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The human vertebral column at the end of the embryonic period proper

2. The occipitocervical region

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INTRODUCTION

The development of the human vertebral column at the end of the embryonic period proper has been described and illustrated recently (O'Rahilly, Müller & Meyer, 1980). Details of the regional subdivisions are not yet available. The present study was undertaken to fill that gap in regard to the occipitocervical region.

The only systematic account of the embryonic cervical vertebrae is that by Reiter (1944), whose study was limited to embryos between 3 and 11 mm and did not include reconstructions. The craniovertebral region was investigated by Sensenig (1957) in embryos of Stages 10–23, but no reconstructions were included and little information on Stage 23 was provided. Isolated examples of reconstructions were published by Hayek (1923; 23·4 mm), Strian (1963; 14 and 27 mm), and Aaron, Gueriot-Colasse & Singer (1966; 17 mm). The present study is the first systematic account of the cervical region based on reconstructions of staged embryos.

MATERIALS AND METHODS

Serial sections of nine embryos of Stage 23, 8 post-ovulatory weeks (O'Rahilly, 1973), belonging to the Carnegie Collection were studied: 27 mm (4 embryos), 28 mm (1), 30 mm (3), and 31 mm (1) crown–rump. One series was sectioned coronally, another transversely, and the remainder sagittally. The stains included haematoxylin and eosin, alum cochineal and azan, and one specimen had been treated with silver. The thickness of the sections varied from 12–50 μm. Graphic reconstructions based on every second to every eighth section were prepared from each of the embryos. In addition, sagittal sections of an early fetus (33 mm crown–rump) treated with silver were studied and reconstructed for comparison.

RESULTS

Centra

The cervical centra, which consisted of hyaline cartilage, were arranged in a gentle arch, concave forwards (Fig. 1C). They were relatively wide from side to side and narrow anteroposteriorly (Fig. 2). The notochord ascended either through the

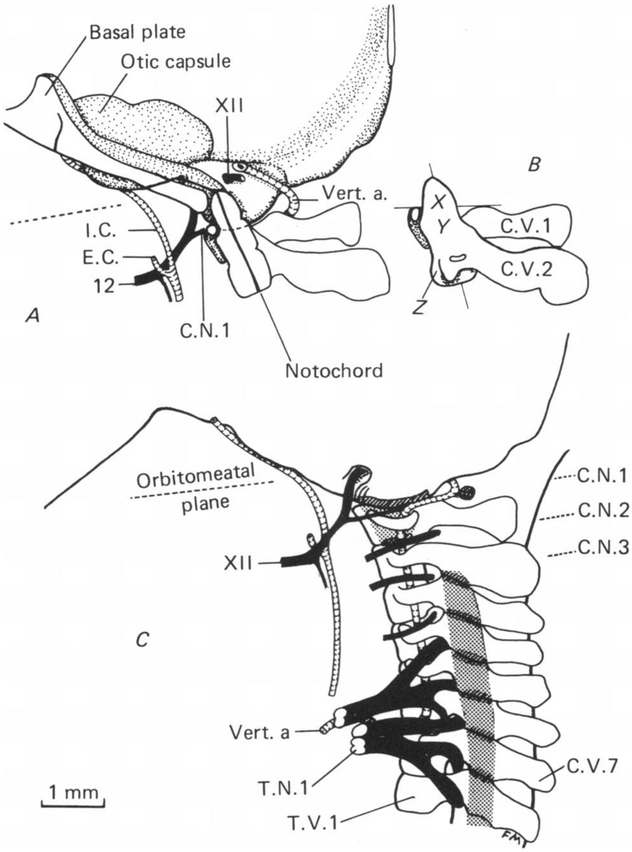

Fig. 1 (A–C). Graphic reconstructions of the base of the skull and cervical vertebrae of a 27 mm embryo (no. 5422). (A) Medial view of the right half, showing the notochord ascending through the median axial column. The notochord displays a loop immediately before entering the basal plate. The external (E.C.) and internal (I.C.) carotid arteries, as well as the vertebral (Vert. a.), are included. The hypoglossal nerve (XII) enters the occipital cartilage some distance above the atlanto axial joint and later receives the first thoracic nerve (C.N. 1) and then gives off the superior root of the ansa cervicalis. (B) Left lateral view of the axis (C.V. 2) superimposed on the right half of the atlas (C.V. 1). The three parts of the median axial column are marked *X*, *Y*, *Z*. Part *X* is seen to project considerably above the level of the atlas. (C) Left lateral view, showing neural relationships, including the brachial plexus. Posteriorly, the vertical line passing medial to the neural processes represents the posterior border of the spinal cord. The two stippled areas indicate the columns formed by the articular processes and facets. The main column is situated behind the exits of the spinal nerves, whereas the atlanto-occipital and atlanto-axial column lies in front of the exits of the first and second cervical nerves (C.N. 1 and C.N. 2).

middle of the centra or a little anteriorly. On reaching the axis (Fig. 1A) the notochord traversed the median cartilaginous column of that skeletal element (Fig. 5C). It then left the tip of the dens (Fig. 3C) and ran through connective tissue (Fig. 4A) for a variable distance before entering the cartilaginous basal plate of the chondrocranium (Figs. 1A, 3A). Although the centra were well separated peripherally by the future intervertebral discs, the perinotochordal area connected the vertebrae into a continuous column. Notochordal enlargements represented nuclei pulposi.

The cartilaginous median column of the axis comprised three parts, which were generally separated by two shallow grooves, especially posteriorly (Figs. 1A, 5C).

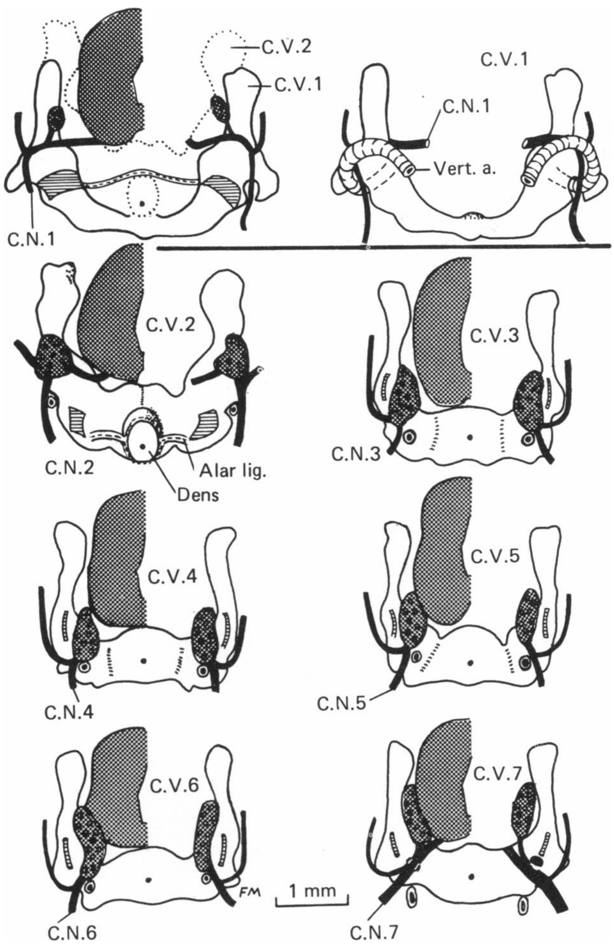

Fig. 2. Graphic reconstructions of the first to seventh cervical vertebrae (C.V. 1–7) of a 27 mm embryo (D-122), superior aspect. The right half of the spinal cord and the spinal nerves and ganglia of both sides are included. The vertebral arteries are shown in the developing first and second cervical vertebrae (C.V. 1, 2) and the complete (third to sixth cervical vertebrae, C.V. 3–6) foramina transversaria. The articular processes or facets are indicated by cross hatching. The notochord is visible in the centra. Two drawings of the first cervical vertebra are provided. That on the left shows the transverse ligament of the atlas; that on the right includes the course of the vertebral artery.

The upper groove corresponded to the position of the transverse ligament of the atlas behind (Fig. 5D). Lines parallel to the base of the axis can conveniently be drawn to indicate the divisions, which will be referred to as X, Y, Z, from above downwards (Figs. 1B, 5D). Posteriorly between parts Y and Z, some fibrous disc material was present. The anterior arch of the atlas usually articulated with part X (Figs. 1A, 5C) and presented an anterior tubercle (Fig. 2). Anteriorly, the arch articulated with the dens (Fig. 7C–E), although a joint cavity was present in only one case. The dens was limited behind by the transverse ligament of the atlas, which was attached to the lateral mass on each side (Figs. 2, 7E). The dens was anchored to the occipital condyles by the alar ligaments (Figs. 2, 3B, 4B), which were very dense. Their fibres ran mostly to the lateral part of the dens, although some ran

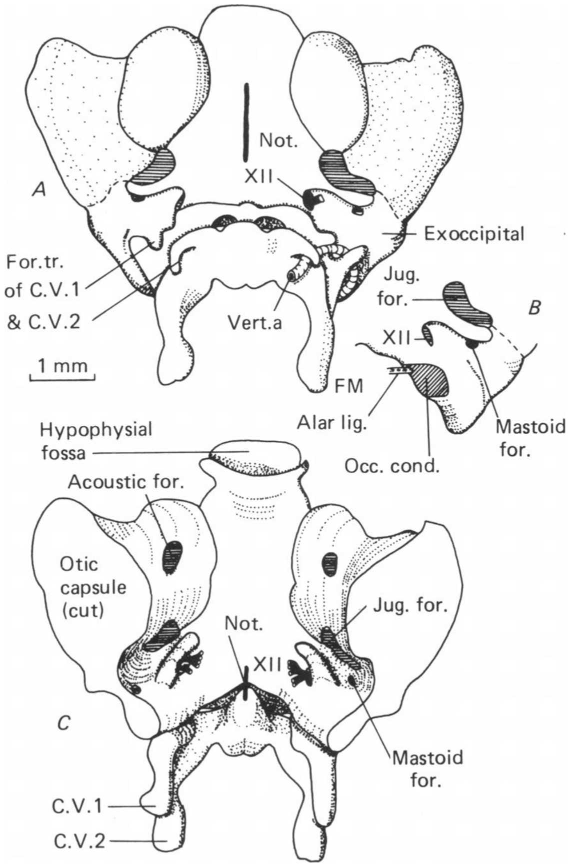

Fig. 3 (A–C). Graphic reconstructions of the base of the skull and the first and second cervical vertebrae (C.V. 1 and 2) of a 27 mm embryo (D-122). (A) Inferior aspect. The notochord (Not.) is visible on the lower surface of the basal plate for part of its course. The foramina transversaria (For. tr.) of the two vertebrae are not yet complete. A part of the future exoccipital is marked. (B) Part of the left occipital region from (A), but with the vertebrae removed, to show the jugular foramen (Jug. for.), the future mastoid foramen or 'foramen paracondyloideum', the exit of the hypoglossal canal (*XII*), the occipital condyle (Occ. cond.) and the alar ligament (the attachment of which is seen also in Fig. 4B). (C) Superior aspect. The notochord (Not.) is seen to bridge the gap between dens and the occipital (cf. Fig. 1A). The five rootlets of the hypoglossal nerve (*XII*) converge to form two bundles.

anteriorly and posteriorly to surround the dens (Fig. 7F). The fibres of the transverse ligament joined the lowermost posterior fibres of the alar ligaments (Fig. 7E, F). Where the notochord left the dens, some mesenchymal cells were arranged in a direction parallel to, and also converging on, the notochord. However, no collagenous fibres were present at the site of the apical ligament of the dens. The dens projected at least to the upper limit of the basal plate (Fig. 1A) and sometimes even extended into the foramen magnum (Fig. 5A).

Neural arches

Each half (neural process) of the incomplete neural arch extended laterally from the centrum and formed a complete or incomplete foramen transversarium (Fig. 2). It then proceeded directly backwards to a variable extent, generally ending along the side of the posterior half of the spinal cord, thereby constituting a normal spina bifida occulta. The tips of at least some of the laminae (e.g. in third and fourth cervical vertebrae) tended to turn laterally (perhaps presaging the bifid spinous process) whereas others faced directly backwards. The laminae of the axis were thicker from side to side and higher as seen laterally (Fig. 1 C).

The foramina transversaria and the vertebral arteries were small except in the atlas (Fig. 2). The transverse processes exhibited more or less distinct anterior and posterior tubercles. The pedicles were in broad continuity with the centra in all the cervical vertebrae (except the atlas) and they were very short. In the fetus, the vertebral arteries entered the sixth cervical vertebra on the right and the fifth on the left side.

The articular processes formed a vertical column that extended upwards to the lower aspect of the axis (Figs. 1 C, 4 C, D). The uppermost three pairs of articular facets, however, were situated on a more anterior plane (Figs. 1 C, 4 C). The interval between the upper, concave articular surface of the atlas and the occipital condyle was filled with dense mesenchyme (Fig. 4 C). In none of the embryos had joint cavitation begun but it had commenced in the fetus at the periphery of the joint. A joint cavity between the dens and the basal plate was present in one embryo (Fig. 7 A, B), and was less developed in the fetus, where it was present between the basal plate and the upper part of the dens only (Fig. 7 D). One embryo had a joint cavity also between the dens and the atlas (Fig. 7 C), although it was not present in the fetus.

The dens of the axis exhibited differences in its relationship to the foramen magnum. In one embryo, for example (Fig. 5 A), it crossed the lower border of the foramen, whereas in other instances (Fig. 5 C, D) it ended at the level of that border.

Cavities were not present in the zygapophysial joints. From the seventh to the third cervical vertebrae the articular facets were arranged sagittally rather than lateromedially, as in the adult (Fig. 6). In the embryo, as in the adult, however, the longitudinal axes of the facets were more or less in line with those of the laminae.

In the fetus, the neural arches of the third to seventh cervical vertebrae had grown more behind the spinal cord than in the embryos, although there was still no median fusion.

Occipital condyles

The condyles were situated in the general area of the future exoccipital and were behind the hypoglossal canal. The extent of the articular surface varied: it was relatively small in one instance (Fig. 3 B) and relatively large in three others (Figs. 1 C, 4 C, 5 A).

Relationship of scapula to vertebral column

The upper border of the scapula reached the level of the fourth/fifth cervical vertebrae in four specimens, the fifth/sixth cervical vertebrae in three, and almost to the third/fourth vertebrae in one instance.

Relationships to nervous system (Fig. 2)

The anteroposterior diameter of the spinal cord was at least twice that of the centra. The spinal ganglia were generally partly in the vertebral canal and partly on the neural arches, medial to the articular processes. The first cervical ganglia were very small (barely larger than the coccygeal) and they were intradural. The first and


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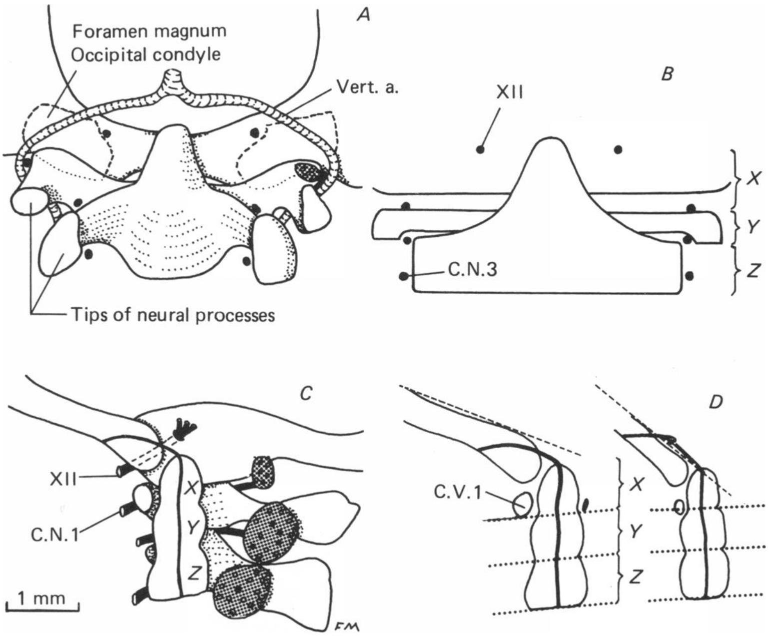

Fig. 5 (A–D). Views of the axis at Stage 23. (A) Posterior view at 31 mm (no. 9226) showing the union of the vertebral arteries to form the basilar, and the tips of the neural processes of the first and second cervical vertebrae forming the normal spina bifida occulta. The positions of the hypoglossal nerves and first to third cervical nerves are indicated by large black dots. On the right hand side, the first spinal ganglion is included. (B) Schematic representation of the first and second cervical vertebrae, and their associated nerves, including the third cervical nerve (C.N. 3). (C) Medial view of the right half at 30 mm (no. 75), showing relationship of nerves and ganglia. *XII*, hypoglossal nerve; C.N. 1, first cervical nerve. (D) Schematic representations of median axial column and its three parts, *X*, *Y*, *Z*. The superior plane of the basal plate, indicated by an interrupted line, is seen to have a variable relationship to the tip of the dens. In the left hand specimen (30 mm, no. 75) the transverse ligament of the atlas is visible in section and is shown in black. In the right hand example (27 mm, no. 5422) a loop is present in the notochord (cf. Fig. 1 A). C.V. 1, first cervical vertebra.

Fig. 4 (A–D). Photomicrographs of the occipitocervical region at Stage 23. (A) Transverse section through the base of the skull at 31 mm (no. 9226), showing the hypoglossal canal in the occipital cartilage on each side. In each canal several small blood vessels are visible, and, lateral to them, two bundles of the hypoglossal nerve. The hypoglossal canal is related laterally to the internal jugular vein (full on one side and empty on the other), posteromedially to the apex of the dens. The notochord can be seen on its way to the basal plate. The future auditory ossicles and the labyrinth are visible on each side in the upper part of the picture. (B) Transverse section at 27 mm (no. D-122), showing again the hypoglossal canal and nerve, together with some additional branches probably representing autonomic fibres. From the medial part of the occipital condyle, collagenous fibres of the alar ligament (Fig. 3 B) diverge medially. Most of these are attached to the dens, although some cross the median plane, especially posteriorly. Portions of the atlas and the second cervical spinal ganglia are also visible. (C–D) Sagittal sections through the cervical vertebrae at 30 mm (no. 4525). The occipital condyle and the first to fourth cervical vertebrae are shown in (C) and the third to seventh cervical vertebrae are visible in (D). The vertical lines in (C) indicate the columns formed by the articular processes and facets (cf. Fig. 1 C). In (D) the fourth to eighth cervical nerves can be seen. The anterolateral tips of the fourth and fifth cervical spinal ganglia appear as dark areas in relation to the corresponding nerves.

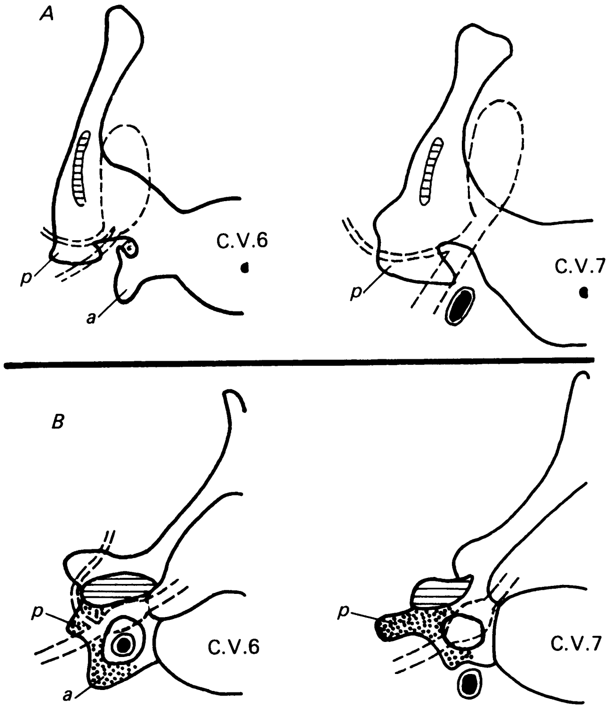

Fig. 6(A–B). Comparison between embryonic (Stage 23) and adult cervical vertebrae. (A) Embryonic sixth and seventh cervical vertebrae (C.V. 6 and 7), showing developing foramina transversaria. In the sixth, the anterior (*a*) and posterior (*p*) tubercles of the transverse process are well developed. In the seventh the anterior lamella is ill developed and the anterior tubercle is ill defined. The articular processes are arranged sagittally and the spinal ganglia lie medial to them. The sixth and seventh cervical nerves are indicated by interrupted lines, and the vertebral artery is shown. (B) Adult sixth and seventh cervical vertebrae (C.V. 6 and 7), showing foramina transversaria completed by 'intertubercular lamellae'. According to Cave (1975), the costal element (shaded with dots) includes posterior tubercle, lamella, and anterior tubercle. The articular processes are arranged coronally and the spinal ganglia are largely in front of them. The anterior tubercle of the seventh vertebra is still ill defined.

second ganglia lay behind the corresponding articular facets and they were relatively lateral. The much larger second ganglia even extended laterally beyond the neural arch. The third to seventh ganglia lay mostly medial to the articular processes, and they were too elongated to fit into the intervertebral foramina. The third to eighth cervical nerves emerged in front of the articular processes, whereas the first and second appeared behind the corresponding articulations (Figs. 1C, 2). The ventral rami of the seventh and eighth nerves resembled those of the first thoracic in their course. The cervical nerves and ventral rami from the second to sixth cervical lay

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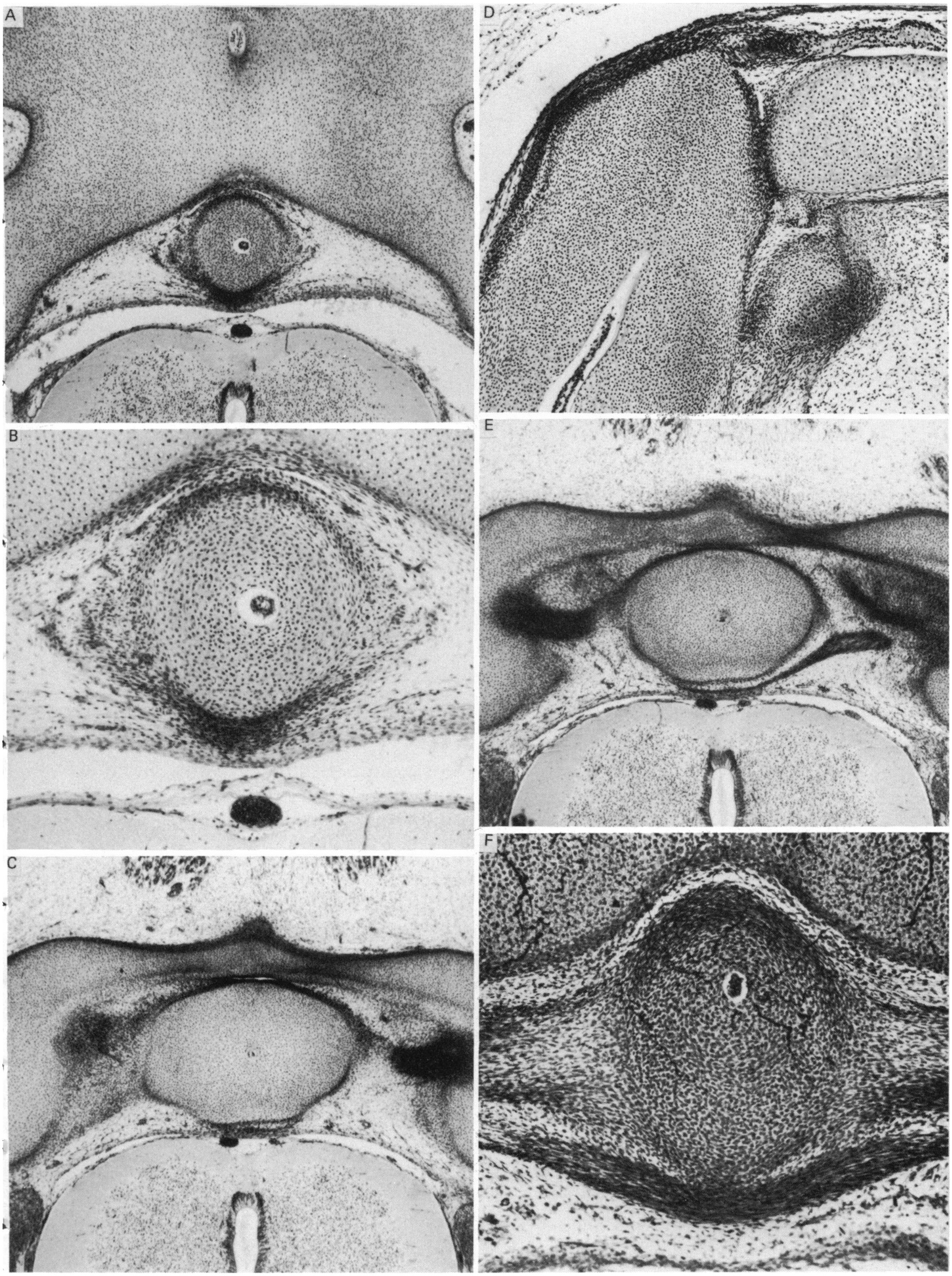
Fig. 7(A–F). Photomicrographs of the atlanto-axial region. (A–B) Occipito-axial joint at 31 mm (no. 9226), showing the beginning articular cavity. (C) Median atlanto-axial joint at 31 mm (no. 9226), possibly showing the beginning of cavitation. (D) Occipito-axial joint in a 33 mm fetus (no. 5852), showing peripheral cavitation. The median atlanto-axial joint contains loose tissue (cf. F). The notochord is evident in the dens and can also be seen lying on the upper surface of the basal plate before entering the cartilage. (E) Transverse ligament of atlas at 31 mm (no. 9226) (cf. first cervical vertebra in Fig. 2). (F) Alar and transverse ligaments at 27 mm (no. D-122). The occipito-axial joint contains loose tissue (cf. D).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lateral to the vertebral artery. The ventral ramus of the first cervical nerve was at first below the vertebral artery and then crossed the vessel medially (Figs. 1C, 2).

The fourth to seventh cervical nerves gave twigs to the vertebral artery. The vertebral nerve, *sensu strictu*, derived from the inferior cervical ganglion, entered the foramen transversarium of the seventh cervical vertebra and, at this stage, ascended no higher than the sixth, at least in the two silver-impregnated specimens.

The many rootlets of the hypoglossal nerve became reduced to three to five bundles immediately before entering the hypoglossal canal (Fig. 3C). At this stage, the hypoglossal canal was undivided in all cases, although it usually contained two divisions of the hypoglossal nerve (Fig. 4A), as well as branches from the vago-accessory complex (Fig. 4B).

DISCUSSION

Bardeen (1908) emphasized that the fully formed "cartilaginous cervical vertebrae have essentially the shape of the adult osseous cervical vertebrae" and that "even before the end of the second [prenatal] month of development distinct cervical characters may be distinguished". The general appearance, however, is considerably modified by the normal spina bifida occulta that occurs in embryos (Fig. 2) and early fetuses.

Among the characteristics of the cervical vertebrae that have for centuries attracted attention, the following are particularly of developmental interest: (1) the peculiarities of the first two vertebrae and the problem of the body of the atlas; (2) the occipitocervical complex as interpreted in vertebral theories of the skull; (3) the relationships of the cervical nerves to the articular pillars of the vertebrae; (4) cervical ribs and the costal element of the transverse processes.

(1) *The median axial column*

The cartilaginous median column of the axis comprises three elements, listed here as X, Y, Z (Fig. 5). These three parts are still visible in the fetus, as has been verified during the present study in 15 specimens from 32 to 79 mm. Calcification occurs in Z (the centrum of the second cervical vertebra) by 120 mm (Töndury, 1958, Fig. 112; Noback & Robertson, 1951, give 69–120 mm as the range) and ossification appears bilaterally in Y by 200 mm (Töndury, 1958, Fig. 113*a*; Noback & Robertson, 1951, give 135–161 mm). In the newborn (Frame, 1960, Fig. 5) the ossification centres for Y and Z are clearly visible. Although most of the postnatal body is ossified from the Z centre, the uppermost portion is formed from the Y centre, so that the dens appears sunken into the body (Köhler & Zimmer, 1968, Fig. 1161; von Torklus & Gehle, 1972, Fig. 29). It has been claimed that the remains of an 'interaxo-odontoid disc' between the Y and Z centres are detectable throughout life (Fischer *et al.* 1969). A constant (Köhler & Zimmer, 1968) or inconstant (von Torklus & Gehle, 1968) centre for the tip of the dens first appears during the second postnatal year (or even earlier) and fuses with the main mass at the tenth to twelfth year.

It is generally agreed that part Z is the centrum of the axis. Part Y is frequently interpreted as the centrum of the atlas (Cave, 1938; Kladetzky, 1955; Sensenig, 1957) but this has also been denied (Ludwig, 1953, 1957). Both structures (dens and body of atlas) were present in certain extinct reptiles and "available paleontologic evidence supports the conclusion that the dens evolved as an addition to the atlas body" (Jenkins, 1969). Part X is sometimes interpreted as a 'proatlas' (Cave, 1938;

Reiter, 1944; Sensenig, 1957; Frame, 1960). Moreover, it has been claimed that the pro-atlantal arch is incorporated into the atlas as the dorsal portion of the superior articular facet for the occipital condyle (Presley & Hallam, 1980) and that the pro-atlantal arch even forms the occipital condyles themselves (Ganguly & Singh-Roy, 1964). The pro-atlas is regarded as "the first cervical cranial sclerotome-half [which] remains as a half segment between the occipital and atlantal rudiments" (Sensenig, 1957). It should be kept in mind, however, that, more recently, the resegmentation (*Neugliederung*) theory in general has been queried (for discussion see O'Rahilly & Meyer, 1979) and the implications for the cervical region have not yet been pursued.

The three elements (X, Y, Z) are related to the first (suboccipital), second and third cervical nerves (Fig. 5C), respectively, as pointed out by Cave (1938).

When the upper portion of the dens remains ossifically independent, it is called an os odontoideum. The separation is probably between parts X and Y. Von Torklus & Gehle (1972) have emphasized that it is not between what are here termed parts Y and Z. These authors maintain that Y, although hypoplastic, is fused to the rest of the axis and projects upwards as a 'cupola'. In some instances, merely a small nodule (Bergmann's ossicle; ossiculum terminale) is found at the tip of the dens. Variations in the various anomalies occur, however, and the existence of an 'acquired os odontoideum' needs to be kept in mind.

(2) *The occipital region*

The part of the skull that develops around the notochord is comparable to one or more vertebrae, according to the vertebral theory of the skull proposed originally by Goethe in a letter from Venice in 1790 (Peyer, 1950). Despite subsequent criticisms, as well as gross exaggerations of this interesting proposal, it is basically correct when confined to the posterior part of the skull, or 'spondylocranium' (Lewis, 1920; Singh-Roy, 1967; Müller & O'Rahilly, 1980). Certain differences in the mode of ossification (perichondral versus endochondral), however, need to be kept in mind (Zawisch, 1957).

The number of segments assigned to the occipital region varies considerably. The most thorough studies in the human indicate either four (Sensenig, 1957) or five (Reiter, 1944). The key features taken into consideration are the somites, myotomes, ganglia, and roots of the hypoglossal nerve. The notochord penetrates the basal plate of the skull (Figs. 1A, 5C, D) and Reiter maintained that the site of penetration is the second from last occipital segment.

It has been maintained that "a partial liberation of one of the vertebral elements which normally enter into the composition of the occipital bone" is responsible for some of the variations and anomalies recorded in the craniovertebral region (Gladstone & Erichsen-Powell, 1915; Gladstone & Wakeley, 1925). On the other hand, it has also been proposed that the atlas is best regarded as an isolated cranial bone, that the ontogenetic craniovertebral boundary is between the atlas and axis, and that the assimilation of the atlas is "merely a manifestation of this ontogenetically ascertainable boundary" (Ludwig, 1957).

The foramen magnum is still incomplete at Stage 20 (Lewis, 1920), so that a craniorachischisis is present. By Stage 23, the foramen is bounded by a complete cartilaginous ring (Müller & O'Rahilly, 1980), so that only the rachischisis remains to be eliminated.

Atlanto-occipital joint

The occipital condyle was illustrated in a reconstruction at 26 mm by Hesser (1926), who described it as ellipsoid, and found the articular surface of the atlas to be a well marked socket. This is in agreement with the present findings (Figs. 1 A, C, 4C). An atlanto-occipital cavity was not observed in the embryos but peripheral cavitation was beginning in the fetus. The hypoglossal canal is considerably in front of the condyle at Stage 23 (Figs. 1 A, 3 B).

The occipital condyles are generally believed to arise largely from the exoccipitals but partly from the basi-occipital, the two parts being separated, in infancy, by a synchondrosis. Subdivisions of the articular surface in the adult are found occasionally but appear not to be related to the synchondrosis (Tillman & Lorenz, 1978).

The development of the transverse, alar, and apical ligaments was studied by Ludwig (1953), who believed that the anlagen of all three were already present at 20 mm.

Occipito-axial joint

The close relationship between the basal plate and the dens (Figs. 1 A, 3 C) was referred to by Hayek (1923), who found a temporary joint cavity at 43 mm and in older fetuses.

In the adult, a median facet is rarely found on the anterior border of the foramen magnum for articulation with the dens of the axis (Le Double, 1903). In other instances, a projection from the occipital (the third condyle) may (or may not) articulate with either the apex of the dens or with the upper border of the anterior arch of the atlas (*op. cit.*).

The dens at first occupies a high position in relation to the basal plate (Fig. 5 D) and may even enter the foramen magnum (Fig. 5 A). This is in agreement with Hayek (1923), who made similar observations in specimens between 25 and 35 mm. The relationships are reminiscent of those seen postnatally in so-called basilar impression, which is an occipital hypoplasia (von Torklus & Gehle, 1972). The dens descends relative to the basi-occipital during the fetal period. Failure of this "caudal shift at the cranial end of the vertebral column" may be responsible for certain anomalies in the craniovertebral region, e.g., an articular facet on the anterior margin of the foramen magnum (Frame, 1960).

Other joints

The sagittal arrangement of the cervical intervertebral (zygapophysial) joints (Fig. 6) was observed at 26 mm by Huson (1967), who found that they are arranged coronally by 50 mm.

(3) *Neural relationships*

The hypoglossal nerve is found to comprise three to five bundles, which is in agreement with Sensenig's (1957) observations. No indication of a divided hypoglossal canal was noted in the present series. Such divisions, which are claimed to represent neural processes of an occipital vertebra, have been seen in embryos, especially 6–15 mm (Inglemark, 1947), late fetuses (Augier, 1931), the newborn and adult (Ingelmark, 1947).

The cervical spinal ganglia are situated mainly medial to the articular processes (Fig. 6A) and not yet in the intervertebral foramina, as maintained by Sensenig

(1957). The articular processes shift from a sagittal to a coronal position later on, and this alteration appears to be associated with a corresponding change in the location of the spinal ganglia, whereby they enter the intervertebral foramina (Fig. 6B).

Although the vertebral nerve could not be traced higher than the sixth cervical vertebra, Kimmel (1959) found it as high as the fourth at 20 mm.

(4) *Cervical ribs*

As Cave (1975) has 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'." In the cervical region, Cave believes that the costal element consists of the major lateral portion of the descriptive transverse process, including the posterior tubercle, 'intertubercular lamella' and anterior tubercle.

In the seventh cervical vertebra, the anterior lamella of the transverse process is frequently ill developed (Fig. 6A) and may lack an anterior tubercle. Although separate cartilaginous centres are not found, the anterior lamella presents a separate centre of ossification, endochondral in origin, in one third of early fetuses (49–150 mm), being first seen at 62 mm (Meyer, 1978). Excessive development of this centre gives rise to a cervical rib in less that 1 % of adults. Cervical ribs occur almost exclusively in association with the seventh cervical vertebra although they have been recorded for all the cervical vertebrae except the atlas (Sensenig & Hall, 1957). There is at present no known basis in the cartilaginous skeleton that would indicate the future appearance of a cervical rib.

SUMMARY

The present investigation of the cervical region of the vertebral column at eight post-ovulatory weeks is the first such study based on precise reconstructions of staged embryos.

At the end of the embryonic period proper, a typical vertebra is a U-shaped piece of cartilage characterized by spina bifida occulta. The notochord ascends through the centra and leaves the dens to enter the basal plate of the skull. The median column of the axis comprises three parts (designated X, Y, Z) which persist well into the fetal period. They are related to the first, second and third cervical nerves, respectively. Part X may project into the foramen magnum and form an occipito-axial joint. Part Z appears to be the centrum of the axis.

The articular columns of the cervical vertebrae are twofold, as in the adult: an anterior (atlanto-occipital and atlanto-axial) and a posterior (from the lower aspect of the axis downwards). Alar and transverse ligaments are present. Cavitation is not found in the embryonic period in either the atlanto-occipital or zygapophysial joints, and is generally not present in the median atlanto-axial joint either.

Most of the transverse processes exhibit anterior and posterior tubercles. An 'intertubercular lamella' may or may not be present, i.e. the foramina transversaria are being formed around the vertebral artery.

The spinal ganglia are generally partly in the vertebral canal and partly on the neural arches, medial to the articular processes. During the fetal period, the articular

processes shift to a coronal position and this alteration appears to be associated with a corresponding change in the location of the spinal ganglia.

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