Fig 2A, 3A). In its ventral end the endocardial tube makes a 90° turn toward the right. The term proximal bend with its lesser and greater curvatures is used for this bend. The endocardial tube distal (downstream) to the proximal bend is referred to as the proximal transverse limb followed by the ascending limb, the distal transverse limb and the terminal limb which is parallel and cephalad to the AV canal.

The endocardial tube is covered by the myocar-
dial tube which shows only two segments: 1) the ventricle, which engulfs the proximal bend, and the proximal half of the proximal transverse limb; 2) the bulbus cordis which engulfs the rest of the endocardial tube. The fold between these two segments is the conoventricular flange (bulboventricular ridge).

Although the site of the future IVF is recognized in the simple primary heart tube, the term IVF is used only when there appears an apparent interventricular septum across the caudal wall of the proximal transverse limb. The borders of IVF at this stage are the following: ventrocaudally the developing interventricular septum, dorsally the wall of the heart tube and cephalically the conoventricular flange (Fig 2B, 3B).

In the 22 somite embryo (2 mm) (embryo XII–8943) the greater curvature of the proximal bend and the dorsolateral wall of the ascending limb expand rapidly. Soon they develop into two saccular chambers, the trabeculated left and right ventricles (Fig 2, 3). Associated with the expansion of the compacta of the ventricles there is also a progressive increase in the diameter of the primary endocardial heart tube as it is represented by the central ends of the trabeculations (Fig 4A, Table 1). The orifice connecting between the lesser curvature of the proximal bend and the expanding left ventricle is in a plane which connects the left wall of the AV canal and the ventro-diaphragmatic margins of the interventricular foramen (Fig 2B, 3B arrows). The IVF, thus, in the early stage of ventricular expansion is neither related to the left ventricle nor to the right ventricle.

During the expansion of the left ventricle, however, there is an extension of the trabeculations on account of the lesser curvature (Fig 2B, C and 3A-D), so that the ventral and the diaphragmatic walls of the left ventricle become longer, and the orifice leading into the ventricle tilts to the position as seen in the mature mitral orifice. As a consequence of the lengthening of the ventral and diaphragmatic walls of the left ventricle, and because of the caudal shift of the right ventricle (Horizons XIII, XIV Fig 3) the interventricular foramen becomes interposed between the developing ventricles (Fig 2, 3).

The Interventricular Foramen 3 (IVF3)

Whereas the IVF2 is a portion of the AV canal, IVF3 again becomes a ring-shaped orifice. The transformation of IVF2 to IVF3 is due to the development of the conus septum and the fusion of the AV cushions.

The term conus is applied here to that segment of the bulbus cordis which extends between the trabeculated right ventricle and the level of the future cusps of the great vessels. The conus is further divided into proximal and distal conuses (Fig 3A-D, 5A-D). In the primitive bulboventricular loop (before the rightward expansion of the AV canal) the dorsal, right and ventral walls of the conus are continuous with the free walls of the right ventricle while the left wall of the conus, the conoventricular flange, roofs the interventricular foramen (Fig 2B). In the mature loop (following expansion of the AV canal) the dorsal wall of the conus arises from the roof of the atrioventricular canal. This portion of the origin of the conus is termed the conoauricular flange (Fig 2D, 4F, 5A) (Tandler’s bulboauricular ridge). The rest of the conus origin remains unchanged. The specific term conoauricular flange is applied for the transverse portion of the conoventricular flange because in the mature heart this structure appears as the aortico mitral continuity. The sagittal portion of the conoventricular flange which remains unchanged and roofs the interventricular foramen is represented in the mature heart by the junctional line of the aorta and the free wall of the left ventricle as well as by the conoventricular septum.

In the conus there are two long spiral endocardial
ridges lining it like "riflings of gun barrel" (Fig 4A-5A). Proximally these ridges appear as swellings, and distally they are narrow. The difference in the shape of the proximal and distal ends of the bulbar ridge caused Tandler to consider them as two sets of different anatomic structures related to a proximal and a distal bulb. According to the same concept with, however, different terminology, the anatomy of these structures is defined as below; the proximal conus ridge No. 1 (Tandler's proximal bulbar swelling A) is located on the ventricular septum ventrocephalad to IVF₂ (Fig 5A). Distal conus ridge 1 (Tandler's distal bulbar swelling A) arises from proximal conus ridge 1 and it runs distally on the right side of the conoventricular flange spiraling to the caudal wall of the distal conus. Proximal conus ridge 3 (Tandler's proximal bulbar ridge B) is located near the extreme right end of the AV canal at the junction between the right ventricle and the conus. The distal conus ridge 3 (Tandler's distal bulbar swelling B) arises from proximal conus ridge 3 and it spirals distally to the cephalic wall of the distal conus. Fusion of distal conus ridges 1 and 3 results in the formation of the distal conus septum and fusion of proximal conus ridges 1 and 3 results in the formation of the proximal conus septum (Fig 5D). The continuity of the proximal and distal conus ridges accounts for the completeness of the conus septum.

The proximal ridge 1 divides the conoventricular flange into two parts. The anterior portion is part of the pulmonary outflow, and the posteroinferior portion is part of the aortic outflow (Fig 5).

Kramer uses the term conus for Tandler's bulbus while Van Mierop uses the term truncus for Tandler's distal bulbus (our distal conus), and conus for Tandler's proximal bulbus. For proximal conus ridges 1 and 3, Kraner and Van Mierop use the terms sinistroventral and dextrodorsal conus ridges, and for distal conus ridges 1 and 3, Van Mierop uses the terms dextroinferior and sinistrolateral truncal swellings respectively. Other investigators do not divide the ridges into proximal and distal segments. Thus, for the entire length of conus ridges 1 and 3, Waterston and Odgers use the terms left and right bulbar ridges and Keith uses the term left and right septal bands respectively.
Just before the fusion of the conus septum, the aortic portion of the conoventricular flange is displaced leftward (embryo XVIII 8909), leaving the IVF unroofed. A new roof, however, is provided for IVF₃ by the inferior edge of the proximal conus septum (Fig 5B). As a result of the leftward shift of the conoventricular flange, part of IVF₂, becomes the "subaortic vestibulum" (Fig 4F). The anterior portion of the conoventricular flange remains unchanged occupying a position of an infundibuloven-
tricular septum. The development of conus ridge 3 at the point of confluence of the conus, AV canal and the ventricular septum results in interruption of the continuity between the aorta and the right ventricular free wall.

By the fusion of the superior and inferior AV cushions (embryo XVIII 9247) the IVF₂ receives its final dorsal margin showing the following borders: cephalically the conus septum (Fig 5B), dorsally the extreme right end of the fused AV cushions and caudally and ventrally the interventricular muscular crest. Closure of IVF₃ will give rise to the septum membranaceum (Fig 4C).

The Development of the Interventricular Septum

There are three basic processes in the development of the interventricular septum: 1) the development of the posterior smooth and posterior trabeculated septums both of which are related to the development of the ventricles, 2) the development of the anterior septum which is primarily derived from conus elements, 3) the development of the septum membranaceum which is derived from the tubercles of the fused AV cushions.

The Development of the Posterior Septum: The measurements of the various components of the interventricular septum in different developmental stages are shown in Table 1 and diagrammatically illustrated in Figure 6. The first evidence for the development of the interventricular septum is seen in the 5.2 mm embryo (XIII, 7433) as a ridge across the caudal wall of the proximal transverse limb. In the subsequent age group the septum consists of two morphologic constituents: 1) a crest which measures 60 microns in height, and which will develop into the posterior smooth septum; 2) a trabeculated portion which measures approximately 200 microns in height and which will develop into posterior trabeculated septum (Fig 4A,B,D,E,6,7). The crest is thicker than the trabeculated portion and its ventricular surfaces are smooth, in contrast to the trabeculated portion of the septum which as its name implies has trabeculated surfaces. The crest and the trabeculated septums are not in the same plane, the crest being somewhat tilted toward the right. As a consequence the junctional line between the crest and the trabeculated septum on the right

Figure 6. Proportional semi-diagrammatic illustrations of the ventricular septum in the developing heart in the various horizons. The dimensions are based on the values given in Table 1. For X, XI, XII, compare Fig 2A and B. Notice the constant diameter of the IVF versus the changing dimensions of the posterior smooth and posterior trabeculated septums as well as of the ventricles and AV canal (magnification approx. x 20).
side is in a more ventral position compared to the left. This right and left relationship of the junctional lines between the smooth and trabeculated portion of the septum is similar to the relationships between the septal band and the junctional line of the smooth and trabeculated septums seen in the mature heart.

In subsequent developmental stages there is a progressive increase in the size of the crest and of the trabeculated septum. By the time that IVF₃ is mature for the formation of the septum membranaceum (horizon XVIII) the horizontal length of the IVF₃ is 200 microns, that of the muscular crest 270 microns and that of the trabeculated septum 830 microns (Table 1). The ratios of these values are: interventricular foramen to muscular septum (crest plus trabeculated septum) is approximately 1:6 and crest to trabeculated septum is 1:3. These horizontal proportions are similar to the proportions along the outflow tract of the mature heart between the septum membranaceum, the posterior smooth septum and the posterior trabeculated septum. In the vertical orientation the IVF₃ measures 300 microns, the crest 140 microns and the trabeculated portion 160 microns. The proportions thus are: IVF to muscular septum is 1:1 and crest to trabeculated septum 1:1. In the mature heart similar proportions along the base are found between the septum membranaceum and the muscular septum.

The Development of the Crista Supraventricularis: While the posterior septum in the mature heart represents a further development of the embryonic posterior septum, the crista supraventricularis is a descendant of the conoventricular septum as well as conus ridges 1 and 3. As Keith¹¹ pointed out because of the expansion of the conus and the ventricles, part of the free wall of the conus assumes a septal position. This portion is most probably represented in the mature heart by the anterior portion of the anterior septum. The posterior portion of the anterior septum is derived from the development of conus ridge 1. Following the fusion of conus ridges 1 and 3 a septum is formed between the pulmonary and aortic outflows, and this conus septum involves the midportion of the crista supraventricularis of the mature heart.

While conus ridge 3 contributes to the conus septum, it also accounts for the development of the parietal portion of the posterior half crista (Fig 5B).

The parietal position of an originally septal structure is due to the shortening of the conus. At the time that the conus septum is formed, the length of the conus is equal to the length of the right ventricle, each measuring about 1.5 mm in length (Fig 3D).

In the mature heart the infundibulum is only one-third of the length of the right ventricle. The shortening of the conus which occurs after the completion of the conus septum⁵⁻¹¹ brings the aortic and pulmonary valves to a close proximity with the ventricles. The “sinking”¹² of the aortic valve toward the septum results in exteriorization of the posterior part of the conus septum. This portion in the mature heart appears as the parietal component of the crista supraventricularis.

During the shortening of the conus, the distal conus septum which, because of its twist, is perpendicular to the proximal septum is telescoped into the latter without losing its orientation. Although the distal conus septum is not identifiable in the mature heart, its original orientation is preserved and it is represented by the aorta being posterior to the pulmonary artery.

The Development of the Septum Membranaceum: A sine qua non condition for the development of the septum membranaceum is completion of the IVF₃, which means normal development of the posterior smooth septum along its junction with the IVF₃. Normal development of the proximal (inferior) end of the proximal conus septum and normal fusion of the AV cushions.

The closure of the IVF₃ takes place during horizons XVII to XIX. In the 11 mm embryo (XVII 8969) a mesenchymal tissue arising from the right end of the inferior atrioventricular cushions grows ventrally (Fig 4E, 5B, C). This mesenchymal bud may be divided into an upper (cephalic) and a lower (caudal) half. The lower half, the “spur,”¹⁰ develops on the right aspect of the crest of the ventricular septum (Fig 4D, 7C). In the frontal section, this spur is caudal compared to the atrioventricular bundle and the interventricular foramen. In subsequent stages this cushion extension develops to become the posterior half of the septal leaflet of the tricuspid valve (Fig 4E, 7D). Its peculiar position on the muscular septum correlates well with the anatomy of the septal leaflet of the tricuspid valve of the mature heart.¹³

The upper half of the inferior mesenchymal extension is known as the right inferior tubercle (Fig 4E, 5B, 8A). This tubercle grows along the diaphragmatic margins of IVF₃ obliterating it from below¹⁰ and it also supplies cushion tissue for the development of the anterior half of the septal leaflet of the tricuspid valve. During the obliteration of the IVF, the atrioventricular bundle retains its position between the muscular crest and the proliferating tubercle.

Obliteration of the region of IVF₃ which is subjacent to the conus septum is done in the...
following way. In horizon XVIII a mass arising on 
the right lateral wall of the atrioventricular junction 
protrudes well into the tricuspid channel (Fig 5B, 
C, 8A).

This lateral mass which we term the combined 
lateral mass is continuous both with the lateral 
atrioventricular cushion and the caudal end of the 
proximal conus ridge. Fusion between the com-
bined lateral mass and the right superior tuber-
cle divides the tricuspid channel into a superior tract 
which is the bulboauricular canal (Fig 4B, 5C, 
8A) and an inferior tract which is the tricuspid 
canal. The obliteration of the bulboauricular canal 
results in the formation of the pars atrioventricular 
of the septum membranaceum (horizons XIX). Lack 
of closure of this canal, we believe, responsible for 
the anomaly known as left ventricular right atrial 
communication.

Fusion of the right superior and the right inferior 
tubercles results in a completion of the pars 
interventricularis of the septum membranaceum. 
(Fig 8B, C) and it is through the combined lateral 
mass that the septum membranaceum is continuous 
with the inferior margin of the conus septum.

In embryo XIX 8092 where the septum mem-
branaceum has just been formed and can still be 
histologically recognized (Fig 4C) the proportions 
of the dimensions of the septum membranaceum, 
posterior smooth septum and the trabeculated sep-
tum are similar to those of the mature heart.

Late Developments in the Posterior Septum of the 
Right Ventricle

Following the formation of the septum mem-
branaceum the septal band and the moderator 
bands become more and more obvious as a specific 
structure (Fig 4, 3C, D, G, 7A-D). Both develop 
along the junctional line between the crest and the 
trabeculated septum, as part of the papillary muscu-
lar system of the tricuspid valve.

In horizon XXI and particularly XXII (Fig 4G, 
7D) undermining underneath the cushion spur on 
the right side of the septum is obvious. As a result 
of this undermining the septal leaflet of the tricuspid 
valve splits off from the septum and the right surface 
of the posterior smooth septum becomes trabecu-
lated. Based on pathologic material an interrela-
tionship between the development of the septal leaflet 
of the tricuspid valve and the trabeculations on the 
right side of the posterior smooth septum was pre-
viously suggested.

Discussion

Despite the minor differences in the description 
of the formation of the septum membranaceum most 
investigators agree that this portion of the ventricu-
lar septum represents the closure of the last version
of the interventricular foramen and that most of this part of the septum is derived from AV cushion tissue. This concept is well-demonstrated by measurements done during this study, and from the determination of the position of the atrioventricular bundle as related to the developing membranous septum.

The muscular ventricular septum of the mature heart represents three developmental portions: the posterior smooth and posterior trabeculated septum (collectively the posterior septum) and the anterior septum. A diverse opinion is found about the development of each of these.

The posterior septum was usually considered as a single developmental unit. Mall, Kramer, and Murray felt that it is formed by actively growing tissue. Tandler, Frazer, and Streeter on the contrary were of the opinion that both ventricles expand on both sides of the inactive interventricular septum. DeVries and Grant felt that condensation of trabeculae between the two ventricles contributes to the formation of the ventricular septum. Odgers speaks about a balanced growth in which he describes generalized growth of the heart, on one hand, along with active growth of the margins of the interventricular foramen, on the other hand. In his description, however, it is not clear whether he refers only to the formation of the septum membranaceum or if he refers also to the formation of the muscular septum.

The present study indicates clearly that from its first appearance the embryonic interventricular septum consists of two morphologic structures, a smooth crest above and a trabeculated part below. Whatever the mechanism of their development is, they represent two separate anatomic structures (Fig 4). It is interesting to speculate about the different nature of their development. As seen in various horizons, these two components of the muscular septum progressively increase in size with growth of the embryo. The centrifugal growth of the trabeculated part scarcely explains the constant increase in the height of the smooth crest. The possibility exists though that the smooth nature of the crest results from "deposition" of trabeculae so that the junction between the trabeculated and the

Figure 8. A) Left ventricular view of the various structures in the vicinity of the IVF; B) right view. The formation of the pars interventricularis of the septum membranaceum by proliferation of the inferior and superior tubercle; C) the various components of the ventricular septum following the closure of the IVF. Junctional line: 1 (J1) is between the posterior smooth and trabeculated septum. J2 is between the proximal conus ridges 1 and 3. J3 is between the combined lateral mass and right superior tubercle (central portion of the septum membranaceum) and J4 between the anterior and posterior smooth septums.
smooth parts of the septum is constantly displaced centrifugally, creating the false impression of the growth of the crest. There are, however, two points which indicate that active growth of the crest is more than a false impression: (1) the appearance of solid crest prior to the expansion of the ventricles; (2) the progressive expansion of the size of the primary heart tube while the diameter of the IVF remains constant indicates a competitive process between expansion and centripetal proliferation.

A hint of the dual developmental origin of the muscular septum is derived from pathologic material. This refers to a peculiar VSD along the junctional line between the posterior smooth septum and the posterior trabeculated septum. This VSD is usually characterized by its long axis being perpendicular to the long axis of the heart, and by the occasional incidence of two or more VSD's along the same line in the same position (Fig 9).

Absence of the posterior smooth septum was demonstrated in one case of isolated VSD\(^2\) (Fig 9)

**Figure 9.** A) Supracristal VSD located between the right and left pulmonary cusps. This defect is located at the distal end of the imaginary fusion line of the conus septum; B) left ventricular view of two different types of VSD's. D\(_1\) is a defect along the junctional line between the anterior septum and the posterior smooth septum with involvement of the pars interventricularis of the septum membranaceum. Four arrows point to four small VSD's along the junctional line between the posterior smooth and posterior trabeculated septums; C) right view of same as B, the multiple defects are hidden by the septal band. The dashed line indicates the junction between the infundibulum and the right ventricle; D) left ventricular view of heart showing complete absence of the posterior smooth septum; E) left ventricular view of AV canal malformation, note the absence of the posterior smooth septum. Ao: aorta; AS: anterior septum; CVS: crista supraventricularis D\(_1\); VSD LP: left pulmonary cusp; MB: moderator band; MV: mitral valve; PMC: papillary muscle of the conus; PSS: posterior smooth septum; PTS: posterior trabeculated septum; PV: pulmonary valve; RP: right pulmonary cusp; SLTV: septal leaflet tricuspid valve.
and this appears to be a characteristic feature in the majority of the specimens showing AV canal malformation (Fig 9E).

The other constituent of the muscular septum is the septal portion of the crista supraventricularis.

Review of the literature will show that the term, crista supraventricularis, has a different meaning to various investigators. Wolff,20 and later Grant21 applied the term to the muscular mass intervening between the pulmonary and tricuspid valves. Van Mierop8 considers the crista the same structure as we do, except that there is no statement in his embryologic map about the left ventricular aspect of the crista. Abbott22 did not relate the crista to the interventricular septum at all, while Keith,11 Lev,23 Becu24 and others include in the crista the parietal and the septal bands.

Also the term anterior septum as found in the literature is not completely defined. According to Lev,22–25 the anterior septum includes the region which is anterior to the septal band. The inferior end of the anterior septum, however, is not determined and the state of the apical portion of the septum is not clarified.

The term, crista supraventricularis, as used in the present study, is applied to the infundibular septum, part of which takes in the mature heart a parietal position.

As shown by Grant,21 the muscular architecture of the crista (excluding the anterior half of the anterior septum) consists of two main layers: 1) a deep one, the fibers of which are in the same orientation as the crista and they occupy the entire length of the crista; 2) a superficial layer which consists of few components. The most superficial components of the superficial layer are the superior end of the septal band and septal end of the parietal bands. The junction between these two bands is marked by the fibrous bulbar raphé. Keith,11 Lev22–25 Grant,21 and Rokitansky26 felt that the septal band is derived throughout its entire length from the proximal conus ridge 1, and this was the basis for using the septal band as a border between Lev’s posterior and anterior septums. The embryologic background for this concept is based upon the incorrect observation made by Keith11 and Rokitansky26 that the proximal conus ridge 1 extends well into the ventricle to give rise to the septal band.

However, as shown in the present study the conus septum and the proximal conus ridge 1 do not extend beyond the level of the IVF. A description similar to the present one was also given by Van Mierop,8 Kramer7 and particularly by Tandler7 and Odgers10 who specifically described the fading away of the proximal conus ridge 1 near the IVF (Fig 4A, 5A).

There are also two anatomic objections against considering the septal and parietal band derivatives of the bulbar ridges and for considering the bulbar raphé as their fusion line: 1) the bulbar raphé is localized below the left pulmonary cusp (Fig 1). This localization of the fusion line between the conus ridges is wrong, since it is well accepted that the septation of the conus occurred at a level between the left and right pulmonary cusps; 2) as pointed out by Grant,21 the bulbar raphé is only a superficial structure. The main bulk of the crista is formed by the deep horizontal uninterrupted muscular bands negating a specific dual origin.

A confirmation of the validity of the imaginary conus fusion line as an important anatomic structure is derived from pathologic material. It was previously shown that infundibular VSD’s which most probably represent fusion failures of the conus ridges are distributed along this line.3 (Fig 9A).

Since the border between the right ventricle and the infundibulum extends along the line passing through the upper edge of the septum membranaceum and the papillary muscle of the conus, the portion of the septal band which is superior to this line is in the conus and the portion below it is in the ventricle. The ventricular portion of the septal band was regarded by Tandler27 as part of the moderator band, or as he termed it “trabecula septomarginalis.” A similar opinion was held by Grant21 and Van Mierop.8 Although the term moderator band was originally applied to the free muscle bundles traversing through the right ventricular cavity,28 these muscle bands include also a varying length of the septal components. Developmentally the ventricular part of the septal band and the moderator band are indistinguishable from each other, both developing along the junction between the smooth and trabeculated septums, being part of the papillary muscular system of the tricuspid mechanism.

A confirmation for dividing the septal band into infundibular and ventricular portions is derived from pathologic conditions. This refers to the VSD along the junction between the infundibulum and the ventricle.3 This defect, when viewed from the right ventricle, (Fig 9B, C) may cut near the papillary muscle of the conus into the septal band along the infundibuloventricular junction. In the left ventricular view, the defect extends anteriorly along the junctional line between the anterior septum and the posterior smooth septum.

The comparative cardioanatomy may also give support to the concept that the muscular septum consists of three separate developmental structures.

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In the heart of a frog there is an interventricular septum which is equivalent in its dimensions and shape to the trabeculated posterior septum of the human heart. On the basal side of the septum there is an interventricular foramen which is equivalent in size to that portion of the human ventricular septum which consists of the posterior smooth septum, the anterior septum and the septum membranaceum.

The interventricular septum in the frog appears as a fine mesh with rather large holes, and it certainly does not function as a partition between two circulations. The absence of specific conduction tissue in the frog indicates that the primitive trabeculated septum functions mainly in the distribution of the propagating pulse. It seems thus that the solid nature of the trabeculated septum of the human heart is a late development of the primitive posterior trabeculated septum, and that the posterior smooth septum, the anterior septum and the septum membranaceum are later additions in the partitioning of the heart.

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