The Conotruncus

I. Its Normal Inversion and Conus Absorption

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SUMMARY

The processes which are involved in the development of the normal outflow tracts of the ventricles are the following: The ostium bulbar torsion accounts for the concordant flow between the ventricles and the proximal conuses. The leftward shift of the ostium bulbi accounts for the partial overriding of the aorta over the left ventricle. The truncal rotation accounts for the twisted relationships of the great vessels and for the definitive interrelationships of the semilunar valves. The aortic conus absorption accounts for the aorticomital fibrous continuity. These processes are not necessarily linked to each other. In the normal, mature heart the conus is represented by the subpulmonary portion of the right ventricular outflow tract.

Additional Indexing Words:
Conus  Truncus  Heart embryology  Heart anatomy  Bulbus cordis

In THE CURRENT literature the term conus (infundibulum) has three different connotations. The first is exclusively embryologic, and it applies to a clearly definable structure in the human embryonic heart. The second connotation is anatomic, and it is used by some to describe the subpulmonary portion of the right ventricle, while others use it to connote the entire outflow tract of the right cardiac chamber. The third connotation denotes those outflow portions of the ventricles of the normal, as well as of the malformed heart, which are believed to be derived from the embryonic conus. Accordingly, then, the conus is elevated to a similar "status" as the other cardiac chambers, being recognized as a definitive segment of the heart, with its own embryology, anatomy, and pathology.

The discrepancy in the literature about the meaning of the term conus evolves from the fact that comparison between snapshots of embryonic patterns at various age groups with definitive normal and malformed patterns of the conuses reveals no apparent similarities to indicate any developmental relationship. Still, use of different terminologies for the changing patterns of the same developmental structure makes as much sense as the use of different names for the left ventricle of the embryo, of the definitive normal, or of the definitive malformed heart.

In order to better understand the polymorphic nature of the conus we recently restudied its normal embryology with particular emphasis on its morphologic dynamics, i.e. the succession of patterns from one age group to another and to its eventual fate in the normal definitive heart. During that study a number of critical conal developments, some of which are not recognized in the literature in English, were elucidated and are to be described in this report.

Material and Methods

The study of embryos was done in the Department of Embryology at the Carnegie Institution of Washington in Baltimore. Existing serial
sections of 37 normal human embryos of horizons XI-XIX were studied under the microscope. The heart of each of these embryos was traced with the aid of a camera lucida in 60X magnification. Various components of the heart were measured. These measurements were performed directly on the microsections that offered the best projection for the particular measurement. Thus, for example, the length of the conus was measured on sagittal sections.

A cardboard reconstruction model of the conus of embryo XV 3512* was made specifically for that study.

*The serial number of each embryo in the Carnegie collection is marked by a Roman numeral which indicates the horizon, and an Arabic serial number. Each horizon equals approximately 2 days of age.

Part of our investigations, which included the embryology of the ventricles and the ventricular septum, was previously reported.8

A consideration of the information in the German literature on the embryology of the conus reveals that there are indeed only two original contributions in this report; namely, the geometric measurements of the conotruncus and the elucidation of the “migration” of the conus septum toward the ventricles. To provide the reader with a clear picture, however, a full description of the embryology of the conus, as observed by the authors, is presented. In order to eliminate repetitive observations of others, references have been supplied in the body of the description. Observations, however, which are either original or are differently interpreted in the literature are specifically discussed.

Figure 1
Developmental semidiagrammatic illustration of the right and left ventricles. The septal and parietal portions of the crista supraventricularis represent the embryonic conus septum. The septal crista is also referred to as the infundibular or conus septum of the definitive heart.

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Definition of Terms

General Terms

Figure 1 shows the relevant developmental components of the definitive heart. Controversies about developmental aspects are discussed in the text. (The discussion in this text will be restricted to the conotruncus.) The developmental aspects of the ventricular portion of the septum were discussed elsewhere.9 The definition of the various segments of the primary heart tube and the embryologic terminology used in this text are given in figure 2 and are largely based on DeVries' report.10

Embryonic Ventricles

Except for the developing right and left ventricles, the entire heart tube is referred to as the primary heart tube.10, 11 The left ventricle is recognized at early stages as a trabeculated territory involving only the greater curvature of the first curve (figs. 2, 3). The lesser curvature opposite the developing left ventricle is smooth and morphologically remains part of the primary heart tube. The greater and lesser curvatures together are termed, in the German literature, proampula.2, 9 The right ventricle is the trabeculated territory involving only the right wall of the metaampula, or ascending limb (figs. 2, 3). The left wall of that segment remains smooth, being part of the primary heart tube.10 During horizon XIV the A-V canal, which initially drained into the proampula, expands toward the right, and by doing so it comes to override the dorsal aspect of the interventricular foramen (IVF) (fig. 3). As a result, the A-V canal gains an access to the right ventricle, and it also becomes continuous with the conotruncus.

Conotruncus and Ostium Bulbi

The metaampula is continuous distally with the conus. The border between these two segments is the ostium bulbi, or the conoventricular junction. On the right the ostium bulbi is the transition from the trabeculated ventricular endocardium to the smooth conal endocardium. On the left the

![Diagram of the Heart of Embryo in Age Group XI](http://circ.ahajournals.org/)

Figure 2

Drawings of a cavity model of a heart tube in horizon XI. The heart tube is convoluted in such a way that it forms five straight segments (limbs), and in-between them, four curves or bends. The proximal segment of the heart tube (starting at the venous end) is the A-V canal. It is oriented posteroinferiorly. Next comes the first curve or proximal bend. In this curve, the heart tube makes a 90° turn toward the right to become the proximal transverse limb, or the interventricular foramen. In curve 2 the heart tube makes a 90° turn cephalically to become the ascending limb, and in curve 3 the heart tube turns in 90° medially to form the distal transverse limb. In curve 4 the heart tube turns in 90° toward the back of the embryo to form the terminal limb, which is cephalad and parallel to the A-V canal. Each curve has a greater and a lesser curvature. The lesser curvature of curve 2 is the conoventricular flange. LV = left ventricle; RV = right ventricle. (Reproduced by courtesy of Carnegie Institution of Washington, by permission.10)
ostium bulbi is the lower edge of the conoventricular flange (fig. 2). During horizon XIV the ostium bulbi shifts toward the left to cephalically override the IVF. This critical process provides the conus with an access to the left ventricle (fig. 4).

Figure 3
Upper row are drawings of cavity models of embryos in horizons XI (A), XIII (B), and XVI (C). The lower row are semidiagrammatic illustrations of hearts of these age groups. A1 and B1 are left views, and C1 is a right view. The ventral walls have been removed. The conotruncal ridges in C1 are shown. The proximal end of conotruncal ridge 1 divides the conoventricular flange into the aortic part (below the ridge) and the pulmonary part (above the ridge). The A-V cushions have been removed from the A-V canal. The junction between the conus and the A-V canal is the conoauricular flange, and the roof of the IVF is the aortic conoventricular flange. (Reproduced by courtesy of Carnegie Institution of Washington, by permission.)

Figure 4
Tracings of human embryonic cardiac frontal microsections showing the process of leftward shift of the conoventricular junction. Compare the relationships between the conoventricular flange (CVF) and the ventricular septum (VS) (A) before, (B) during, and (C) after completion of the leftward shift. The numerals that follow the serial numbers of the embryos indicate the numbers of the microscopic slide, the row, and the microsection on the slide.
The conotruncus is a collective term used for the conus and the truncus arteriosus. The conus includes the left wall of the ascending limb, the distal transverse limb, and the proximal end of the terminal limb (figs. 2, 3). The truncus, which follows the conus, includes the midportion of the terminal limb. Internally, the conus and truncus are differentiated by the number of their endocardial cushions. There are two longitudinal endocardial cushions in the conus and four in the truncus. From their first appearance the conotruncal ridges are arranged in a spiral course, like riflings of a gun barrel (figs. 3C1, 5B). Conus ridge no. 1 (bulbar ridge A) starts proximally on the anterior wall of the conoventricular junction and spirals through the left wall of the conus to the dextroinferior wall of the truncus. In the same way, conus ridge no. 3 (bulbar ridge B), which starts on the back wall of the conoventricular junction, spirals along the right wall of the conus, to end on the sinistrosuperior wall of the truncus (fig. 5B).

The conotruncal ridges may be looked upon as the lines of fusion of the two walls of the conotruncus. These two walls are the parietal walls of the aortico and pulmonary truncoconuses. Most of the conoventricular flange is part of the aortico conus, while the right wall of the proximal conus is part of the pulmonary pathway. Distally, the aortico truncus is on the right, whereas the pulmonary truncus is on the left (fig. 5B).

The spiral course of the conotruncal ridges is probably a result of the 90°–110° counterclockwise torsion (looking downstream) that the ostium bulbi underwent during the formation of the bulboventricular loop. (In this report the authors rely on Pernkopf’s2 and Davis’s13 descriptions of the rotation of the ascending limb during the formation of the bulboventricular loop.) Truncal

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**Figure 5**

Frontal diagrammatic illustration of the conotruncal inversion and conus absorption. The ventral wall of the conotruncus and ventricles has been removed. The cross-hatched area is the aortic conus. The pulmonary conus is unshaded. (A) Situation in which a conotruncal inversion did not occur. (Normally, it is nonexistent because inversion of the ostium bulbi occurs during the formation of the loop.) Notice that the aortic conotruncus is on the right, and conus ridges 1 and 3 are on the posterior and anterior conus walls, respectively. (B) The situation seen in horizon XV in the normal human embryo. The proximal conuses are in a postinversion relationship with the aortic conus relatively left sided, and the pulmonary conus, right sided. The distal conus septum is fused as in horizon XVI. (C) As a result of rotation of the truncus (horizon XVII) completion of the conotruncal inversion is achieved. Notice that conotruncal ridges 1 and 3 reversed their interrelationships. (D) Absorption of the bilateral proximal conuses brought the distal conus septum toward the ventricular septum, and absorption of the distal aortic conus accounts for the fibrous continuity between the aortic and mitral valves.
Figure 6

Photomicrographs of human embryonic hearts of the Carnegie collection. Left column shows left view of sagittal sections of embryos: (a) XV 8966 6.1.5, (c) XVII 6519 22.1.2, (e) XIX 1390 13.3.2. Right column shows frontal view of frontal sections of embryos: (b) XV 8997 12.2.4, (d) XVII 8998 19.3.3, (f) XVII 353 14.2.2. The length of the conotruncus is compared with the arterial trunks in the left column. The conotruncus extends from the cono-ventricular junction (CVJ) to aorticotruncal aortic sac junction (ATAJ). The aortic sac (trunk) extends between the distal end of the truncus and the pericardial reflection (PR). In a the
ridges no. 2 and 4 are restricted to the truncus and are found on the left and right truncal walls.

The truncus is continuous distally with the aortic sac (ventral aorta) (fig. 6) which is devoid of endocardial cushions.

In horizon XVI truncal ridges 1 and 3 fuse to form the truncal septum (fig. 6). At the same time, the septum aortopulmonale grows from the dorsal wall of the aortic sac toward the truncal septum to fuse with it. As a result of the fusion of these two septa the aortic sac is divided into the ascending aorta and the pulmonary artery; the truncus is divided into the aortic and pulmonary trunci, or valves.1, 2, 9

Observations
Rotation of the Truncus
Once the septum aortopulmonale and the truncal septum are fused, the truncus rotates about 90–110° in a counterclockwise direction (looking downstream) (figs. 5, 6). This counterclockwise rotation (torsion) of the truncus, which follows the earlier counterclockwise rotation of the ostium bulbi, thus unwinds the coiled course of the conotruncal ridges (fig. 5). As a result, the aortic truncus is transferred to the same side as the aortic conus (left side) and the aortic and pulmonary trunks become coiled,2, 9 the situation seen in the definitive heart. During the period of truncal rotation, the distal portion of the conus septum is being formed by the fusion of conus ridges 1 and 3 (horizons XVI, XVII).

Absorption of Conus and "Migration" of the Conus Septum
A second critical process involving the ventricular outflow tracts is the marked shortening of the conus and the equivalent lengthening of the aorta and pulmonary arteries.2, 9, 14 During the period of unwinding of the conotruncus, the aortic conotruncus is reduced in length from 700 to 400 μ (horizons XVI, XVII) (figs. 6, 7). During the formation of the conus septum (by fusion of the distal portions of the conus ridges), the length of the aortic conotruncus further decreases to 220 μ (horizon XIX). Of these 220 μ the truncus measures about 200 μ, while the conus only measures 20 μ. A concurrent process to the shortening of the aortic conus is the lengthening of the ascending aorta. This is indicated by the increase in the distance between the aortic valve and the pericardial reflection on the ascending aorta (figs. 6, 7). This distance increased from 260 μ in horizon XVI to 710 μ in horizon XIX. The length of the pulmonary conotruncus is reduced from 880 μ in horizon XV to 600 μ in horizon XIX (figs. 6, 7). As a result of the shortening of the conus the distal conus septum is "conveyed" toward the heart (fig. 5D). In horizon XVII, when the conotruncus has already been reduced to about half its original length (fig. 7), the distal conus septum provides, in its new location, the new cephalic border for the IVF (transforming IVF2 to IVF3).9 (During cardiogenesis the IVF is constantly remodeled showing three anatomic versions destined IVF1–IVF3. IVF1 is the proximal transverse limb of the bulboventricular loop. IVF2 is bounded by the sinus septum, conoventricular flange, and the A-V cushions. In IVF3 the conus septum replaces the leftward-shifted conoventricular flange.) After closure of the IVF (formation of septum membranaceum) muscular elements arising from the right ventricle invade the conus septum. This invasion is most conspicuous in the region of conus ridge 3.9, 15 Once the conus septum is muscularized it receives the anatomic appearance of the crista supraventricularis. Once the shortening of the conus has been completed, the aortico and pulmonary trunci receive their final shapes as semilunar valves. The endocardial cushions (or ridges) which fill the aortic and pulmonary trunci hollow out on their

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conotruncus is long and the arterial trunk short (see fig. 7 for measurements). In e the length proportions are reversed. The truncal rotation is shown in the right column. The truncal septum (TS) which is vertical "b" is horizontal in f. Truncus ridge 4 (TR4) is another indicator for the truncal rotation. AS = atrial septum; ATAJ = aortico-truncal aortic sac junction; CVJ = conoventricular junction; DC = dorsal A-V cushion; PC = pulmonary conus; PR = pericardial reflection; SM = septum membranaceum; TR = truncal ridge; TS = truncal septum; VC = ventral A-V cushion.

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distal ends to form the cup-shaped sinuses and their related semilunar leaflets (fig. 6). Conus ridges 1 and 3 contribute to both semilunar valves, giving rise to the right and left cusps in each valve.

**Discussion**

As described in the German literature, this study indicates that there is an absolute, rather than relative, reduction in the length of the conus, particularly of the aortic conus. During horizons XV–XIX the length of the aortic conotruncus decreases from 880 to 220 μm (200 μm of which are in the truncus) (fig. 7). The length of the ascending aorta increased during that period from 100 to 710 μm. These values indicate that during the time that the aortic conus became shorter by about 600 μm the ascending aorta became longer by about the same degree (figs. 6, 7). The length of the truncus during that period did not change significantly.

The effect of the conus absorption on the definitive anatomy of the heart is twofold. First, the bilateral absorption of the proximal part of the conus accounts for the “migration” of the distal conus septum toward the heart where it assumes its definitive position in the interventricular septum (fig. 5). Secondly, the additional absorption of the distal aortic conus accounts for the fibrous continuity seen in the mature heart between the aortic and mitral valves (fig. 5).

Grant’s opinion that the conus ridges do not fuse, hence, receives partial support. It was Keith and Van Praagh who developed the concept that the fibrous aortic conital continuity was indicative of the absence of the aortic conus. According to them, the presence of a muscular band interrupting this continuity would indicate persistence of the aortic conus. Van Praagh broadened this concept and, in a number of publications, accurately elucidated the anatomy of the conus in various cardiac malformations. The geometric measurements of the present study also confirmed

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**Figure 7**

Measurements in microns of the length of the right ventricle (RV), the left ventricle (LV), the conotruncus, and the aortic trunk in various embryonic age groups. The frontal view of the rotation of the truncus and the timing of septal fusions is illustrated for comparison. The numbers in the illustrations refer to the conotruncal ridges. Abbreviations as in figure 6.

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<th>LENGTH RV μm</th>
<th>LENGTH AORTIC CONOTRUNCUS μm</th>
<th>LENGTH POLYMORPH SEPTAL REFLEXION μm</th>
<th>TRUNCAL ROTATION</th>
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previous observations about the inversion of the conotruncus,\textsuperscript{2, 9} of which two points are of particular significance: (1) The inversion of the conotruncus occurs in two stages. The first, the inversion of the ostium bulbi (proximal conus), occurs as early as at the time of the D-looping, whereas the second stage, which is the completion of the inversion, occurs only at a later stage by the rotation of the truncus. (The term D-looping was used by Van Praagh to describe the formation of the D-loop of the primary heart tube.\textsuperscript{19}) (2) The torsion of the truncus occurs only after the septum aortopulmonale has been completed, and about half of the torsion is completed before any shortening of the conus is apparent.

It is due to the ostium bulbar rotation that the proximal ends of the conotruncal ridges are located in such a position that there is an anatomic concordance between the left ventricle and the proximal aortic conus, and between the right ventricle and the proximal pulmonary conus (fig. 5). The truncal torsion simply follows in a manner similar to the previous proximal torsion, bringing the semilunar valves to the same sides as their proximal conuses and unwinding the spiral course of the conotruncal ridges. In addition, as a result of the rotation of the truncus, the aorta spirals around the pulmonary artery to a position found in the definitive heart. We were unable to find evidence for the commonly accepted concept that the septum aortopulmonale twists as it grows toward the conus septum.\textsuperscript{3, 14, 20}

While Keith\textsuperscript{17} and Lev\textsuperscript{5} linked the truncal rotation to the shrinking of the aortic conus, Van Praagh assumed that inversion of the conotruncus was due to the growth of a subpulmonary conus.\textsuperscript{19} As shown here, however, (figs. 6, 7) half of the truncal torsion is completed before any change of the conus length is apparent, and the inversion of the proximal conus occurs before there is any evidence of the existence of the conotruncal ridges.

The borders of the anatomic conus also need some clarification. While in the embryo the border between the conus and the ventricle stands out, this is not the case in the definitive heart. As observed by Tandler\textsuperscript{15} and Asami\textsuperscript{9} once the conus septum has been formed it is invaded by muscular elements which grow from the right ventricle. The conus septum receives, thus, the shape of the crista supraventricularis (or the definitive conus septum), and it becomes anatomically indistinguishable from the muscular right ventricle.

Comparison between embryonic and definitive hearts indicate that the conus, or infundibulum, in the mature heart includes only the subpulmonic territory\textsuperscript{2-4} (fig. 1).

The more common concept in the American literature, however, is different. According to Lev\textsuperscript{5} and Grant\textsuperscript{6} the conus, or infundibulum, includes the septal band, the moderator band, and the parietal band. Lev, who introduced this concept to the American literature,\textsuperscript{5} adopted it from Keith.\textsuperscript{17} Neither Keith nor Spitzer, however, mentions the embryologic basis on which they selected these anatomic landmarks.\textsuperscript{21} More recently Lev (Unpublished observations) wrote: "Embryologically the term conus is used synonymously with the term bulbus by most people. This constitutes only part of the outflow tract of the right (and also the left) ventricles. This, as pointed out by Van Mierop and others lies beneath the pulmonary trunk. We must not confuse the anatomic term conus with the embryologic." The thesis of this work, however, is that there is only one conus which, in the normal heart, constitutes the small subpulmonary region of the outflow tracts of the ventricles, and as any other organ it has its own embryology and pathology.

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