The Timing and Sequence of Events in the Development of the Human Vertebral Column During the Embryonic Period Proper *

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Summary. A documented scheme of the early development of the human vertebrae is presented. It is based on (1) reports of workers who personally studied staged human embryos, and (2) personal observations and confirmations. The necessity of studying staged embryos in order to determine the precise sequence of developmental events is stressed.

Key words: Human embryo – Vertebrae – Somites – Notochord – Developmental stages.

Introduction

Since the early studies of the development of the vertebrae by Remak, Kölliker, Froriep, and von Ebner, many articles have appeared, although relatively few on human embryology. Publications on both comparative and human development have recently been evaluated in an important review by Verbout (1976), who discusses and, with Baur (1969), rejects the resegmentation *(Neugliederung)* on which most accounts have long depended. This problem, and the related question of whether intervertebral fissures are artifacts, await further studies for a completely convincing solution. The present article is concerned rather with the relationship of observed developmental features to embryonic staging.

The importance of embryonic staging (O'Rahilly, 1973a) in developmental studies has already been shown in published accounts of several body systems and organs (reviewed by O'Rahilly, 1979). In all of these investigations it has been stressed that the term "stage" is being employed in its technical, embryological sense, and hence that such expressions as "at the 18 mm stage" should
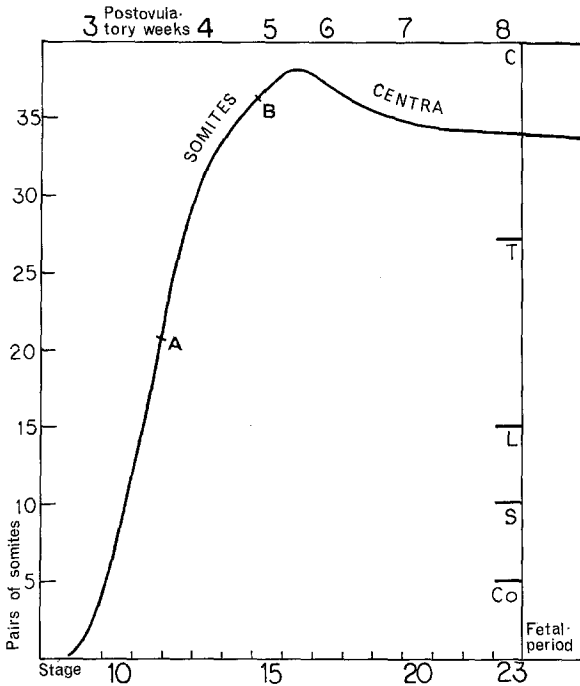
Fig. 1. Graph showing the numbers of pairs of somites in relation to stages and ages, based on 29 human embryos, most of which belong to the Carnegie Collection and most of which have been recorded in the literature. The somites first appear at stage 9, increase in number rapidly between 3 and 4 weeks, and reach their maximum at stages 15–17. Variations occur but their extent is difficult to assess. Point A represents the moment when the first pair of somites disappears, and point B indicates when occipital somites are no longer counted

be replaced by "at 18 mm C.-R." In other words, the length of an embryo is a single criterion that is not *per se* adequate to establish a "stage."

Material and Methods

The scheme presented here is based on first-hand reports of workers who personally studied staged human embryos, supplemented by personal observations. Only staged embryos have been considered, that is, those specifically assigned to one of the recognized Carnegie stages (formerly termed "horizons") of human development (O'Rahilly, 1973a, 1979). It should be noted that Carnegie stages are always assigned Arabic numerals whereas the so-called horizons are given Roman numerals. Although this staging system, which is now in international usage (Blechschmidt, 1973), had not been established at the time of the earlier investigations (prior to 1942), nevertheless, because some of the embryos studied formerly were staged subsequently, it is now possible to refer certain specimens to specific stages, and this has been done here. An important example is the material studied by Bardeen and Lewis in various publications and listed by O'Rahilly and Gardner (1975, Table 1). In addition, certain embryos have been assigned to stages on the basis of their somitic count.

The ages given throughout this article are in postovulatory days (O'Rahilly, 1973a), and the pitfalls of comparisons between the macaque and the human have been avoided.

Results

Sequence of Events

Stage 7 (ca 0.4 mm; ca 16 Days)
   Notochordal process appears (O'Rahilly, 1973a)
Stage 8 (ca. 1–1.5 mm; ca 18 Days)
   Notochordal canal appears in notochordal process (O'Rahilly, 1973a)
   Floor of notochordal canal may begin to disappear, resulting in grooved
   notochordal plate and formation of neurenteric canal (O'Rahilly, 1973a)
Stage 9 (ca 1.5–2.5 mm; 1–3 Pairs of Somites; ca 20 Days)
   Notochordal plate is intercalated into endoderm (O'Rahilly, 1973a)
   Neurenteric canal may be completely patent, partly patent, or completely
   closed (O'Rahilly, 1973a)
Stage 10 (ca 2–3.5 mm; 4–12 Pairs of Somites; ca 22 Days)
   Notochord first appears as a solid cord caudally, and notochordal tissue
   extends from tip of foregut to caudal region (Corner, 1929)
   Neurenteric canal may be open or closed (O'Rahilly, 1973a)
   Sclerotomic cells migrate ventromedially from somites (Sensenig, 1949)
   Neural crest is first visible (Corner, 1929)
Stage 11 (ca 2.5–4.5 mm; 13–20 Pairs of Somites; ca 24 Days)
   Notochord shows dorsal evagination, becomes tubular, and is separated
   from both gut and neural tube, but it shows no lumen (Sensenig, 1949,
   1957)
   Occipital, cervical, and thoracic somites may be distinguishable, e.g., 3 Occ.,
   7 C., and 10 T. in a 20-somite embryo (Davis, 1923)
Stage 12 (ca 3–5 mm; 21–29 Pairs of Somites; ca 26 Days)
   Notochord shows homogeneous eosinophil sheath (Sensenig, 1949)
   Occipital, cervical, thoracic, and lumbar somites may be distinguishable,
   e.g., 2 Occ., 8 C., 12 T., and 2 L. in a 24-somite embryo (Johnson, 1917).
   However, after 20 pairs of somites, first somite seen is probably S. 2 (Arey,
   1938)
   Sclerotomic migration extends ventral and dorsal to notochord, and dorsally
   to form neural processes (Sensenig, 1949)
   Intrasclerotomic fissures are barely discernible in some specimens (Personal
   observations)
   Myotomes are flattened (Sensenig, 1957)
   Aortae give off many dorsal branches (Blechschmidt, 1973)
   Neural crest has reached level of upper limb buds (Gardner and O'Rahilly,
   1976)
Stage 13 (ca 4–6 mm; 30 or More Pairs of Somites; ca 28 Days)
   Occipital, cervical, thoracic, lumbar, and sacral somites may be distinguish-
   able, e.g., 2 Occ., 8 C., 10 T., 5 L., and 3–4 S. in a 28- to 29-somite embryo
   (Gage, 1905); and coccygeal somites may be present, e.g., in 35-somite em-
   bryos (Bardeen and Lewis, 1901; Ingalls, 1907)
   Intrasclerotomic fissures are distinctly seen in most embryos of this stage.
   Thus cranial and caudal sclerotomites are distinguishable (Personal observa-
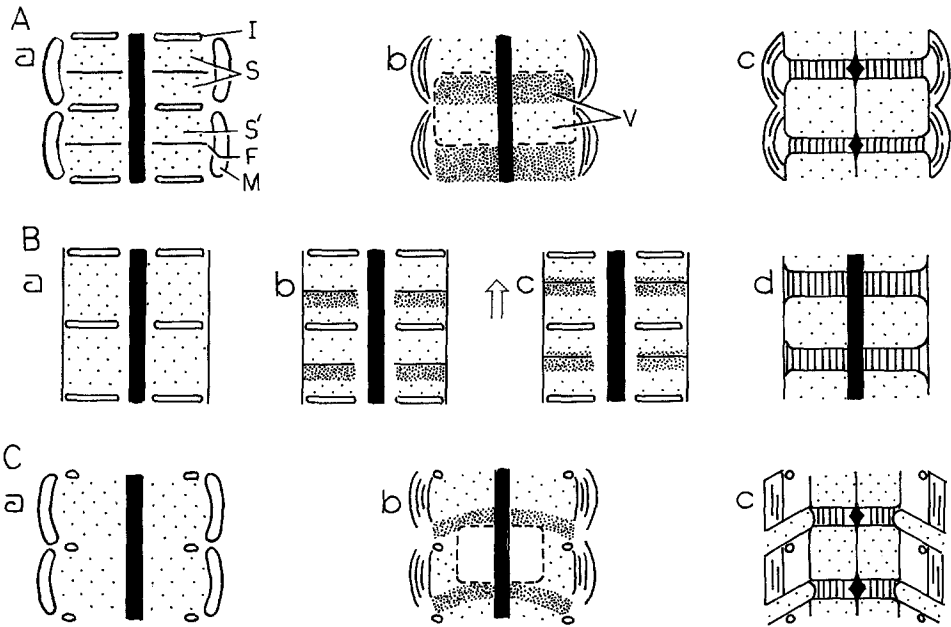   tions)

Fig. 2A–C. Summary of the chief theories of vertebral development. **A** In Remak's classical theory of vertebral segmentation, the sclerotomes (*S*), bounded laterally by myotomes (*M*), medially by the notochord, and cranially and caudally by intersegmental vessels (*I*), are bisected by an intrasclerotomal fissure (*F*) into cranial and caudal sclerotomites (*S'*). The caudal sclerotomite becomes more condensed (in *b*) and unites with the loose cranial sclerotomite of the next sclerotome to form the vertebral Anlage (*V*). The definitive vertebra (in *c*) is intersegmental in position and the muscles formed from the myotomes function between vertebrae. **B** In Prader's (1947) theory of vertebral resegmentation, condensed caudal and loose cranial sclerotomites are formed (in *b*). The condensed tissue of the caudal sclerotomite, together with the intrasclerotomal fissure, becomes displaced cranially (*arrow*) so that the sclerotomites are no longer equal in size and the fissure becomes surrounded by dense tissue (in *c*). The condensed tissue around the fissure and derived from both cranial and caudal sclerotomites differentiates into the intervertebral disc (in *d*). **C** In Baur's (1969) theory, the myotomes are bounded medially by a homogeneous, unsegmented mesenchymal mass (in *a*) without sclerotomal divisions, although intersegmental vessels reveal somitic boundaries. Dense and loose zones appear (in *b*) with no evidence of resegmentation. The dense zones develop into the intervertebral discs and ribs (in *c*), whereas the loose areas differentiate into the vertebral centra. The muscles formed from the myotomes are attached to the ribs but not to the centra. *Abbreviations:* *F* intrasclerotomal fissure; *I* intersegmental vessel; *M* myotome; *S* sclerotome; *S'* sclerotomite; *V* vertebral Anlage

Cellular vertebral rudiments are distinguishable from "meninx primitiva" (Sensenig, 1957)
Anlagen of ribs appear (Sensenig, 1949)
Ventral roots of spinal nerves appear before dorsal (Sensenig, 1957)
Neural crest cells are becoming mingled with those of somitic origin (Sensenig, 1951)
More than twenty pairs of spinal ganglia are appearing (Blechschmidt, 1973)
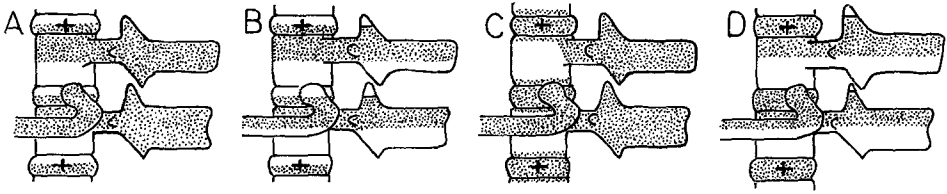Typical myotomic plates are present (Sensenig, 1957)

Fig. 3A–D. Scheme of the derivatives of the sclerotomites. **A** In Bardeen's theory (1905) the intervertebral disc and the centrum each develop from both sclerotomites. The following theory is basically similar. **B** In Reiter's theory (1942), based on resegmentation, the intervertebral disc develops from both sclerotomites at the site of the transient intervertebral fissure. **C** In Wyburn's theory (1944) a strictly horizontal linear relationship is not found. The intervertebral disc, neural arches, and ribs are derived entirely from the caudal sclerotomite whereas the centrum develops from both sclerotomites. The intervertebral fissure becomes incorporated into the centrum. **D** In Sensenig's theory (1949) the intervertebral disc differentiates entirely from the caudal sclerotomite, the intervertebral fissure occupies its cranial boundary, and the pedicles arise from both sclerotomites

Stage 14 (ca 5–7 mm; ca 32 Days)

Segmental flexures of notochord are developing (Sensenig, 1957)

Notochord possesses a cellular perichordal sheath (Sensenig, 1957)

Notochord ends in a prechordal strand, which is inserted into dorsal wall of craniopharyngeal pouch (O'Rahilly, 1973b)

Intrasclerotomic fissures are seen in most embryos (Personal observations)

Caudal sclerotomites are becoming more condensed than their cranial counterparts. The latter contain spinal nerves, ganglia, and intersegmental vessels (Personal observations)

Primary perichordal centra and (future intervertebral) discs are distinguishable (Sensenig, 1957)

Anlagen of articular processes appear (Sensenig, 1949)

Adult complement of spinal ganglia is present (Blechschmidt, 1973)

Brachial and lumbosacral plexuses are forming (Blechschmidt, 1973)

Many myotomic plates are detectable (Blechschmidt, 1973)

Stage 15 (ca 7–9 mm; ca 33 Days)

Notochord is thicker in future discs than in centra at stages 15 and 16 (Sensenig, 1949)

Intrasclerotomic fissures are absent in most embryos of stages 15 to 18 (Personal observations)

Occipital somites are still distinguishable, e.g., 3 Occ., 8 C., 12 T., 5 L., 5 S., and 5 Co. in a 38-somite embryo (Bardeen and Lewis, 1901)

"Meninx primitiva" is well developed (Sensenig, 1951)

Stage 16 (ca 8–11 mm; ca 37 Days)

Notochord appears segmented (Blechschmidt, 1973)

Adult complement of ribs is present (Blechschmidt, 1973)

Ventral rami of most spinal nerves are present (Blechschmidt, 1973)

Stage 17 (ca 11–14 mm; ca 41 Days)

Rostral end of notochord is becoming surrounded by cranial base (Blechschmidt, 1973)

Dens of axis is detectable (Blechschmidt, 1973), although it is not separated from atlas (Sensenig, 1957)

Chondrification begins in primary centra and in basi-occiput (Sensenig, 1949, 1957)

Mesenchymal ribs show head, neck, and tubercle (Sensenig, 1949)

Dorsal rami of many spinal nerves are present (Blechschmidt, 1973)

Future prevertebral and postvertebral musculatures are becoming separated (Sensenig, 1957)

Stage 18 (ca 13–17 mm; ca 44 Days)

Cartilage appears in laminae (Sensenig, 1949)

Neural arches extend dorsally to mid-level of spinal cord, and their tips are united by membrana reuniens (Sensenig, 1949)

Spinal ganglia are entering intervertebral foramina (Sensenig, 1951)

Stage 19 (ca 16–18 mm; ca 48 Days)

Articular processes and pedicles are chondrified (Sensenig, 1949)

Stage 20 (ca 18–22 mm; ca 51 Days)

Atlanto-occipital and atlanto-axial joints are detectable (Sensenig, 1957)

Dens is separate from anterior arch of atlas (Lewis, 1920)

Stage 21 (ca 22–24 mm; ca 52 Days)

Thoracic part of vertebral column is about 5 mm in length (Friedland and de Vries, 1975)

Stage 23 (ca 27–31 mm; ca 57 Days)

Tips of neutral processes of cervical vertebrae curve laterally, indicating their future bifid condition (Sensenig, 1957)

Spinal ganglia are largely within intervertebral foramina (Sensenig, 1951)

Epidural cavity is forming (Sensenig, 1951)

Approximate lengths of portions of vertebral column: C., 5 mm; T., 8 mm; L., 4 mm; S., 3 mm (Friedland and de Vries, 1975).

Discussion

Although the maximum number of pairs of somites in the human is frequently given as 42–44, they are never all visible at one time. Moreover, at the end of stage 11 (20 somites), the first pair disappears (Arey, 1938), so that the count is diminished by one pair thereafter. In various embryos described in the literature (and the meagre data indicate that considerable variation may be found), occipital somites have been noted from stages 11 or 12 until stage 15, after which they are no longer counted. Thus Bardeen and Lewis (1901) list 3 occipital somites in a 38 s. embryo of stage 15 but none in a 34 s. embryo of stage 16. By stage 17, a solid clivus has formed. The number of occipital somites is said to be at least 4 (Sensenig, 1957) or 5 (Reiter, 1944). According to Sensenig (1957), "the somites disappear" at stage 17. Thereafter, in order to continue the convenience of a numerical index, the number of centra can be noted.

In Fig. 1, the usual numbers of somites and centra are shown in relation to age, without allowing for variation. It can be seen that the somites first appear at stage 9 (3 postovulatory weeks) and increase in number rapidly between

3 and 4 weeks. The maximum number present at any one time is to be found at stages 15–17 (5–6 weeks), which is basically in agreement with the statement by Bardeen in Keibel and Mall (1910) that the maximum number of "vertebrae" (36 or occasionally 37) is "reached in embryos from 8–16 mm. in length." It is likely that the large number is due at first to the presence of several occipital segments and, later, when the occipital somites can no longer be distinguished, to an increasing albeit variable number of coccygeal segments. The greatest number of pairs of somites found at any one time is of the order of 38.

The main components of the human vertebral column (vertebrae, intervertebral discs, ligaments, and periosteal coverings) are completely mesodermal in origin, as far as is known. (Certain portions of the skull are believed to be derived from the neural crest.)

For simplicity, the ontogeny can be divided into two broad phases: sclerotomic and vertebral (Williams, 1959).

In the sclerotomic period, the sclerotomal cells from the ventromedial aspect of the paraxial, somitic mesoderm are usually said to migrate medially[1] into the matrix-filled space surrounding the notochord and neural tube (Feller and Sternberg, 1934; Marin-Padilla, 1966). Whereas a small proportion of these cells form an accumulation directly adjacent to the neural tube to intermingle with a small contingent of neural crest cells and constitute the undifferentiated primitive meninx (Holmdahl, 1934; Sensenig, 1951), the vast majority of them become concentrated around the notochord to form the perichordal blastema, and also lateral to the ventral portion of the neural tube to form the neural processes. These sclerotomic concentrations form a continuous, undifferentiated, homogeneous column which retains its segmental origin: it is separated by partitions containing the intersegmental vessels given off by the aorta. Most authorities believe that a resegmentation (*Neugliederung* of Remak) occurs within these segmental sclerotomes, involving the presence of a partial, transverse intrasclerotomic fissure (intervertebral fissure of von Ebner), continuous with the myocoele (Ingalls, 1907; Reiter, 1944). A redistribution of cells, perhaps under the influence of the spinal ganglia and the ventral nerves (Flint, 1977), occurs to form condensed caudal and loose cranial sclerotome-halves or sclerotomites.

The vertebral period commences, according to the resegmentation theory (Fig. 2), by the union of the caudal sclerotomite of one sclerotome with the cranial sclerotomite of the next succeeding segment to form the definitive vertebral Anlage. In so doing, the membranous primordium becomes intersegmental with respect to the original somite and its myotome, the intersegmental vessels become intrasegmental, and the intrasclerotomic fissures come to represent the boundaries between successive vertebral elements. Such a resegmentation has received wide acceptance in all vertebrate classes for many decades, although recently sufficient doubts have been raised to warrant seeking more convincing evidence to validate this concept (Baur, 1969; Verbout, 1976; Blechschmidt

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[1]   It has recently been proposed (Gasser, 1979) that "sclerotomal cells do not migrate medially during normal embryonic development of the rat." The remnant of the somite moves dorsolaterally, and the trailing cells that are left proliferate, causing the subsequent increase in density of the perichordal tissue

and Gasser, 1978). Essential to this evaluation in the human is the controversial existence of an intrasclerotomic fissure. Such a fissure has been observed, for example, by Bardeen (1905), Ingalls (1907), Wyburn (1944), Prader (1947a, b), Sensenig (1949), Peacock (1951), Walmsley (1953), Töndury (1958), and the present investigators, and has been correlated with anomalous appearances of the vertebral body (Remagen, Hienz, and Wiedermann, 1970). Nevertheless, its existence has been denied by several competent investigators (Blechschmidt, 1957; Baur, 1969; Verbout, 1976). Critiques of various theories of vertebral development have been provided by Williams (1959) and Verbout (1976). Figure 3 depicts some of the variations of these theories that have been described for the human.

The derivation of the various components of the vertebral column from the dense and loose mesenchymal primordia characteristic of the sclerotomic phase is extremely complex, and its description depends on the species studied, the state of preservation of the embryonic tissues, and the interpretation of the author. In the human, for example, the precise derivatives of the caudal and cranial sclerotomites, whether a result of resegmentation or not, are quite variably described (Fig. 3). In general, however, it can be stated that the cranial sclerotomite is concerned primarily with the development of the vertebral centrum, whereas the caudal sclerotomite differentiates, for the most part, into the different processes (neural, costal) and the intervertebral disc.

Precise data concerning the embryonic stages during which the various cellular phenomena involved in sclerotomic differentiation take place have been documented in the present study. Chondrification of the vertebral blastema, early in the vertebral phase, likewise occurs during the embryonic period proper. These data have also been documented in the present study, although the sequence of appearance within the various levels of the vertebral column has not been detailed. Moreover, the atlanto-occipital and atlanto-axial region (Ludwig, 1953 and 1957) presents special problems that are outside the scope of the present paper.

Centres of chondrification occur bilaterally in the vertebral blastema within a glycosaminoglycan-rich (in the chick) matrix (Strudel, 1971), containing collagenous fibres (Minor, 1973) identified as Type 2 in the chick (von der Mark et al., 1976). Separate chondrific centres appear on each side of the centrum and in each neural and costal process, and eventually fuse in the fetal period to form a single cartilaginous vertebral model. The onset of ossification of the vertebrae takes place during this period and varies with the vertebral level. Precise data based upon C.-R. lengths are available in the literature, e.g., Teissandier (1944), Noback and Robertson (1951), O'Rahilly and Meyer (1956), Bagnall et al. (1977a, b).

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