


# The Embryonic Ascent of the Kidney Revisited

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## ABSTRACT

Although the embryonic kidney's ascent is well established, the intermediate morphological changes that occur during the process are unclear. To evaluate the morphological events that accompany the kidney's ascent, we examined serial sagittal sections from 24 embryos at 5–7 weeks gestation. Six specimens had bilaterally ascending kidneys that were between the levels of the second to fifth lumbar vertebrae, and each kidney had a primitive renal cortex surrounding clusters of ampullae, which branched from the pelvis, and a dense tissue band that connected the renal cortex with the embryonic adrenal cortex or celiac ganglia, and there was no adipose capsule or renal artery. The tissue band contained abundant nerve twigs from the major splanchnic nerve; thus, it was conceivable that it was sufficiently rigid to support the length of the retroperitoneal tissue mass that included the embryonic adrenal cortex, celiac ganglia, and kidney. The lumbar vertebral body's height was much shorter than that of the ascending kidney. However, the lower vertebral column's curvature was often maintained, even when the kidneys had ascended. Therefore, vertebral column straightening was not the only factor required to drive the ascent. Together with the growth of the thorax and liver, the adrenal cortex, ganglia, and kidney appeared to change simultaneously at a position relative to the vertebrae. The renal artery established a connection to the renal cortex after the ascent. Evaluations of frontal sections from five additional specimens suggested that from its initial position, the kidney extended upwards between bilateral umbilical arteries. *Anat Rec*, 302:278–287, 2019. © 2018 The Authors. The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology published by Wiley Periodicals, Inc. on behalf of Wiley-Liss, Inc.

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Abbreviations: AD = adrenal; AO = aorta; C2 = the second cervical vertebra; CA = celiac artery; CIA = common iliac artery; DC = descending colon; GL = celiac sympathetic ganglia; IVC = inferior vena cava; J = jejunum; K = kidney; L1, L2, L3, L4, L5 = the first, second, third, fourth, and fifth lumbar vertebrae, respectively; M = mesonephros; MA = mesonephric artery; MD = mesonephric duct; MSN = major splanchnic nerve; OV = ovary; OA = ovarian artery; OD = ovarian duct; P = pancreas; RA = definite renal artery; SMA = superior mesenteric artery; SCV = subcardinal vein; ST =

stomach; T = testis; TA = testicular artery; T1, T2, T11 = the first, second, and eleventh thoracic vertebrae, respectively; UA = umbilical artery; UR = ureter; VAS = vas deferens

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## INTRODUCTION

The ascent of the embryonic kidney from the level of the sacral vertebrae to that of the first lumbar vertebra is well established. One driving force underlying this ascent is the straightening of the body, which involves the rapid longitudinal growth of the lumbosacral vertebrae and a reduction of the flexion at the lumbar level (Hamilton et al., 1976; Parrott et al., 1994; O'Rahilly and Müller, 1996). However, to our knowledge, the process that involves kidney sliding along the vertebral column has not been demonstrated photographically, which may relate to the short timeframe in which this event occurs. Unlike sagittal sections of the embryonic kidney, horizontal sections do not clearly demonstrate the changes that occur in and around the kidney at the level of the vertebrae. Few collections of serial sagittal sections of human embryos exist worldwide, and we believe that the kidney's morphology in sagittal sections when the organ is at an intermediate location, for example, the lower lumbar level, may provide insights that could lead to a reevaluation of the kidney's ascent process.

O'Rahilly and Müller (1996) explained that, during the kidney's ascent, it "taps" segmental blood vessels at increasingly higher cranial levels, and that the last (most superior) vessel to be tapped becomes the renal artery. Such switching of the arteries that feed the ascending kidney was first postulated by Felix (1912) in the so-called, "ladder theory." However, Hinata et al. (2015) reported that the final renal artery appears after the kidney's ascent to the level of the first lumbar vertebra has been established, and that the segmental mesonephric arteries disappear from the area around the ascending kidney. Thus, it seems unlikely that the kidney uses the mesonephric arteries as a ladder for the ascent. Moreover, the absence of an arterial supply appears to enable the kidney to slide during the ascent.

The kidney's ascent accompanies a change in the orientation of the renal hilum from a ventral orientation to a medial orientation, that is, a 90° rotation, but opinions differ regarding this movement. Hamilton et al. (1976) and Parrott et al. (1994) believed that the ascending kidney underwent a medial rotation of 90°, while O'Rahilly and Müller (1996) considered that the change may be caused by an increase in the growth of the lateral lip of the hilum, rather than being caused by an actual rotation. Consequently, the aim of this study was to determine the intermediate morphology of the kidney during its ascent to reevaluate the mechanism underlying the ascent, contribution of the segmental arterial supply, and possible ureteric elongation using rare collections of sagittal sections of embryonic kidneys held in Göttingen, Germany and Madrid, Spain.

## MATERIALS AND METHODS

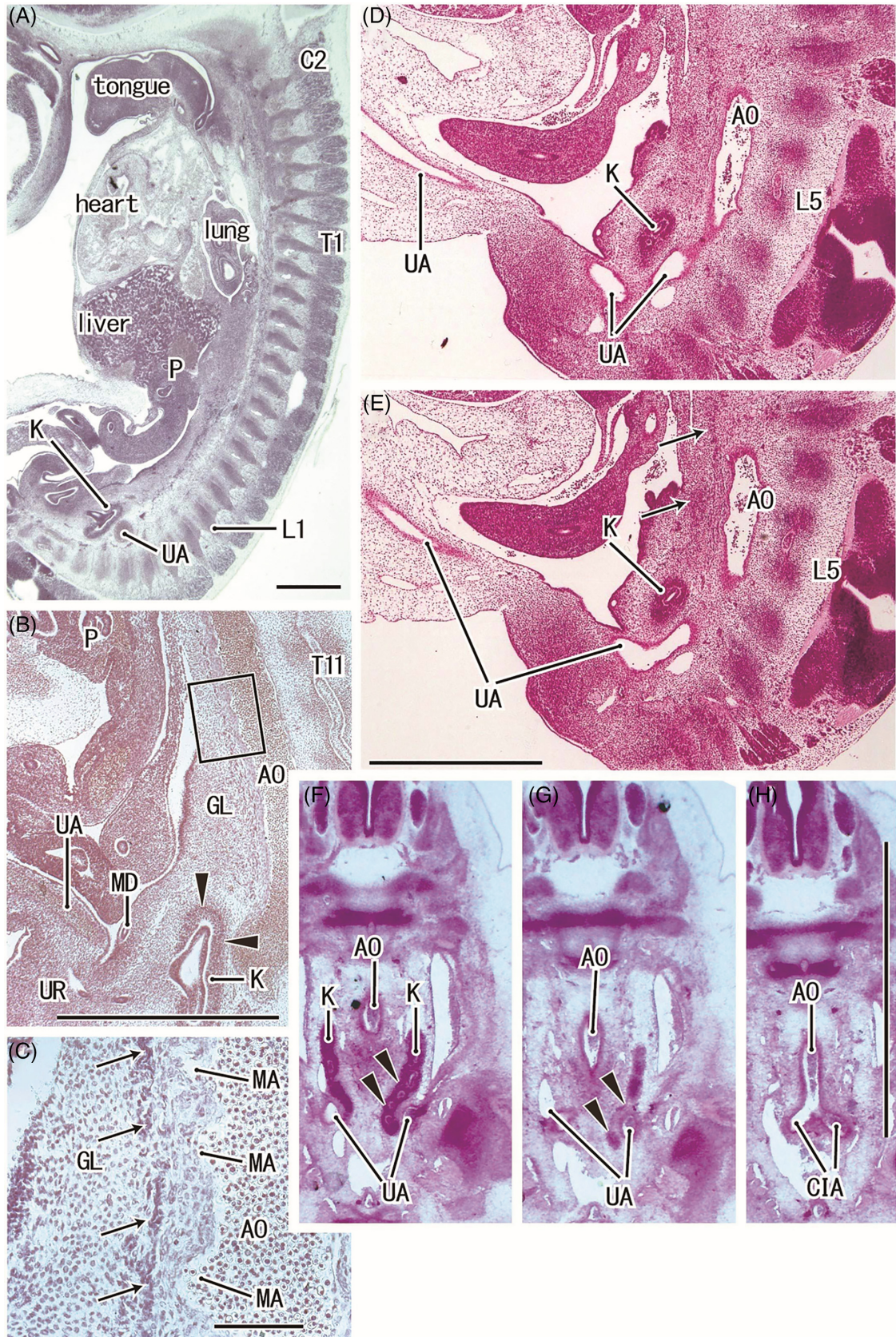
This study was performed in accordance with the principles of the Declaration of Helsinki 1995 (revised in 2013). We evaluated serial sagittal sections of 24 embryos at 5–7 weeks gestation that had crown-rump lengths (CRLs) of between 10 and 28 mm. Half of the specimens that were in the Blechschmidt Collection at the Medical Museum of Georg-August-Universität Göttingen, which were first described by Radlanski and Renz (2010), were prepared as serial sagittal sections. Most of the sections were stained with hematoxylin and eosin (HE), and a small number were stained using azan or Masson's trichrome staining protocols. The use of this collection did not require specific approval from the university. The other sections comprised part of a large collection kept at the Institute of Embryology at the Complutense University of Madrid that were derived from miscarriages and ectopic pregnancies at the university's Department of Obstetrics. Most of these sections were stained with HE, and a small number were stained using azan, orange G, or silver staining protocols. Madrid University's ethics committee approved the use of the Spanish specimens (B08/374). The thickness of the sections ranged from 5 to 7 µm. Photographs of the sections were taken using a Nikon Eclipse 80 microscope (Nikon Corporation, Minato, Tokyo, Japan).

To determine the topographical anatomy of the kidney in its initial position below the aortic bifurcation, we examined frontal sections of the five embryos with CRLs of 11 to 14 mm at 5 weeks gestation. Four of these specimens belonged to Madrid University, and the fifth specimen belonged to the Congenital Anomaly Center of Kyoto University (no. 244992; Carnegie stage 18). One of the authors (A.I.) had taken photographs of the fifth specimen in Kyoto during a previous study (Hinata et al., 2015).

## RESULTS

### Inferior Pole of the Metanephros was Below the Aortic Bifurcation Initially

The kidney was composed of two to four oval-shaped or triangular-shaped pelvises, and a belt-like cap of mesenchymal tissue surrounded each pelvis in four of the 24 sagittally sectioned specimens that had CRLs of 10, 11, 13.4, and 15 mm (Fig. 1). The mesenchymal cap opened to form a medial or ventral site that connected the pelvis to the ureter (Fig. 1B). There were no fibrous structures bundling or surrounding the renal pelvises, and no glomerular or tubular structures had developed. The inferior pole of the kidney was always located below the aortic bifurcation initially, but the superior pole extended above the bifurcation. Thus, the positions of the kidneys relative to the levels of the vertebrae varied among the specimens,



**TABLE 1. Summary characteristics of the sagittal sections of the embryos**

Specimen identification	CRL and gestational age	Class	Kidney height	Figure reference	Vertebral column	Arteries	Connection to adrenal tissue
IW-10-3	10 mm, 5 weeks	In	L5-S2		Ventrally curved	UA attached	
27-3-54	11 mm, 5 weeks	In	S1-S2		Ventrally curved	UA attached	
19-1-59	13 mm, 5 weeks	Im	L2-L4	Figure 2D	Ventrally curved	UA attached	Connected
5-1-66	13.4 mm, 5 weeks	In	L4-L5	Figure 1A	Ventrally curved	UA attached	
8-12-50	13.5 mm, 5 weeks	Im	L3-L5	Figure 2A	Ventrally curved	UA attached	Connected
2-19-68	15 mm, 6 weeks	Im	L2-L4	Figure 3D	Ventrally curved		Connected
GV3	15 mm, 6 weeks	Fi	L1-L3		Ventrally curved	ND	
IW-16	15 mm, 6 weeks	In	S1-S2	Figure 1D	Almost straight	UA attached	
18-3-48	16 mm, 6 weeks	Im	L4-L5	Figure 3A	Ventrally curved		Connected
17-4-52	16.8 mm, 6 weeks	Im	L2-L5		Ventrally curved		Connected
18-3-48	17 mm, 6 weeks	Im	L2-L5		Ventrally curved		Connected
IW-33	17 mm, 6 weeks	Fi	L4-S1		Almost straight	ND	
PR	19 mm, 6 weeks	Fi	L1-L4		Ventrally curved	ND	
1-12-51	20.5 mm, 6 weeks	Fi	L1/2-L4		Ventrally curved	RA identified	
G-I 20	20.5 mm, 6 weeks	Fi	L1-L3		Almost straight	RA identified	
BOT	21 mm, 6 weeks	Fi	L1-L3		Almost straight	ND	
B-O	21 mm, 6 weeks	Fi	L1-L4		Almost straight	ND	
13-7-49	21 mm, 6 weeks	Fi	T12/L1-L3		Ventrally curved	RA identified	
GV7	22 mm, 7 weeks	Fi	L1-L3		Ventrally curved	RA identified	
22-4-52	22 mm, 7 weeks	Fi	L1-L3		Ventrally curved	RA identified	
IW-43	24 mm, 7 weeks	Fi	L1-L3	Figure 5	Almost straight	RA identified	
24-6-49	26 mm, 7 weeks	Fi	L1-L4		Almost straight	RA identified	
IW-41	27 mm, 7 weeks	Fi	T12/L1-L2		Almost straight	RA identified	
IW-111	28 mm, 7 weeks	Fi	L1-L3	Figure 4	Almost straight	RA identified	

The “ventrally curved” and “almost straight” vertebral column are based on observations at the lumbosacral level; they do not include a curvature at the coccygeal, thoracic, or cervical level of the vertebrae.

Abbreviations: CRL, crown rump length; Fi, final location at a level of the first lumbar vertebra; Im, intermediate level along the vertebral column; In, initial morphology with a mesenchymal cap and an inferior pole below the aortic bifurcation; L, lumbar; ND, renal artery not detected in and around the final kidney; RA, renal artery; S, sacral; T, thoracic; UA, umbilical artery.

from the fourth lumbar vertebra to the second sacral vertebra (Table 1). The positions of the left and right kidneys relative to the levels of the vertebrae differed slightly, but the difference was less than the length of one vertebra. The kidneys were always adjacent to the ventral, medial, and/or superior aspects of the umbilical artery (Fig. 1A, E); therefore, they appeared to be moving over the arch of the umbilical artery. The origins of the mesonephric arteries were occasionally found on the internal aspects of the aortic walls (Fig. 1C). At the superior pole, the kidney was initially adjacent to relatively dense, belt-like tissue that extended superiorly (Fig. 1E), and in the dorsal part of the belt-like tissue, a nerve-like structure was present near the kidney that ran parallel to the aorta (Fig. 1C), which was most likely candidate tissue for the celiac ganglia. A ventral curvature of the lumbosacral

vertebral column was always evident, and loosely packed tissue occupied the area between the kidney and the vertebral column. The mesonephros was seen on the cranial side of the metanephros. These kidneys are denoted as “In” in Table 1.

In addition, an examination of the frontal sections of five embryos showed that the kidneys extended superiorly beyond the aortic bifurcation within the immediate ventromedial area between the bilateral umbilical arteries (Fig. 1F–H). Hence, rather than moving over the umbilical artery, the kidney extended vertically from its initial position, and after passing through a narrow space between the bilateral arteries’ origins, it turned laterally to extend further superiorly. We did not find a mesonephric artery that supplied the kidney in its initial position.

Fig. 1. Kidney below the aortic bifurcation at 5 weeks gestation. (A–C) Sagittal sections of an embryo with a crown-rump length (CRL) of 13.4 mm. (D and E) Sagittal sections of an embryo with a CRL of 15 mm. (F–H) Frontal sections of an embryo with a CRL of 14 mm. (A) The right kidney (K) in its initial location is adjacent to the umbilical artery (UA) at the levels of the fourth to fifth lumbar vertebrae. (B) A plane that is 0.2 mm medial to panel A. A mesenchymal cap surrounds each of the pelvises (arrowheads). Belt-like tissue, which is a candidate for the future celiac ganglia (GL), extends inferiorly along the aorta (AO) to reach the kidney. (C) A higher magnification view of the square in panel B showing tissue that contains nerve-like structures (arrows). (D and E) are adjacent sections at the same magnification. The right kidney is on the umbilical artery in its initial position at the level of the first and second sacral vertebrae. The arrows indicate a candidate for the celiac ganglia. (F–H) Frontal sections of the pelvis; the interval between (F) and (G) is 0.05 mm and that between (G) and (H) is 0.1 mm. The kidney extends upwards from its initial position and passes through the immediate ventromedial side of the umbilical artery (F). Above the artery, the kidney makes a turn to the lateral side (arrowheads in F and G). The aortic bifurcation is located on the dorsal side of the kidney (H). Panels F–G are at the same magnification. All the sections are stained with hematoxylin and eosin. Scale bars: 1 mm (A, B, E, and H) and 0.1 mm (C). For definitions of the other abbreviations, see the common abbreviations for the figures.

### Ascent of the Metanephros to Locations Between the Levels of the Second to Fifth Lumbar Vertebrae

In 6 of the 24 specimens that had CRLs of 13, 13.5, 15, 16, 16.8, and 17 mm, the kidneys did not reach the level of the first lumbar vertebra, but their entire parts were located at an intermediate level above the aortic bifurcation, that is, between the levels of the second to fifth lumbar vertebrae. These kidneys were oval and had smooth surfaces. A continuous mesenchymal structure, or the primitive renal cortex, surrounded the clusters of ampullae branching from the pelvis (Figs. 2 and 3). However, a space that would have been indicative of the adipose capsule and/or the renal fascia was absent from the area around the kidney. In five of the six embryos, the kidneys were long and they extended along the lengths of three or four vertebrae; specifically, the third to fifth or the second to fifth lumbar vertebrae. One of the six embryos carried short kidneys that extended along the lengths of two vertebrae. The difference in height between the left and right kidneys was less than the length of one vertebra.

Like the kidney that was in its initial position, a dense tissue band was evident that connected the early renal cortex with the embryonic adrenal cortex or celiac ganglia (Figs. 2C–E and 3C–E). This band-like tissue was comprised of high densities of small cells that contained abundant developing nerve twigs that connected to the major splanchnic nerve (Fig. 2C) and/or the lumbar nerve plexus. In two of the six embryos, the umbilical artery was attached to the inferior aspect of the kidney (Fig. 2B), and the ventral curvature of the lumbosacral vertebral column was evident. In four of the six embryos, the intrahepatic vena cava was connected to the subcardinal vein through a tight connection between the right embryonic adrenal cortex and the liver. Sometimes, a candidate for the renal artery was found (Fig. 3C), but it was difficult to trace it to either the renal cortex or the aortic origin. Likewise, a mesonephric artery did not supply the ascending kidney. The mesonephros was seen not only on the ventral side, but also on the caudal side of the metanephros. The kidneys at an intermediate height or location are denoted as “Im” in Table 1.

### Superior Pole of the Metanephros at and Above the Level of the First Lumbar Vertebra

Most of the specimens (14/24) carried a kidney that was surrounded by a narrow space or a candidate adipose capsule. This space or capsule separated the kidney from the vertebral column, embryonic adrenal cortex, and celiac ganglia. The kidney contained glomerular and tubular structures and was at the level of or was above the first lumbar vertebra (Figs. 4 and 5); thus, the kidney extended along the levels of the first to third or first to fourth lumbar vertebrae. The mesonephros was seen on the caudal side of the metanephros.

We were often able to identify the entire course of the renal artery from its aortic origin at the levels of the second lumbar vertebra or the second to third lumbar vertebral border (Figs. 4E and 5G) to the renal cortex (Figs. 4B and 5C,D). Sometimes, the artery was not found (ND in Table 1), possibly because of damage caused by irregular

tissue staining during the histological processing of the tissue. The subcardinal vein always passed close to the ventral side of the kidney and merged with the retrohepatic vena cava. Notably, the subcardinal vein separated the renal arterial course from the nearby mesonephric artery (Fig. 5F). The uppermost mesonephric artery was identified as the gonadal artery, and it approached the renal artery (Figs. 4D and 5B). The ventral curvature along the lumbosacral vertebral column was absent from eight of the 14 specimens, but it persisted in the other six specimens. The kidneys at their final locations are denoted as “Fi” in Table 1.

### Variability in Metanephric Morphology at 5–6 weeks Gestation

We categorized the positions of the kidneys in the 24 sagittally sectioned specimens into the initial, intermediate, and final locations, according to their craniocaudal levels of the metanephroi. Since our criteria were not based on nephrogenesis or the size of the specimens, 12 embryos that were smaller than 17 mm and had gestational ages of 5 and 6 weeks (Table 1) exhibited considerable variations at all three locations. The inferior poles of the kidneys in four embryos were below the aortic bifurcation, that is, the initial location; the kidneys in six embryos were located between the levels of the second to fifth lumbar vertebrae, that is, the intermediate location; and two embryos' kidneys were at the final location. However, nephrogenesis occurred after the metanephroi had reached their final positions. In all of the specimens examined, the ureters were well canalized.

## DISCUSSION

We have described an intermediate morphology that was present during the ascent of the kidney in six sagittally sectioned embryos. The most striking feature was the temporal connection between the primitive renal cortex and the embryonic adrenal cortex or celiac ganglia after the initial upward movement of the kidney from the level of the aortic bifurcation. The celiac ganglia were much larger than the ascending kidney. Since a fascial space for the future adipose capsule had not yet developed around the kidney at the intermediate location, the primitive cortex was able to directly attach to the embryonic adrenal cortex or ganglia. Moreover, the band-like tissue that connected these structures was dense and mechanically reinforced by the abundant nerve twigs that were present within the tissue. Thus, the kidney, embryonic adrenal cortex, and celiac ganglia formed a longitudinal, retroperitoneal, solid mass at the time of the kidney's ascent, and they were most likely to change their positions relative to the vertebral column together. Hence, a kidney was unlikely to ascend alone, independently of the embryonic adrenal cortex and celiac ganglia.

Variations in the morphology of the metanephric kidney were evident at 5–6 weeks gestation because the current classification was based on the craniocaudal level of the metanephroi, as opposed to being based on the size of the embryo (CRL) or nephrogenesis. However, we always found connections between the ascending metanephros and the cranially-located retroperitoneal structures. The

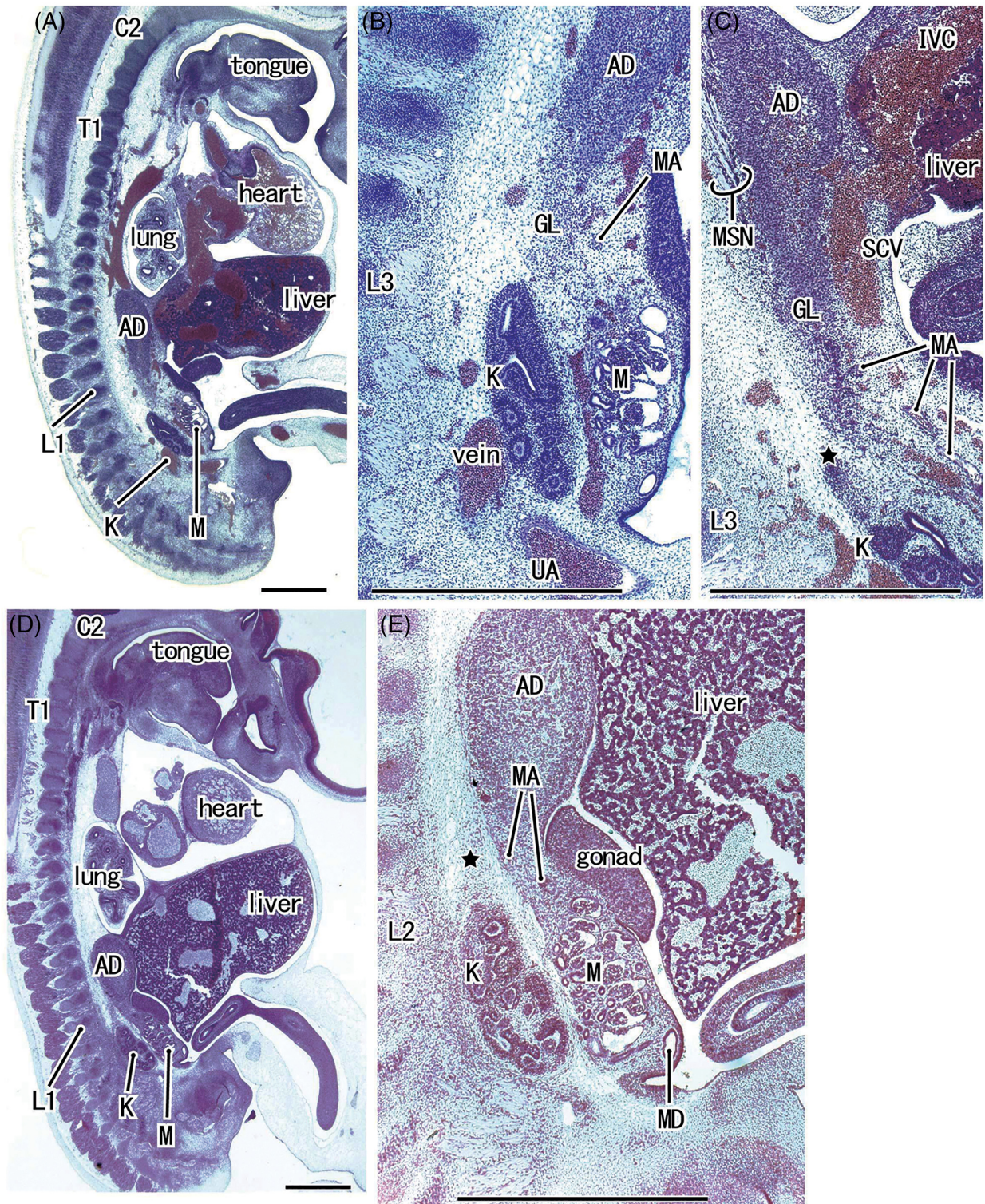


Fig. 2. Ascending right kidney in two embryos at 5 weeks gestation. (A–C) Sagittal sections of an embryo with a crown-rump length (CRL) of 13.5 mm; (D and E) sagittal sections of an embryo with a CRL of 13 mm. (A) A kidney (K) between the levels of the third to fifth lumbar vertebrae. (B) A higher magnification view of the same kidney and the embryonic adrenal cortex (AD) in panel A. (C) A plane that is 0.2 mm medial to panel A in which the developing celiac ganglia extend inferiorly to reach the kidney (star). The major splanchnic nerve (MSN) reaches the ganglia. (D) A kidney (K) between the levels of the second to fourth lumbar vertebrae. (E) A higher magnification view of the kidney in panel D shows band-like tissue that connects the embryonic adrenal cortex and the kidney (star). All the sections are stained with hematoxylin and eosin. Scale bars: all 1 mm. For definitions of the other abbreviations, see the common abbreviations for the figures.

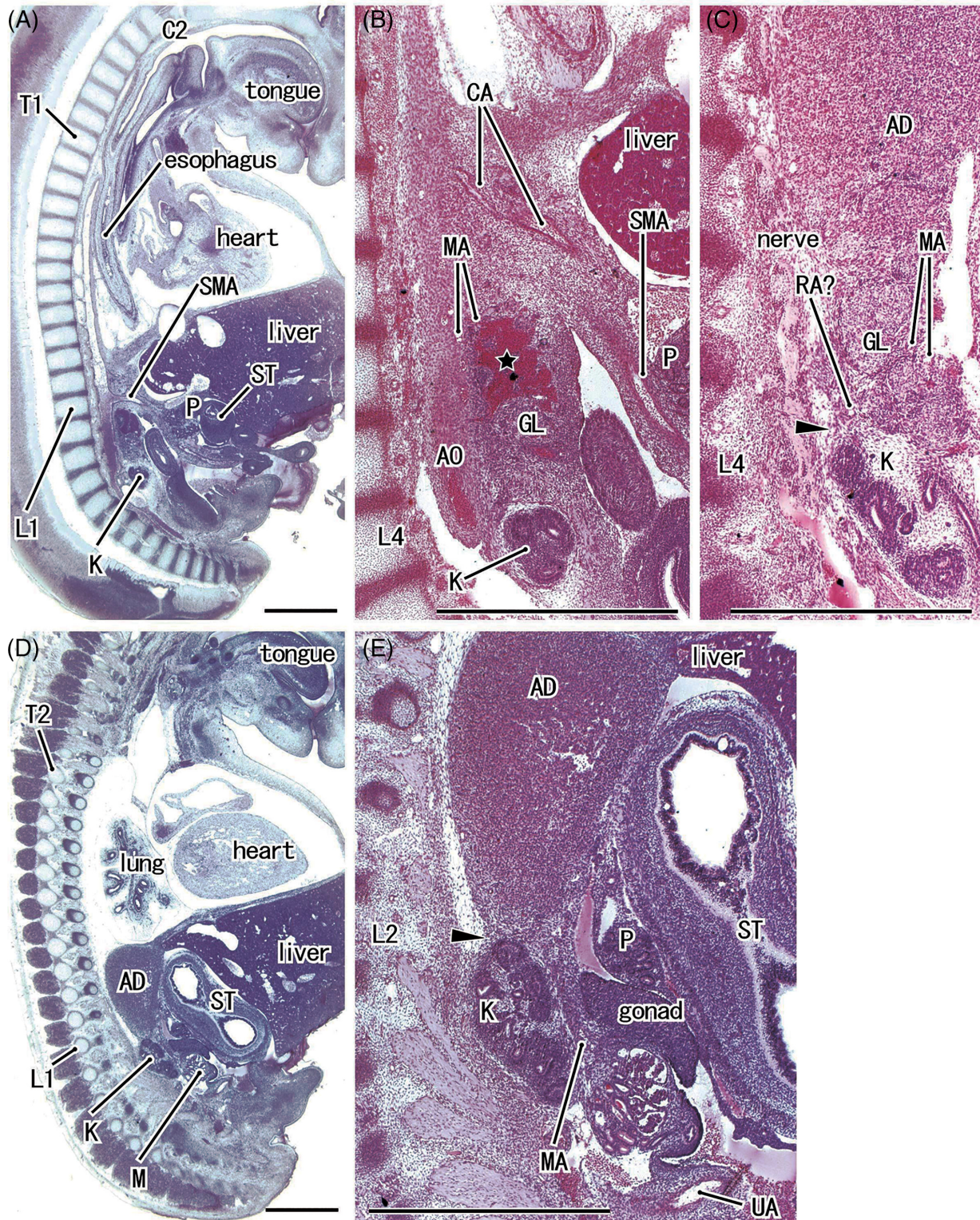


Fig. 3. Ascending left kidney in two embryos at 6 weeks gestation. (A–C) Sagittal sections of an embryo with a crown-rump length (CRL) of 16 mm and a kidney between the levels of the fourth to fifth lumbar vertebrae. (D and E) Sagittal sections of an embryo with a CRL of 15 mm and a kidney between the levels of the second to fourth lumbar vertebrae. (B) A section adjacent to that in panel A shows the celiac artery (CA) and bleeding in the celiac ganglia (GL; star). (C) A plane that is 0.1 mm to the left of the section in panel A. (E) A higher magnification view of the kidney in panel D. In (C) and (E) the embryonic adrenal cortex or ganglia is connected to the kidney (arrowheads). All the sections are stained with hematoxylin and eosin. Scale bars: all 1 mm. For definitions of the other abbreviations, see the common abbreviations for the figures.

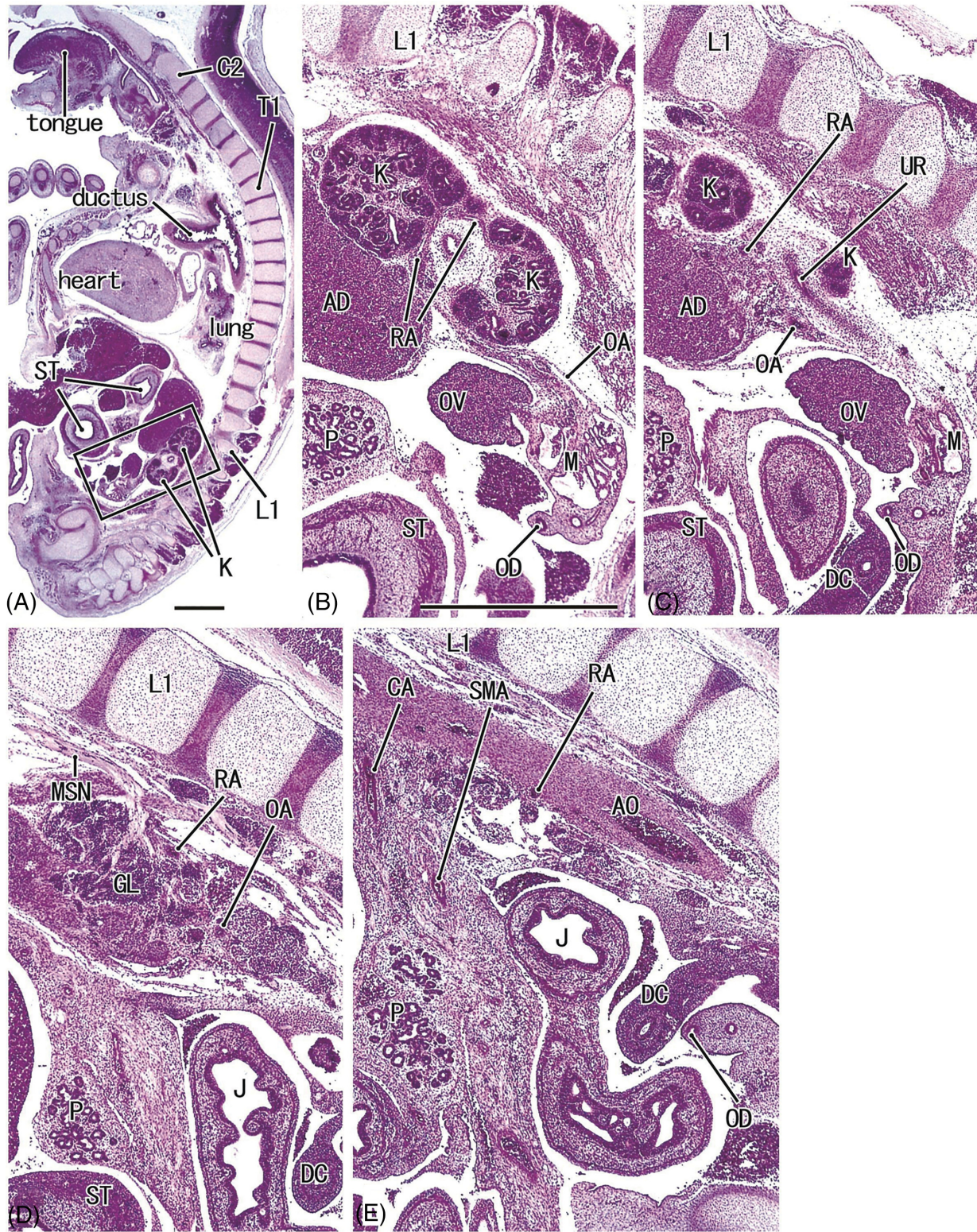


Fig. 4. Left kidney in a female fetus in its final position at 7 weeks gestation. Sagittal sections of an embryo with a crown-rump length (CRL) of 28 mm. (A) The leftmost plane. (B) A higher magnification view of the kidney and embryonic adrenal cortex in panel A. (E) An almost midsagittal plane. The renal artery originates from the aorta (E), runs through the celiac ganglia (C and D), and supplies the renal cortex (B). (D) The major splanchnic nerve reaches the ganglia. (B) The ovarian artery supplies both the mesonephros and ovary. All the sections are stained with hematoxylin and eosin, and panels B-E are at the same magnification. Scale bars: 1 mm (A and B). For definitions of the other abbreviations, see the common abbreviations for the figures.



right embryonic adrenal cortex that was connected to the liver and the ganglia was fixed by a thick, major splanchnic nerve that arose from the level of the thorax.

Therefore, the growth of the heart, lung, and liver along the transverse axis may pull the retroperitoneal mass upwards. Since the lumbar vertebral body was much

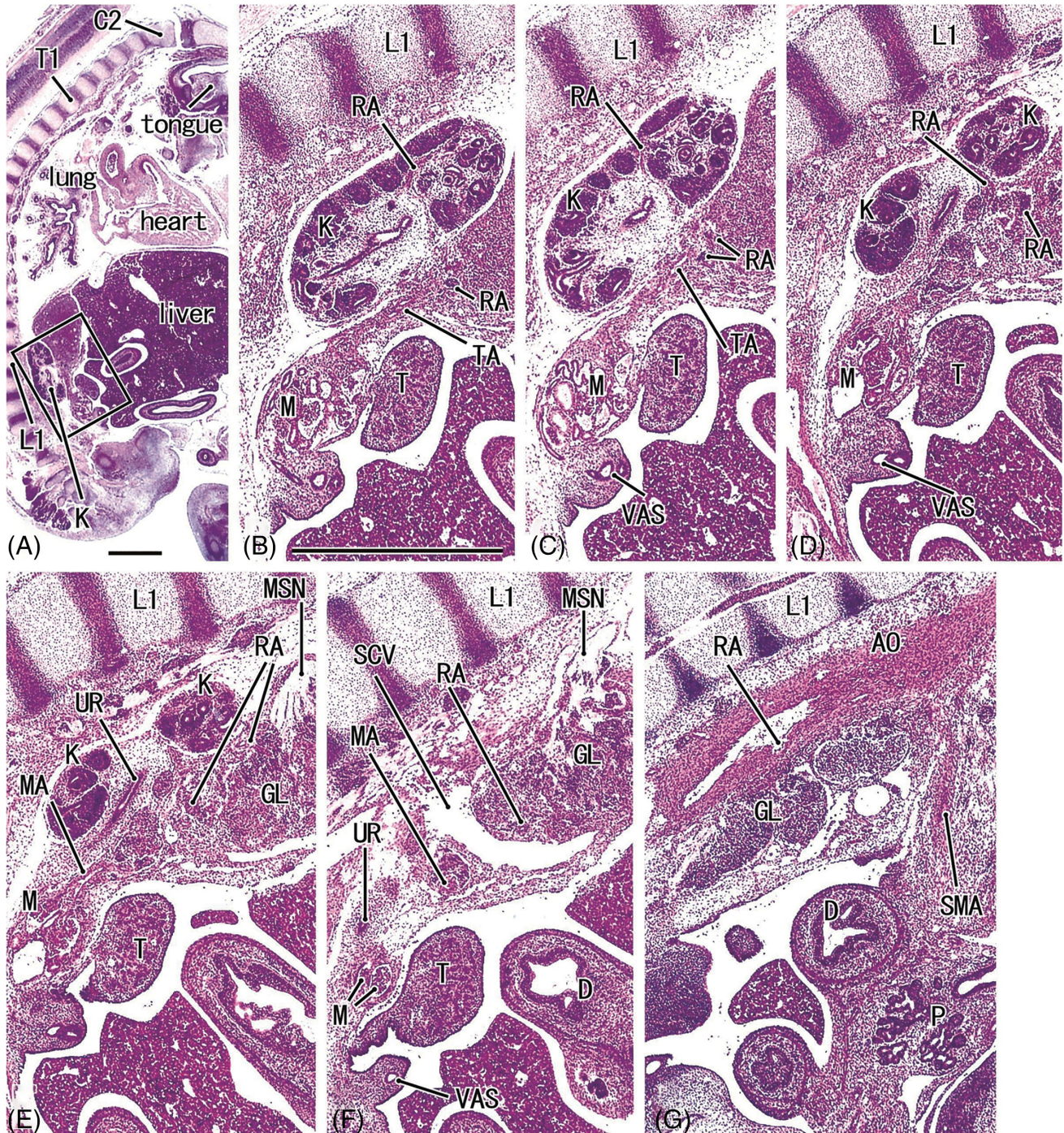


Fig. 5. Right kidney in a male fetus in its final position at 7 weeks gestation. Sagittal sections of an embryo with a crown-rump length (CRL) of 24 mm. (A) The rightmost plane, (B) is a higher magnification view of the kidney and embryonic adrenal cortex in panel A, and (G) corresponds to an almost midsagittal plane. The renal artery originates from the aorta (G), runs through the celiac ganglia on the superior side of the subcardinal vein (D-F), and supplies the renal cortex and the testicular artery supplies both the mesonephros and testis (B and C). (E) The major splanchnic nerve reaches the ganglia. All the sections are stained with hematoxylin and eosin, and panels B-G are at the same magnification. Scale bars: 1 mm (A and B). For definitions of the other abbreviations, see the common abbreviations for the figures.

smaller than the ascending kidney, changes in their relative positions seemed to advance easily and rapidly. In contrast, the ventral curvature of the lumbosacral vertebral column was often maintained, even after the kidney had reached its final location. Therefore, vertebral column straightening was not a major factor that drove the kidney's ascent. When the kidney reached its final location, the connection between the renal cortex and the embryonic adrenal cortex or celiac ganglia was lost, and it was interrupted by the adipose capsule and renal fascia that were developing around the kidney.

The ascent of the kidney from the sacral level to a level above the aortic bifurcation seemed to depend on the growth of the kidney itself, that is, its elongation along the craniocaudal axis. At the beginning of this study, we noted that the umbilical artery was a major obstacle during the early phase of the ascent, because the artery was as thick as the kidney and the bilateral arteries formed a pair of arches that stood upright in the pelvis (Hinata et al., 2015; Naito et al., 2015). Although we initially thought that the kidney moved over the arterial arch based on our examinations of the sagittal sections, our examinations of the frontal sections led us to revise our first impression, and we found that the kidney was slender initially and that it grew upwards through a narrow space between the bilateral origins of the umbilical arteries. On the immediate superior side of the arteries, the kidney growth changed its direction to the lateral site above the aortic bifurcation; thus, the kidney appeared to avoid moving over the thick and high arterial arch. The diversion around the umbilical artery might provide an opportunity for a minor part of the kidney to be left behind as the major part of the kidney ascends, which could underlie the formation of aberrant kidneys, for example, a horseshoe kidney.

The mesonephros was seen on the cranial side of the kidney when it was below the aortic bifurcation, and in this configuration, a ladder of mesonephric arteries was likely to exist. However, the mesonephros was seen on the ventrocaudal side of the metanephros in six embryos that had kidneys at the intermediate location. The caudally-distributed mesonephric arteries were unlikely to provide a ladder to facilitate the further ascent of the metanephros. Moreover, nephrogenesis occurred after the metanephros had reached the final position, indicating that the ascending kidney might not need a glomerular blood flow. Therefore, we can contest the well-known theory that suggests that the ascending kidney receives its blood supply from the aorta at increasingly higher levels until the blood supply from the definitive renal artery at the level of the second lumbar vertebra is reached (Hamilton et al., 1976). Aberrant renal arteries at lower lumbar levels, if present in adults, might not originate from persistent mesonephric arteries, but from possible secondary budding that arises from the aorta. The human embryonic aorta seems to retain the potential for budding after the mesonephric arteries have been obliterated, and this is supported by the abundant retroperitoneal twigs that arise from the abdominal aorta (Turyna et al., 2014). The subcardinal vein separated the renal arterial course from the nearby mesonephric artery, and the renal artery created a common trunk with the artery to the gonad, celiac ganglia, and/or embryonic adrenal cortex instead.

Felix (1912) argued that the elongation of the ureter was responsible for the kidney's ascent, but Parrott et al. (1994) indicated that this was a remote possibility. According to O'Rahilly and Müller (1996), the ureter is solid temporarily but soon becomes recanalized when it expands to create the initial renal pelvis at the sacral level. Since the renal pelvis emerges before the kidney ascends, the upper end of the tubular or recanalized ureter should follow the ascending kidney. The ureter was canalized in all of the specimens examined in this study. However, in contrast to the rapid elongation of a solid tube as occurs, for example, in the early duodenum (Matsumoto et al., 2002), the elongation of a canalized tube seems difficult to achieve through the simple proliferation of the epithelial cells. Naito et al. (2015) demonstrated that the ureter had a loop-like or an arch-like course initially and that it protruded inferiorly along the lateral pelvic wall. We consider that during the kidney's ascent, the ureteric loop is uncoiled to provide an additional, but sufficient, length that corresponds to the distance over which the kidney ascends from the aortic bifurcation to the upper lumbar level. In contrast to the findings from the horizontal sections, a change in the orientation of the renal hilum, that is, the rotation of the kidney, was not clearly demonstrated in the sagittal sections examined in the present study, which represents a limitation of this study.

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