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The human vertebral column at the end of the embryonic period proper. 3. The thoracicolumbar region

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INTRODUCTION

Detailed, well illustrated accounts of the human vertebral column as a whole at the end of the embryonic period and of the cervical vertebrae in particular have been published (O'Rahilly, Müller & Meyer, 1980, 1983). Both these studies were based on precise reconstructions of several embryos of the same stage in order to assess variations and particular attention was paid to the relationships between the vertebral column and the nervous system. Now that the occipitocervical region has been completed, the next two subdivisions, thoracic and lumbar, are studied here in a similar manner. The relationship between the vertebral column and thoracic and abdominal organs during the embryonic period has already been clarified (Müller & O'Rahilly, 1986).

MATERIALS AND METHODS

Serial sections of six embryos of Stage 23, 8 postovulatory weeks (O'Rahilly & Müller, 1987), belonging to the Carnegie Collection were studied: 27 mm (no. 5422, 7425 and D-122), 30 mm (no. 75 and 4525), and 31 mm (no. 9226) in greatest length. One series was sectioned coronally, two transversely, and the remainder sagittally. Stains included haematoxylin and eosin, alum cochineal, and azan, and one specimen was treated with silver. The thickness of the sections varied from 12 to 50 μm. Graphic reconstructions based on every second to every eighth section were prepared from each of the embryos. In addition, a sagittally sectioned and silver-impregnated fetus of 33 mm (no. 5852) was reconstructed for comparison.

The abbreviations C, T, L, S and Co (for cervical, thoracic, lumbar, sacral and coccygeal) will be followed, where appropriate, by either V for vertebra or N for nerve. Thus, TV 6 signifies the sixth thoracic vertebra.

RESULTS

The cartilaginous vertebrae

The parts of a thoracic vertebra and their relationship to the peripheral nerves are shown (TV 8) in Figure 1*a*. This view from above demonstrates that the neural processes (future laminae) are short and slightly bifurcated and that a prominent transverse process is present. The neural processes are united by collagenous fibres, the

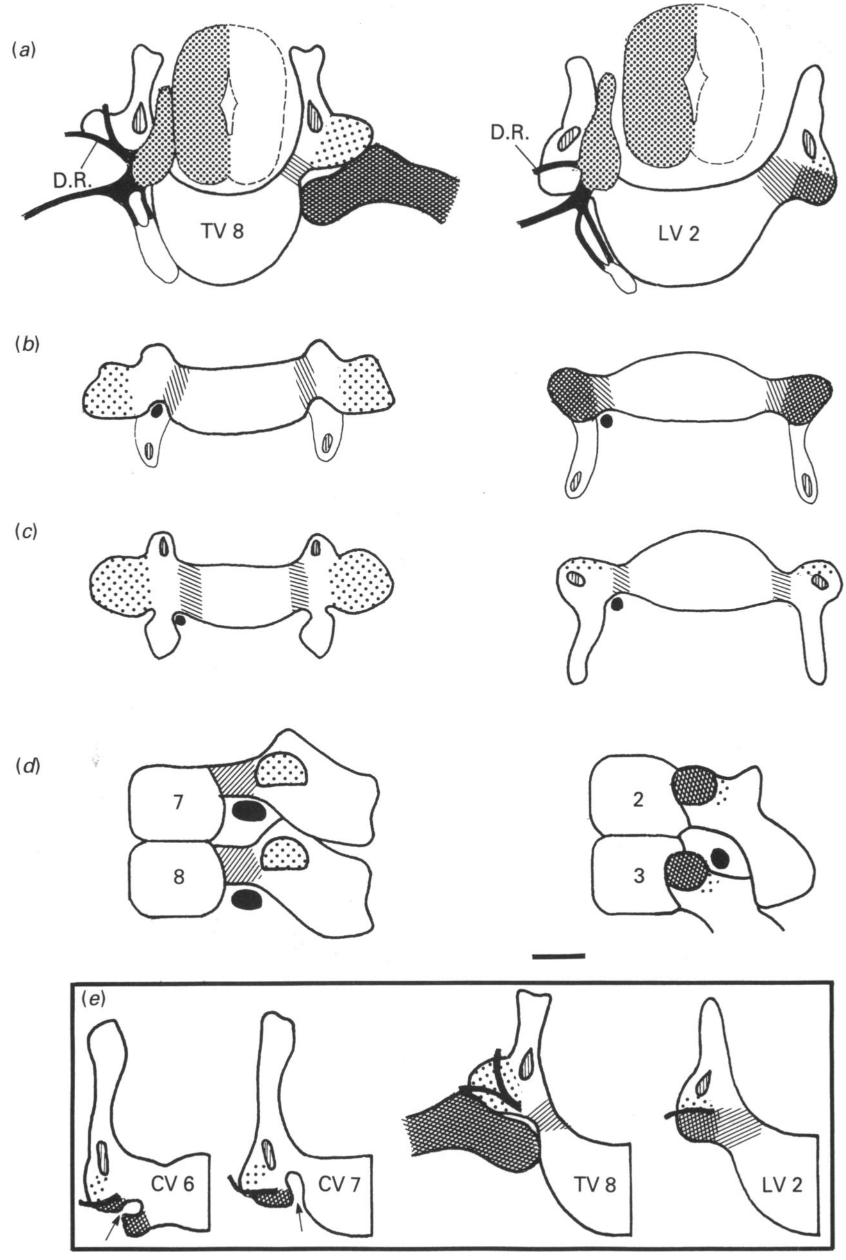


Fig. 1 (*a–e*). Comparison of the general form of TV 8 and LV 2 of no. D-122. (*a*) A view from above; (*b*) from ventral; (*c*) from dorsal; (*d*) from left lateral. The corresponding parts of the vertebrae have the same shading. An embryonic vertebra consists of a centrum and a neural arch, the latter being represented bilaterally by a pedicle (hatched), a transverse process (stippled), and a neural process (future lamina). The costal element is cross-hatched. The neural tube and spinal ganglia are represented by dense stippling. (*e*) Superimposition of dorsal rami (D.R.) on CV 6, CV 7, TV 8, and LV 2. The (cross-hatched) costal elements are ventral to the dorsal rami. The arrows point to the sites of the future foramina transversaria. The bars in Figures 1, 5 and 6 represent 0·5 mm.

innermost of which form the membrana reuniens dorsalis. A comparison of the thoracic vertebrae of different columns reveals some variation in the amount of growth of the neural processes. In one embryo (no. 9226), for example, the laminae are flush with the dorsal limit of the spinal cord whereas in another (no. D-122) approximately one fourth of the lateral surface of the cord is free of skeletal protection (Fig. 1*a*). Little or no variation exists between the thoracic vertebrae of any one specimen (except for TV 1 which, in some features, resembles a cervical vertebra). The neural processes of TV 1 and TV 12 are slightly further apart than those of TV 2–11 (in nos. 9226 and D-122). When the tips of the neural processes are approximately aligned, and also the ventral limits of the centra (Fig. 1*e*), the dorsal rami of the thoracic and lumbar nerves are seen to be situated much further dorsally than are those of the cervical nerves. A similar relationship applies to the true transverse processes.

The lumbar resemble the thoracic vertebrae in many respects. However, what appears to be a transverse process corresponds to a costal element and the true transverse process (future accessory process) is reduced to a small area between costal and articular processes. A mamillary process could not be detected.

Costovertebral and intervertebral joints

Three facets are present for Ribs 2–10: one on the future body*, another on either the pedicle or the front of the transverse process for the corresponding rib and a third on the future body for the subjacent rib. The first rib is different from Ribs 2–11 in that it articulates with the body of its own segment and with that of the segment above, namely the future body of CV 7. Only one facet for the corresponding rib is present for Ribs 11 and 12. This corresponds already to the adult pattern. The zygapophysial joints (Figs. 1, 3*b*, *c*) form a continuous column from the thoracic to the sacral region.

Spinal nerves and autonomic nervous system

The spinal ganglia of the thoracic nerves lie partly on the pedicles (Figs. 1*a*, 2*b*, *c*). The spinal nerve is very short and lies in the upper half of the intervertebral foramen (Fig. 3*d*). The arching course of the ventral rami of TN 3–9 is related to the widening thoracic cage, whereas TN 1 and 2 are in line with CN 7 and LN 3–5 (Fig. 4). The dorsal rami of TN 3–9 pursue a similar course, and the general pattern of a dorsal ramus (Fig. 1*a*) is as follows. It first runs along the line between the transverse process and the tubercle of the rib, there giving off a twig to the joint capsule. It then divides; one twig follows the posterior border of the rib and a second runs dorsally and crosses the transverse process. A small twig from the proximal part of the dorsal ramus runs to the joint between the head of the rib and the future vertebral body.

The ganglia of the sympathetic trunk are not well demarcated but share a common primordium, which is represented by a continuous mass of dark cells and fibres. At most levels two rami communicantes are evident (Figs. 2, 5).

The ventral rami of LN 1 and 2 resemble more the thoracic than the lumbar nerves (Fig. 4*b*), whereas the course of LN 3–5 is similar to that of the sacral nerves (Fig. 4*c*). The dorsal rami of TN 10–12 are arranged in a pattern similar to that of the sacral nerves. An important difference, however, is that the dorsal rami of the sacral nerves leave the vertebral canal by foramina that develop into the future dorsal foramina. The dorsal roots are horizontal only in TN 1, whereas the roots of TN 2–12 descend obliquely (Fig. 3*a*, *b*). The descent of the dorsal roots of the thoracic nerves amounts

* When the neurocentral joints become established later in fetal life, it can be seen that a rib articulates with the neural arch but not with the centrum.

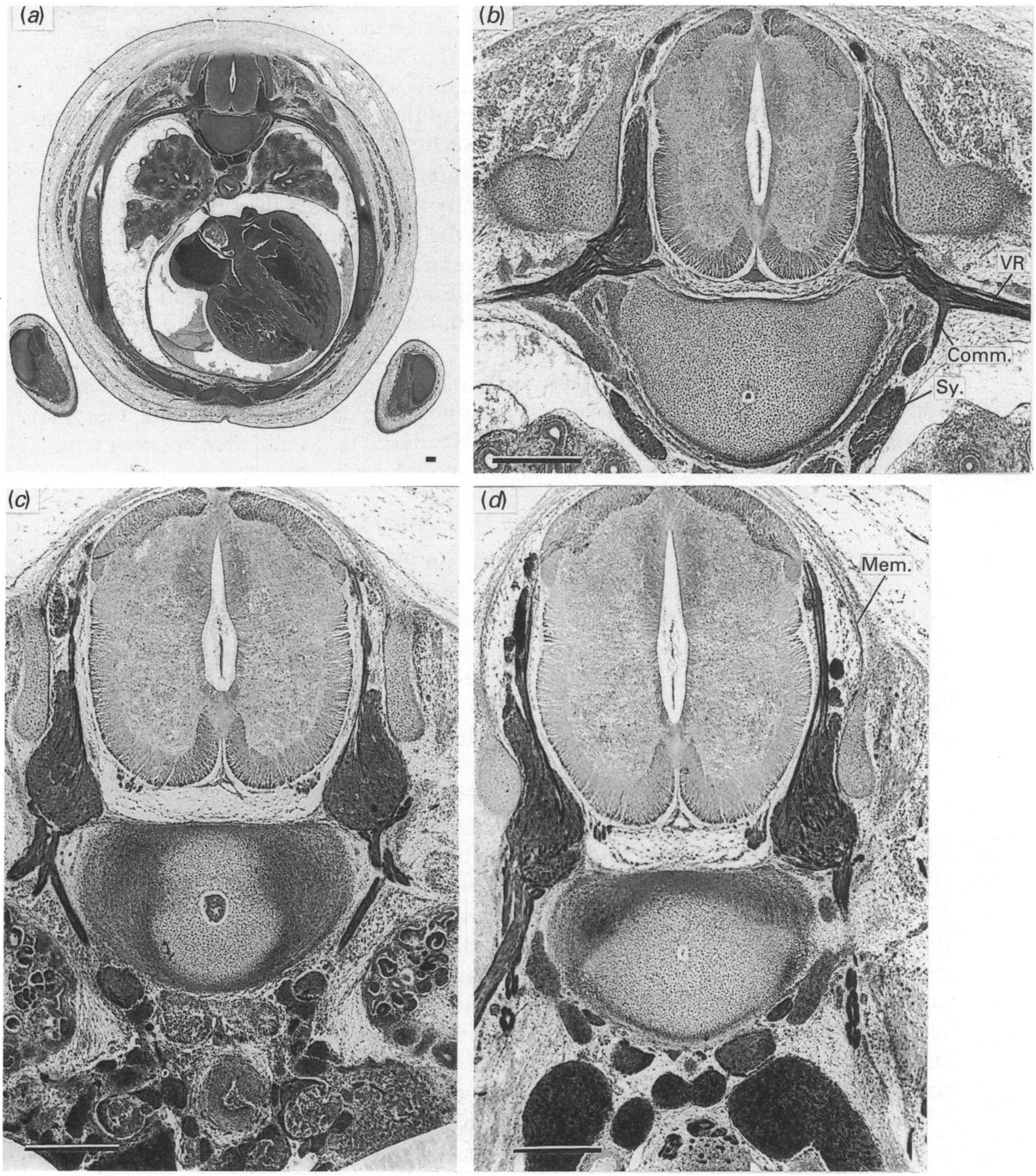
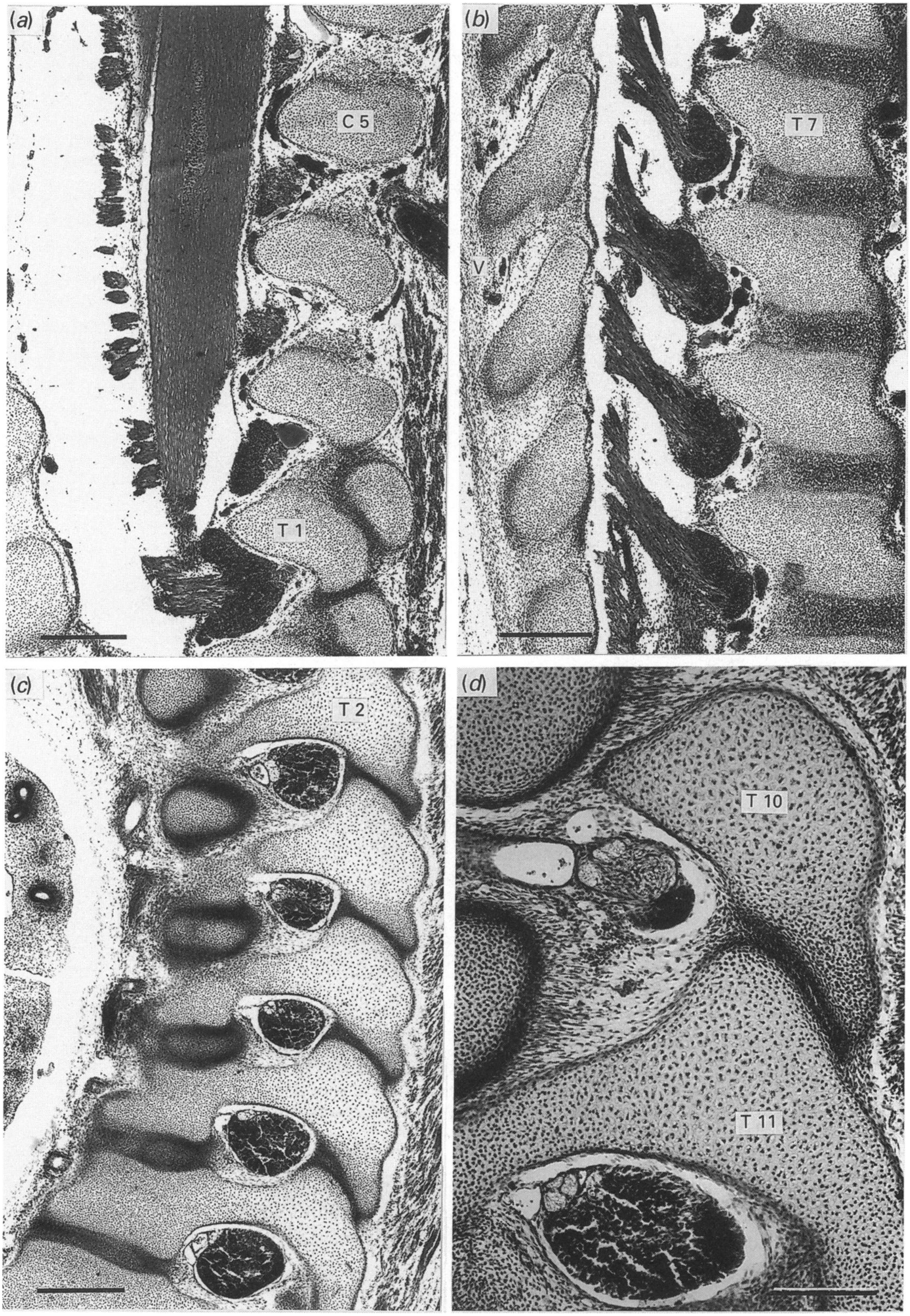


Fig. 2(*a–d*). (*a*) and (*b*) Transverse sections through TV 6 and TV 8, respectively, showing the relationship to (*a*) heart and lungs, and (*b*) spinal nerve. Spinal ganglia and portions of the dorsal and ventral roots, as well as the spinal nerves, ventral rami (VR), rami communicantes (Comm.) and sympathetic ganglia (Sy.). *Cf* Figure 1(*a*). (*c*) Transition between TV 12 and LV 1, showing the peripheral part of the intervertebral disc and the expanded intersegmental part of the notochord. Some metanephric tissue is also visible; (*d*) LV 5. Note the membrana reuniens dorsalis (Mem.) between the neural processes in (*b*)–(*d*). The bars in Figures 2 and 3 represent 250 μm.

Fig. 3(*a–d*). (*a*) and (*b*) Sections of no. 5852 showing cervical and thoracic vertebrae, and dorsal roots. Dorsal is to the left, ventral to the right. The dorsal roots of CN 5 to TN 1 in (*a*) follow the same horizontal direction. The vertebral artery (V) is entering between CV 5 and CV 6. Descending dorsal roots begin in segment 2 of the thoracic cord and can be seen for TN 7–10 in (*b*). (*c*) Intervertebral foramina and articulations of TV 2–6. (*d*) Details of intervertebral foramen between TV 10 and 11.


(a)
C 5
T 1
(b)
T 7
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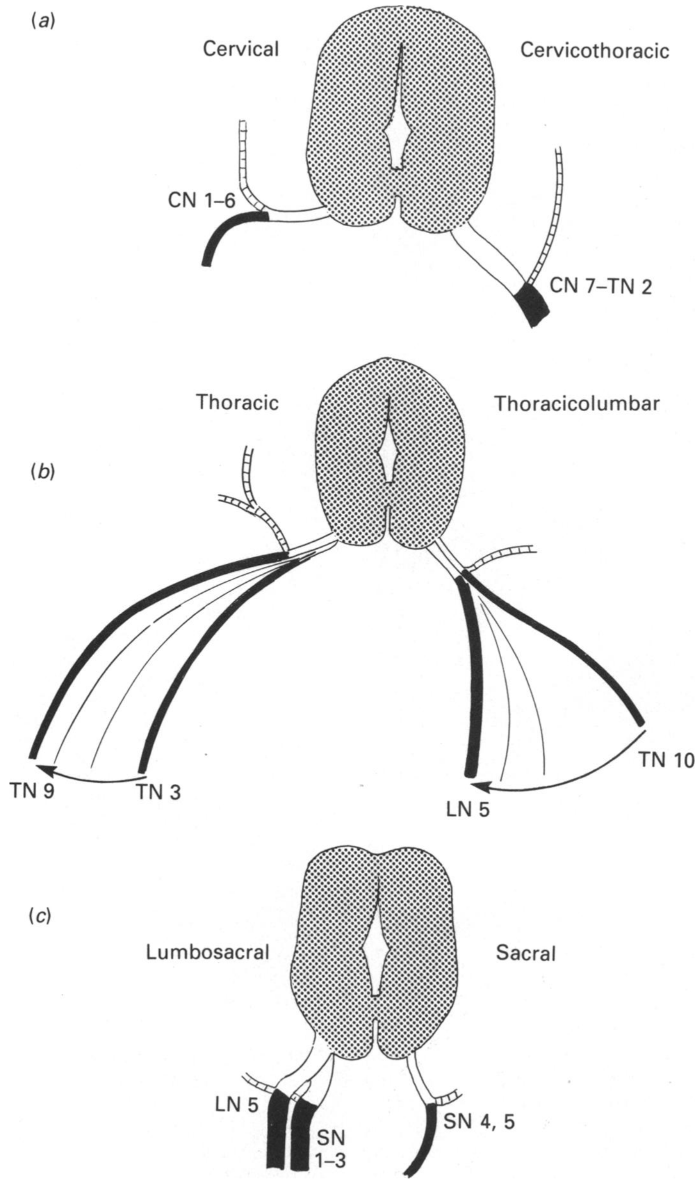

Fig. 4(*a–c*). Comparison between spinal nerves. (*a*) CN 1–6 possess a relatively long spinal nerve, which then divides at almost a right angle into dorsal and ventral rami of similar calibre. The pattern changes from CN 7 to TN 2: the ventral ramus becomes much thicker then the dorsal. (*b*) The arching course of TN 3–9, as well as 10–12, is followed by LN 1. (*c*) The lumbar nerves then run almost in a sagittal plane, which is occupied also by the sacral nerves. The roughly right angle between spinal nerve and dorsal ramus corresponds to the adult appearance. Ventral roots and spinal nerves, white; dorsal rami, hatched; ventral rami, black.

to approximately half a segment; the dorsal roots of the lumbar segments are steeper, and the difference in level between spinal cord and vertebral units is approximately one segment. The steeper course in the lumbar region corresponds to the greater height of the lumbar vertebrae.

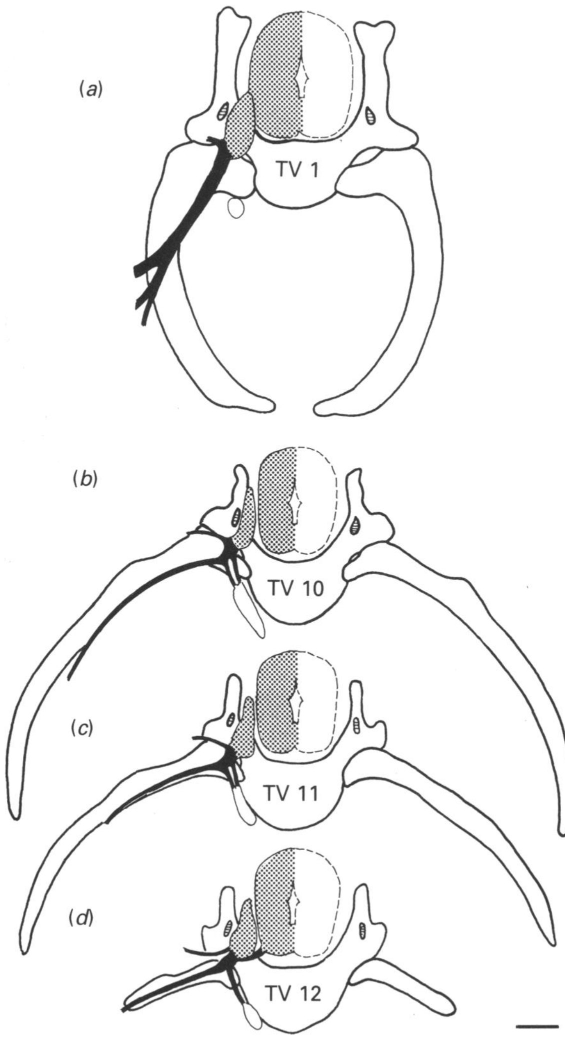

Fig. 5(*a–d*). Thoracic vertebrae and ribs (D-122) seen from above. In (*a*) the head of the massive first rib articulates with both CV 7 and TV 1. TV 1 resembles more the cervical vertebrae than it does the following thoracic elements. Its large neural processes are bipartite and reach further dorsally. The neural structures are CN 8 and the cervicothoracic ganglion. (*b*) TV 10 and TN 9; rami communicantes to the sympathetic ganglion (shown in white) are present. (*c*) TV 11 and TN 10; (*d*) TV 12 and TN 11. In all instances the ribs are ventral to the dorsal rami.

The sternum and scapula

The right and left sternal bands are almost completely united and they are connected to the vertebral column by Ribs 1–7. The scapula (Fig. 6) is high in position, at the level of CV 4/6 to TV 4/5, as illustrated previously by O'Rahilly *et al.* (1980, Fig. 2). The bifurcation of the trachea is at TV 3/4 and the heart (Fig. 2*a*) extends from TV 2 to 8.

Proportions of the thoracic and lumbar vertebral column

The mean percentages of the different subdivisions of the developing vertebral column from Stages 16 to 23 were calculated and plotted (Fig. 7). Both thoracic and lumbar parts change little during the three weeks that elapse between these stages.

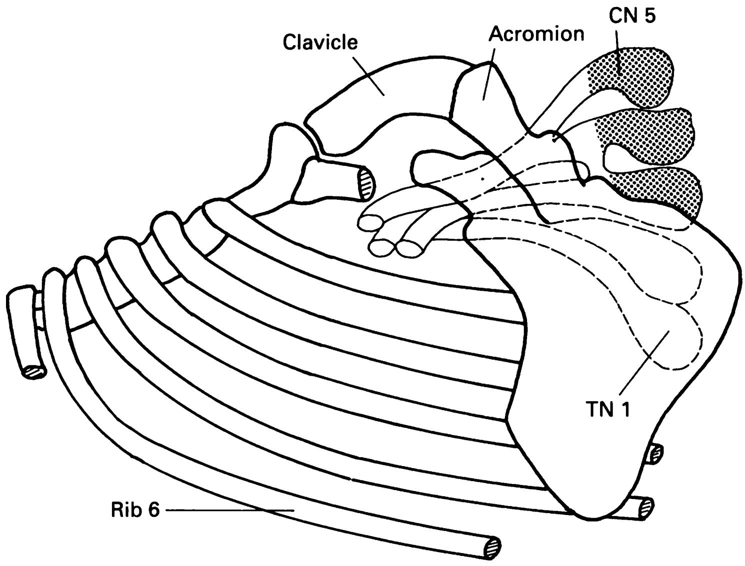

Fig. 6. Scapula and brachial plexus in left lateral view (no. 5422). Seven true ribs articulate with the sternum. The level of the scapula in this embryo is CV 4 to TV 4/5. The lateral, medial and posterior cords of the brachial plexus are sectioned.

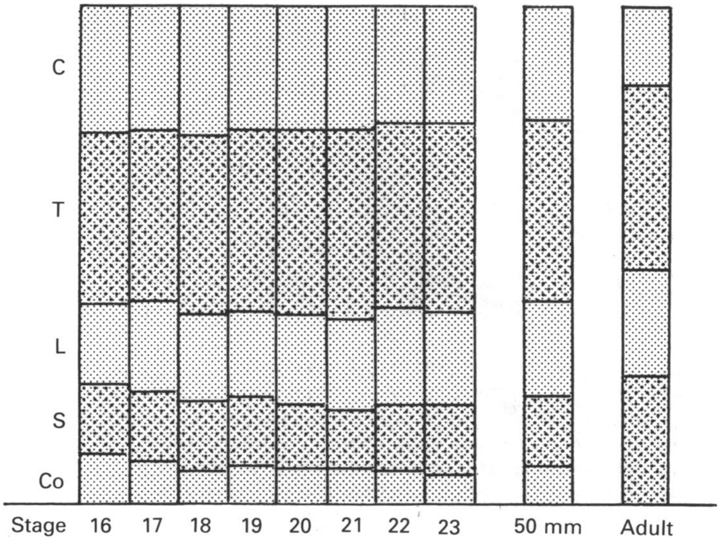

Fig. 7. The relative proportions of the regional subdivisions of the vertebral column from Stage 16 (5 weeks) to Stage 23 (8 weeks) and later. The data for the embryos are means derived from the figures given in Table 7 in Müller & O'Rahilly (1986); those for a 50 mm fetus and for the adult are calculated from Bardeen (1905*b*, Tables A, B).

Their slight increase is at the expense of the cervical and coccygeal parts of the column. The height (calculated from the mean) of one individual vertebra is highest in the lumbar (3·74 %), second highest in the thoracic (3·14 %) followed by the cervical (3 %), the sacral (2.8 %) and finally the coccygeal (1·2 for five, or 1·5 for four vertebrae).

Intervertebral discs

The lumbar discs are thicker than those in the thoracic region. The peripheral part already shows signs of organisation into the future annulus fibrosus and an expansion of notochordal cells represents the nucleus pulposus (Fig. 2*d*).

DISCUSSION

Bardeen (1905*a*) studied the development of the thoracic vertebrae and subsequently (1905*b*) that of the lumbar vertebrae in a series of embryos and early fetuses up to 50 mm. These significant sources of information are of particular interest because the specimens later became a part of the Carnegie Collection and hence their stages are now known (O'Rahilly & Müller, 1987, Appendix 1). Reiter (1942, 1944) included embryos up to approximately Stage 18 in his study of the development of the human vertebral column. Although Sensenig (1949) included Stage 23, his illustrations extend only to Stage 19. Moreover, all these authors, especially in regard to their illustrations, concentrated on the mesenchymal phase.

At Stage 23 a thoracic or a lumbar vertebra is a continuous cartilaginous element but, when ossification begins and progresses during the fetal period, the neonatal pattern of three primary osseous areas is gradually attained. The neurocentral joint on each side (Jonata, 1938, Fig. 35) then allows a clear distinction to be made between the centrum and the neural processes. When the neurocentral synchondroses become obliterated during childhood, the vertebra once more becomes a continuous, but this time an osseous, element.

The entire vertebral column at Stage 23 shows a normal spina bifida occulta totalis (O'Rahilly *et al.* 1980, Fig. 5). The membrana reuniens dorsalis (of von Recklinghausen) is a thin layer between the, as yet unfused, neural processes. It completes the neural arch and closes the vertebral canal from the surface epithelium and the subjacent mesenchyme. The development of the membrane was closely followed in embryos of 24 mm and larger, as well as in fetuses, by Ask (1939). Many vertebral anomalies arise during the embryonic period proper, e.g. butterfly vertebrae such as that recorded at 63 mm by Müller, O'Rahilly & Benson (1986).

Macalister (1892–93) noted the relationship between the first rib and CV 7 in the adult, but found only a capsule and not an articular surface.

Invertebral joints

Whereas many features of the adult vertebrae are already present at the end of the embryonic period proper, some changes are yet to come in the intervertebral joints, as pointed out by Huson (1967). The definitive disposition of the articular facets of the zygapophysial joints, for example, is present only in the cervical region at 26 mm and, in the other regions, changes in the direction of the articular surfaces continue until after birth.

The lumbar intervertebral disc at 29 mm was described and illustrated by Peacock (1951, Fig. 9). Definite fibres of the annulus fibrosus are present, and a "specialized peri-notochordal cartilage" surrounds the "notochordal reticulum."

Neural relationships and homology

The neural relationships of the developing skeletal elements have been found to be of considerable aid in the determination of homologous parts within the vertebral column. Clarification of corresponding parts has not previously been possible within the embryonic period proper. In the thoracic region (Figs. 1, 5) the ribs are situated ventral to the dorsal rami. In (at least the lower) cervical and in the lumbar region at Stage 23 (Fig. 1 *e*), the areas ventral to the dorsal rami are considered to be the costal elements. Furthermore, in the thoracic region the transverse processes more or less underlie the dorsal rami. In (at least the lower) cervical region at Stage 23, the 'true' transverse element is therefore merely a small area in the vicinity of the posterior tubercle of the future descriptive transverse process; in the lumbar region at Stage 23, the 'true' transverse process is a similarly small area.

Holl (1882), from his study of ossification centres, believed that the lateral process* of a lumbar vertebra is comparable to (*ist gleich zu setzen*) the transverse process of a thoracic vertebra together with its associated rib, a conclusion supported by the embryonic data of the present study. As has been well remarked, "the regional status of a vertebra is determined by the ontogenetic fate of its pleurapophysis (costal element) which, in the thoracic region, remains independent as the obtrusive rib, but elsewhere becomes incorporated into the descriptive 'transverse process'" (Cave, 1975).

At Stage 23 the vertebral column and the neural tube are coterminous, i.e. the spinal cord ends at the last coccygeal vertebra (O'Rahilly *et al.* 1980, Figs. 3, 4). The termination of the cord is in the sacral region from about 45 to 90 mm (Barry, 1956, Fig. 3). Associated with this displacement is a change in the angulation of the dorsal roots of the spinal nerves, as shown for SN 1 at 30–221 mm in a well-known drawing published by Streeter (1919, Fig. 2).

The directions of the dorsal roots of the spinal nerves reflect differences in growth gradients between vertebral column and spinal cord. In general, at Stage 23 the cervical roots are horizontal, the thoracic sloping caudally, the lumbar even more so, and the sacral again horizontal. Within two weeks, at 46 mm, the sacral have acquired a slope similar to that of the lumbar dorsal roots (Barry, 1956, Fig. 5). This is interpreted here to signify an increased longitudinal growth of the sacral part of the vertebral column (centra and/or discs). A comparison of the embryonic information with the fetal data (45 mm to term) of Barry suggests that the first differential growth is at the lumbar level, followed at almost the same time by the thoracic component, and then, early in the fetal period, by the sacral region. The upper cervical roots show a slight caudal slope even at 19 mm (attributed by Barry to increased nuchal flexure) and differential growth in that region becomes marked after 175 mm.

The characteristic regional variation in angulation of the spinal nerves and their roots is complicated by changes between the intradural and extradural portions of their course, particularly in the lower cervical and upper thoracic regions, as has been described in the adult (Nathan & Feuerstein, 1970).

Lumbar ribs

Extrathoracic ribs may be found occasionally in the adult, especially in the cervical (see O'Rahilly *et al.* 1983) and lumbar regions. Their presence has been related to the possible development of individual centres for the costal elements of cervical and lumbar vertebrae, as has been detailed by several writers, although such centres have not been observed by the present authors. Müller (1906) maintained that, as in the cervical region, all lumbar vertebrae (at 15–23 mm) show independent precartilaginous or cartilaginous rib *anlagen*. According to Bardeen (1908–09), "in the lumbar

* Holl (1882) used Rosenthal's term *Seitenfortsatz* (Processus lateralis) for the combined transverse and costal elements of developing lumbar and sacral vertebrae, although his usage was not entirely consistent.

vertebrae it seems probable that there are separate centres of chondrification for each of the costal elements. These appear later than the centres for the ribs in the thoracic region and they very quickly fuse with the cartilaginous transverse processes. Usually they bear no close resemblance to the true ribs." Frets (1909), who examined embryos from 17 to 22 mm, believed that the lateral processes of all lumbar vertebrae appear as precartilaginous thickenings of the intermuscular septa and that they possess individual cartilaginous centres. He stressed that the lateral processes of LV 1 are round in form and different from the rod-shaped ribs. Reiter (1944) found lumbar rib *anlagen* that (at 9–10 mm) were not distinctly separate from the centra, and that the costal processes of LV 1 were only a little smaller than Ribs 1 and 12. He showed a mostly blastemal "lumbar Rib" 1 beginning to fuse with the transverse process, and a "lumbar Rib" 5 beginning to fuse with the centrum and transverse process at 22·2 mm (his Figs. 6, 7). Prenatal vertebral variations were reviewed in detail by Peters (1927), who also studied 87 specimens of the Hochstetter Collection, in which he found rudimentary thirteenth ribs (at 25·8, 26·5, 28·3, 40·6 and 66 mm) and free LV 1 costal processes (at 54, 66 and 73 mm). In the mouse, in contrast to the above studies, von Bochmann (1937) failed to find independent cartilaginous centres of the lumbar lateral processes.

In the fetal period, several authors have noted ossification centres that they have claimed to be cervical and lumbar ribs. For example, in their alizarin red study of the skeleton of 136 specimens (14–235 mm), Noback & Robertson (1951) found "seventh cervical ribs" in 34 cases (57–235 mm) and "first lumbar ribs" in 3 instances (97–134 mm).

In summary, several authors who have studied the matter believe that separate cartilaginous centres form in the costal processes of most, if not all, developing vertebrae: the range given by Bardeen (1908–09) is "from the first cervical to, and sometimes possibly including, the first coccygeal." A distinction needs to be made, however, between such centres, whether cartilaginous or osseous, and ribs. So-called cervical ribs in the fetus are simply separate ossific loci within the cartilaginous costal elements of CV 7, and are present in nearly one third of fetuses up to 150 mm (Meyer, 1978), as compared with an incidence of less than 1 % for cervical ribs in the adult. Bardeen (1908–09) proposed that the cartilaginous centres for the costal elements of LV 1 should not "be classed as ribs... unless they bear so strong a morphological resemblance to the ribs as to seem to come in series with these," which "normally is not the case." Lumbar ribs in the adult vary considerably in both length and form, as shown by Schertlein (1928), who was able to distinguish lumbar ribs from lumbar transverse processes in radiographs.

Further precision can now be added in that, although the costal elements of LV 1 do not resemble ribs in form (Müller, 1906, Fig. 8, 15 mm), they are, in all the lumbar vertebrae, in series with the ribs, as shown here by the neural relationships.

The sternum

The sternum develops from bilateral sternal bands, suprasternal structures and a ventral rudiment (Klíma, 1968). The sternal bands are partially fused at 22–23·5 mm (Reiter, 1942) but signs of the fusion can still be seen caudally at 32 mm (Müller, 1906, Fig. 17). The seven true ribs are already united with the sternal bands at 17 mm (ibid). On comparative and experimental grounds, it may be that the sternum should be regarded as appendicular (a part of the pectoral girdle) rather than axial (Seno, 1961).

The scapula

Vertebral levels of various structures during the embryonic period proper became securely established when somitic and vertebral interrelationships were clarified by Müller & O'Rahilly (1986). It has been shown, for example, that the scapula does not descend during the embryonic period proper, although it does so between that time and adulthood. Congenital elevation of the scapula is no longer considered as a simple failure of descent but rather as part of a complex that may include diastematomyelia and the split notochordal syndrome.

SUMMARY

The present study of the thoracicolumbar region continues an investigation of the vertebral column at 8 postovulatory weeks (the end of the embryonic period proper) by means of graphic reconstructions.

The cartilaginous vertebrae have short neural processes associated with the normal spina bifida occulta present at this time. The separate cartilaginous centres that several authors believe to exist in the cervical and lumbar costal elements, but which have not been observed by the present authors, have been thought to be the forerunners of extrathoracic ribs. A distinction needs to be made, however, between such centres and ribs. Similarly, in the fetal period, ossific loci in the costal elements of CV 7 are very frequent, whereas cervical ribs in the adult are relatively rare. The neurocentral joints, and hence the boundaries between neural arches and centra, are unclear before ossification has begun and has progressed during the fetal period. The sternal bands are almost completely united and the scapula is high in position.

Neural relationships aid in the determination of homologous parts within the vertebral column, but clarification of corresponding parts has not previously been possible within the embryonic period. Areas ventral to the dorsal rami are ribs in the thoracic region and costal elements in other regions. Areas underlying the dorsal rami are transverse processes in the thoracic region and minute 'true' transverse elements in the cervical and lumbar regions. Thus, the descriptive lumbar transverse processes correspond to the true transverse processes and the ribs in the thoracic region.

The dorsal rami of the thoracic nerves pass between the transverse processes and the tubercles of the ribs and then divide. The ventral rami of lumbar Nerves 1 and 2 resemble the thoracic in their course, whereas those of Nerves 3–5 are similar to the sacral. The thoracic dorsal roots are sloping and, associated with the greater height of the lumbar centra, the lumbar roots even more so. The directions of the various dorsal roots reflect differences in growth gradients between vertebral column and spinal cord. The thoracic and lumbar portions of the column change little in proportion during the embryonic period proper.

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