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KEYWORDS: intervertebral disc, scanning electron microscopy, collagen fibril.

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THREE-DIMENSIONAL ARCHITECTURE AND DEVELOPMENT OF LUMBER INTERVERTEBRAL DISCS

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Abstract. The three-dimensional architecture of the collagen framework of human lumbar intervertebral discs was studied with scanning electron microscopy and polarized light microscopy concentrating on the fibrillar interconnection between the intervertebral disc and the vertebral bodies. The fibrillar framework of the annulus fibrosus and the cartilage end-plates encircled the nucleus pulposus as a closed-pack system in the adult. This closed-pack system developed in the seventh embryonic month and was completed by the tenth month. In general, fibrils composing the framework in the fetus were thinner than in the adult. There was no fibrillar interconnection between the cartilage end-plate and subchondral bone. In the inner one-third of the annulus, obliquely oriented fibrillar lamellae interconnected with the cartilage end-plate. In the outer two-thirds, the fibrillar bundles of the lamellae were firmly anchored into the vertebral bodies. This fibrillar anchoring system was already present in the full-term fetus although the vertebral rim was not ossified.

Key words: intervertebral disc, scanning electron microscopy, collagen fibril.

Human intervertebral discs consist of three different anatomical components: a nucleus pulposus in the center, an annulus fibrosus surrounding the nucleus concentrically, and cartilage end-plates separating the nucleus from the adjacent vertebral bodies. Intervertebral discs are important for connection of the vertebral bodies and a shock absorber during weight bearing and movement of the spine. It is necessary to study the mechanical architecture of the intervertebral disc to understand the physiological and pathological conditions of the disc.

Coventry and his associates (1) have reported details of the anatomy and pathology of the discs with light microscopy. Fibrillar structure of the intervertebral disc has been observed with polarized light microscopy (2), X-ray diffraction (2) and transmission electron microscopy (TEM) (3-6). Inoue and Takeda (7-9) have reported on the fine structure of intervertebral discs with scanning electron microscopy (SEM), and have suggested a closed-pack system as a shock absorber. However, there have been little investigation of interconnections between either the cartilage end-plate and vertebral body, or the annulus fibrosus and vertebral body.

In the present study, stereoscopic observation of intervertebral discs demonstrated the fine interconnections between the annulus, cartilage end-plates and vertebral bodies. Prenatal development of collagen framework of the intervertebral disc was also investigated.

The results are discussed from the view points of morphology, biomechanics and embryology.

MATERIALS AND METHODS

Human lumbar intervertebral discs (L_{4-5} level) with associated vertebral bodies were obtained from seven adults aged 18, 22, 28, 38, 46 and 56 years old, and from four fetuses (one from the fifth embryonic month, two from the seventh month and one from the tenth month). Each adult specimen was divided sagittally with a bone sectioner. Two slices of about 6 mm thickness were obtained from the central part of each specimen and observed with soft X-ray. One slice for light microscopy was fixed in 10% formalin and another slice for SEM was fixed in 2.5% glutaraldehyde. Light microscopic sections were stained with hematoxylin-eosin, Masson trichrome, van Gieson and safranin 0, and were observed with conventional and polarized light microscopy. The specimens for SEM were again cut into two groups; one group was post-fixed with 1% osmium tetroxide after washing in phosphate buffer; the other group was decalcified, immersed in chymotrypsin solution and post-fixed. Each sample was dried, evaporated and examined by SEM (U-3 SEM, JEOL Ltd. and field emission type SEM, Hitachi Ltd.). The fetal specimens were cut sagittally with a razor and prepared in the same way as the adult specimens.

RESULTS

Collagen Framework of Adult Intervertebral Disc

In sagittal sections of adult intervertebral discs, the nucleus had only small numbers of cartilage cells and fibroblasts in the matrix. No notochordal cells were seen. The fibers of the nucleus were irregular by arranged. Poor cellularity was also found in the annulus. Regular orientation of the fibers composing the annulus fibrosus was distinct under polarized light microscopy. The width of the lamellae gradually increased from the inner part of the annulus to the outer edge. Peripheral fibers of the annulus blended into fibers of the longitudinal ligament. The cartilage end-plate of ordinary hyaline cartilage contained fibrils runing parallel to the vertebral body.

At the junctional areas of the annulus fibrosus, the nucleus pulposus and the cartilage end-plate, obliquely oriented lamellar fibers of the annulus adjacent to the nucleus connected with the cartilage end-plate at the upper and lower margins of the inner part of the annulus. Fig. 1A clearly shows morphological interconnection between lamellar fibers of the annulus and horizontally-aligned fibers of the cartilage end-plate. The fibers of the nucleus were aligned irregularly and the line of demarcation between the nucleus and annulus was rather distinct in young subjects but becoming less so in adults. Polarized light microscopy clearly showed fibers of the outer two-thirds of the annulus anchored to the vertebral body (Fig. 1B).

SEM examination of the cut surface of the intervertebral disc clearly showed differences in the framework of the collagen fibrils in the nucleus, annulus and cartilage end-plates. The nucleus was made up of an irregular network consisting of collagen fibrils 0.1–15 μm in diameter. Chymotrypsin easily digested the ground substance and denuded the collagen fibrils, and wide spaces were seen among the fibrils. Granular particles probably of mucopolysaccharide-protein complex, 0.01-0.08 μm in size, were attached to some fibrils (Fig. 2). Collagen fibrils of the annulus were regularly arranged with little interconnection, composing lamellar bundles (Fig. 3).

The cartilage end-plate of the adult disc consisted of a dense collagen framework arranged parallel to the vertebral bodies (Fig. 4). The collagen fibrils around a chondrocyte lacuna, however, were arranged circumferentially to form a thick enclosure about the chondrocyte (Fig. 5). On the cartilage surface facing subchondral bone, fibrils of the cartilage end-plate crossed each other and formed a tight collagen meshwork (Fig. 6 and Fig. 7).

Interconnection Between Intervertebral Disc and Vertebral Bodies in Adults

Cartilage end-plate and vertebral body. The vertebrae adjacent to the discs were composed of a cancellous type of bone with rather specialized bony plates, situated above and below. These bony plates were composed of two parts: a centrally situated bony end-plate localized at the subchondral area, and a vertebral rim surronding the outside on the cartilage end-plate. A supporting trabecular line ran beneath and parallel to the bony end-plate (Fig. 8A). The vertebral rim sloped internally to meet the peripheral zone of the subchondral bone (Fig. 8B).

Polarized light microscopy showed differences in the orientation of collagen fibers in the junctional area between the cartilage end-plate and the vertebral body. The collagen fibers of the cartilage end-plate were aligned horizontally and were easily distinguished from those of the subchondral bone (Fig. 1A). Collagen fibrils of the cartilage end-plate and the vertebral body were also clearly demonstrated by SEM observation of the cracked surface. No fibrillar interconnection between the cartilage end-plate and the subchondral bone was detected (Fig. 9). The cartilaginous collagen ran parallel to the vertebral body while the subchondral bone was made up of fibrillar lamellae aligned at oblique angles (Fig. 10). Separation of the cartilage end-plate from the trabecular lamellae was made in the samples cracked after drying (Fig. 11). In the central portion of the end-plate, the vascular buds of the bone marrow with cavities of about 50 μm in size faced the cartilage end-plate directly (Fig. 12).

Annulus fibrosus and vertebral body. The obliquely-oriented fibrillar lamellae of the inner one-third of the annulus interconnected with the cartilage end-plates. In the outer two-thirds, the lamellar fibers were anchored directly into the vertebral rim, forming fibrillar bundles which interwove with the lamellar fibers of the bone trabeculae. The fibrilar bundles in the outermost layers of the annulus mixed with the periosteal fibers of the vertebral body. Polarized light microscopy of the junctional area between the annulus and vertebral rim showed anchoring by these collagen fibers (Fig. 1B).

SEM examinations also showed that the fibrils of the annulus were regularly aligned and interconnected with the vertebral rim (Fig. 13A and B). At high power, collagen fibrils were seen to be anchored firmly into the bony tissue (Fig. 14). In one part, chondrocytes were observed between the fibers of the annulus running vertically (Fig. 13A).

Collagen Framework of Fetal Intervertebral Disc

In the intervertebral disc at the fifth embryonic month, distribution of the notochordal cells in the cyst of the nucleus was observed. The lamellar nature of the annulus fibrosus had already developed at the periphery of the immature disc. However, no fibrillar interconnection was seen between the lamellar fibrils of the annulus and those of the cartilage plate. The ossification center was still obscure, and proliferating and maturing cartilage cells of the growth plate did not show the fine columnar arrangement.

In the seventh embryonic month, the lamellar structure of the annulus developed and expanded upward and downward as well as internally and externally, forming fibrillar interconnections with the cartilage end-plates (Fig. 15A). Under SEM, the lamellar fibers were made up of a fine arrangement of collagen fibrils (Fig. 16). The cartilage end-plate was also made of transverse fibrils running parallel to the adjacent vertebra.

In the full-term fetus, the shape of notochondral cells in the nucleus was unchanged but the volume ratio of the nucleus became comparatively less as the surrounding annulus and cartilage plates increased. Each lamella of the annulus was arranged regularly, but separate from other lamellae. However, collagen fibrils of the lamellae of the full-term fetus already had a regular orientation similar to that of the adult. Fibrillar interconnection between the annulus and the cartilage end-plate had developed in the adult pattern (Fig. 15B). In general, however, each fibril was thinner in the fetus than in the adult.

The cartilage cells in the growth plate showed a columnar arrangement between the cartilage end-plate and the ajacent vertebra (Fig. 15B). The fibrillar arrangement of the cartilage end-plate and peripheral rim was quite different under polarized light microscopy (Fig. 17A and B). Collagen fibrils of the inner part of the annulus interconnected with those of the cartilage end-plate and the fibrils of the outer part wove into the part that corresponded to the vertebral rim (Fig. 18A and B). At this stage, remnants of vascular channels to both the cartilage end-plate and the peripheral rim were still observed, whereas the nucleus and almost all parts of the annulus were avascular.

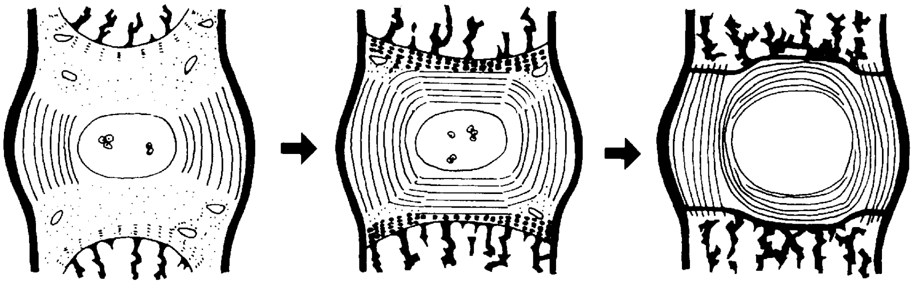
DISCUSSION

The intervertebral disc was first recognized as an anatomical entity by Vesalius in 1555 and was well-known to early anatomists. Recently, extensive investigations of the morphology, biochemistry, physiology and mechanics of the intervertebral disc have been performed (1, 2, 10–13).

Among the many light microscopic studies (1, 5, 11, 14–17), Coventry and his associates (1) have reported more definite details of the discs. Light microscopic studies have shown that the nucleus pulposus is a gel-like substance which contains cells and a meshwork of collagen fibers. The matrix is mostly composed of mucopolysaccharide-protein complex together with water and salts. The annulus fibrosus has a lamellar structure made up of collagen fibers aligned regularly. Decusation of the collagen fibers of one lamella with the fibers of the next lamella contributes to the strength and elasticity of the disc (1, 2, 10, 13, 18).

Stereoscopic observation of the intervertebral disc at ultrastructural level has shown that the nucleus pulposus, annulus fibrosus and cartilage end-plates are built up together as a closed-pack system, which act as a buffer against gravity and torsion (7–9). Shock absorption may be due to a hydrodynamic action caused by the hydroscopicity of the mucopolysaccharide-protein complex in the nucleus (19). Present stereoscopic examinations, however, suggest that shock absorption can be achieved not only by the nucleus but also the annulus and cartilage end-plates encircling the nucleus, since both are composed of extremely tough fibrillar framework (Fig. 19).

The present study clearly demonstrated that the cartilage end-plate contains no fibrillar connection with the collagen of the subchondral bone of vertebrae. This lack of interconnection between the end-plate and the vertebrae may render the disc weak to horizontal shearing forces. Segmental separation of the end-plate such as Macnab (12) described, therefore, may occur with excessive and/



Text Fig. 1. Schematic representation of development of the collagen framework.

or horizontal forces. Spinal osteochondrosis may be also caused by such structural damage to the cartilage end-plate (12, 20, 21), and fibrillation of the cartilage end-plate due to chronic trauma seems to be one of the main factors inducing spondylosis in the adult (11, 21-23). The cartilage end-plate, therefore, is a structure which can be easily destroyed by, or undergo degeneration in response to, shock absorption (12, 13).

Sylvén and his associates (6) reported ultrastructural details of intervertebral discs, especially the fine structure of the nucleus pulposus using TEM. Inoue and Takeda (7-9) using SEM described the three-dimensional architecture of the collagen fibers of intervertebral discs. They suggested that this architecture is a closed-pack system which acts as a shock absorber. However, there has been little investigation of the interconnection either between the cartilage end-plate and the vertebral body, or between the annulus fibrosus and the vertebral body. Especially, the fibrous architecture at the ultrastructural level has received very little attention. SEM surveys in the present study showed that the collagen fibrils in the outer two-thirds of the annulus were firmly anchored into vertebral bodies (Fig. 13A and B, Fig. 14). This anchoring system is the same as that of tendons (24, 25) and is thought to provide resistance against stretching or shearing stresses. However, the human spine in life is subjected to a combination of shear, torsion, compression and tensile forces. According to Shah (26), one of the areas of stress concentration was around the vertebral rims. Many shearing stresses recurring at this junctional part may result in mechanical breakage as suggested by Schmorl and others (10, 13). On the other hand, stretching stresses recurring at the outermost fibers of the annulus fibrosus may cause the "traction spur" of Macnab (12, 27). Macnab has suggested that the traction spur is primarily a result of abnormal motion, whereas the marginal osteophyte is related more to collapse and loss of height of the disc space (12).

The cartilage end-plate is important to nutrition. Impermeability of the cartilage end-plate may interfere with disc nutrition and result in degeneration of the nucleus (16). Nachemson and his associates (28) have stated that permeability of the end-plate is always associated with the presence of "vascular buds". They have also suggested that the absence of marrow space contact with cartilage in the end-plate results in impermeability of the end-plate, which in turn may interfere with disc nutrition and be a cause of disc degeneration (28). The collagen meshwork of the cartilage end-plate probably facilitates the flow of metabolites and water from the vertebral bodies to the nucleus by compression and decompression. Histological studies have shown that there are regions where the marrow spaces are in direct contact with the cartilage end-plate and that the central portion of the end-plate can be permeated by dye (28). Crock and his associates (29) observed radiographically that the vertebral end-plate was perforated by short vertical venous tributaries and according to Maroudas and his associates (30), contact between the disc tissue and the marrow spaces occupied about 10% of bone-cartilage interface. Direct contact was also evident in this study with SEM (Fig. 12). These findings support the idea that diffusion through the cartilage end-plate from vascular channels is a weak arrangement for coping with vertical compression forces, since there is a lack of protection by any hard subchondral bone plates. Internal disc disruption produced by compression fractures of the cartilage end-plate, for example, is related to prolapse of the disc material into vertebral bodies as seen in Schmorl's nodes (13, 31).

To interpret of these findings on the collagen framework in the disc, and the connection between the intervertebral disc and adjacent vertebrae, one must know something about the development of these structures. The endoderm provides the notochord, and the nucleus pulposus of the fetus is a modified remnant of the notochord in the disc region (32). The sclerotome which derives from the segmental mesoderm or somites surrounds the notochord and is responsible for the formation of the vertebral bodies, cartilage end-plates and annulus fibrosus.

The notochord becomes obliterated in the cartilaginous vertebral body and extends at the disc. At the end of the tenth embryonic week, the cells of the notochord lie entirely within the disc. They can, then, be called nucleus pulposus. The cells of the nucleus pulposus undergo mucoid degeneration; they remain as notochord-type cells through birth, even though they gradually disappear after birth. Keyes and Compere (11) have concluded that the nucleus pulposus is formed by proliferation and mucoid degeneration of the notochordal cells, followed by fibrocartilaginous invasion derived from the original mesenchymal intervertebral cells.

In the present study, the slightly differentiated nucleus, annulus and cartilage end-plates were observed at the fifth embryonic month. Although immature, the lamellar structure of the annnlus was already evident. However, these lamellar fibrils of the annulus had no fibrillar interconnection with the undifferentiated cell layer, or the anlage of the cartilage end-plate, which is laid down between the nucleus and the vertebra. The cartilage end-plate occupied much space compared to the nucleus and the annulus, but its fibrillar arrangement was still obscure.

Peacock (32) suggested that the annulus fibrosus differentiates very early in the development of the disc since the mesodermal anlage showed differentiation at 13 mm (about the sixth embryonic week). The lamellar structure of the annulus fibrosus is thought to be oriented in this stage of the development of undifferentiated cells. Well-defined fibers are present at 29 mm (about the tenth embryonic week) (32). Thus, the intricate fiber system develops long before the vertebral column is subject to external mechanical influences. According to Keyes and Compere (11), and Peacock (32), by the 18th embryonic week the structure of the intervertebral disc is similar to that of the adult disc. However, from the present study, the intervertebral disc in the fifth embryonic month (20th embryonic week) cannot be said to have a well-organized structure.

At the seventh embryonic month, the lamellar structure of the annulus develops and has fibrillar interconnections with the cartilage end-plate (Fig. 15A). The end-plate shows transverse fibers running parallel to adjacent vertebra.

In the full-term fetus, the collagen fibrils composing the lamellae have a regular orientation similar to that of adult fibrils. The collagen fibrils of the inner part of the annulus intermingle with those of the cartilage end-plate, while the fibrils of the outer part join the cell layer which becomes the vertebral rim. The fibrillar anchoring system of the annulus by the peripheral rim is already present at full-term even though the peripheral cell layer has not ossified.

Thus, the closed-pack system or the organized collagen structure of the intervertebral disc begins to form at the seventh embryonic month and is completed in the tenth month (Fig. 19). Mechanical factors such as fetal attitude, presentation, position and movement have some influence on the development of the fibrillar structure. Keyes and Compere (17) have stated that the cartilage end-plate and the epiphyseal ring, or the vertebral rim, are genetically one structure and comparable to the articular cartilage and the epiphysis of long bone. However, the alignment of the fibers of the cartilage end-plate is clearly distinguishable from those of the peripheral mesenchymal layer in the full-term fetus (Fig. 17). Peacock (32) showed that the cartilage end-plate develops from the result or the extension of chondrification from the vertebral body. In the present study, however, the cell layer of the cartilage end-plate in the tenth embryonic month clearly separated from the endochondral ossification layer of the vertebral side. It is thought that the cell layer of the cartilage end-plate is derived not from the vertebral side but from the undifferentiated cells which accumulate in early embryonic life and develop as an organized structure under mechanical influences.

The cartilage end-plate continues its function as a part of the disc during the development of the spinal column. On the other hand, the vertebral rim acts as an anchoring ring for the attachment of the annulus in the developing stage as well as in the adult. Stout peripheral fibers of the annulus fibrosus corresponding to Sharpey's fibers develop almost completely around the vertebral rim at the birth. Schmorl (13) believed that the vertebral rim is important only in that it serves to firmly anchor the fibers of the annulus fibrosus.

Degenerative changes of the discs occur gradually after 30 years of age and are marked in aged persons. Coventry *et al.* (1), Hirsch and his associates (5) recognized these changes as: fragmentation of the annulus, fissuring of the cartilage end-plate, and invasion of granulomatous tissue and blood vessels from adjacent vertebral bodies. In disc degeneration, the first morphological change to occur is the separation of a segment of the cartilage end-plate from the adjacent vertebral body (10, 12, 28). On the contrary, Hansen (14) have stated that the nucles is the functional center of the disc and systematically appearing changes in the nucleus are important as primary causes of pathologic changes of the discs and therefore also of all pathologic changes in the intervertebral space. Further studies of the three-dimensional architecture of degenerated discs are necessary for clarifying the pathology of such disc lesions.

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Legends to Figures.

Fig. 1. Polarized light micrograph of an adult disc. A: Horizontally-aligned collagen fibers of the cartilage end-plate (CE) can be easily identified from those of the vertebral body (VB). B: The lamellar fibers of the annulus fibrosus (AF) are anchored directly into the vertebral body. ×40

Fig. 2. High powered view of the collagen fibrils of the adult nucleus. Granular particles, 0.01–0.08 μ in size, attach to the fibrils. ×42,000

Fig. 3. Collagen fibrils of the annulus fibrosus of the adult composing the fibrillar bundles. ×7,000

Fig. 4. Collagen orientation of the cartilage end-plate showing horizontal alignment. ×7,000

Fig. 5. Collagen fibers of the cartilage end-plate encircling the chondrocyte lacuna. ×3,500

Fig. 6. On a horizontally separated cartilage surface which faces the vertebral body, fibrils of the cartilage end-plate cross each other and form a tight collagen meshwork. ×1,800

Fig. 7. High powered view showing the collagen meshwork of the horizontally separated cartilage surface. ×12,000

Fig. 8. Sagittally cut surface of the macerated vertebral body. A: A supporting line (➡) runs beneath and parallel to the bony end-plate. B: Vertebral rims (VR) slope internally to meet the peripheral zone of the bony end-plate.

Fig. 9. Junction (➡) between cartilage end-plate and subchondral bone. ×600

Fig. 10. At the junctional area between the cartilage end-plate (CE) and the vertebral body (VB), collagen fibrils of each tissue show different orientation. ×180

Fig. 11. After drying and cracking, the cartilage end-plate (CE) was separated from the vertebral body (VB). The arrow shows the junction between the cartilage end-plate and the vertebral body. AF: annulus fibrosus. ×60

Fig. 12. Vascular buds (*) from the bone marrow face the cartilage end-plate freely. ×180

Fig. 13. On the cracked surface of the junctional area between the annulus (AF) and the vertebral rim (VR), the continuous anchoring of collagen fibers is observed. A: ×500 B: ×1,500

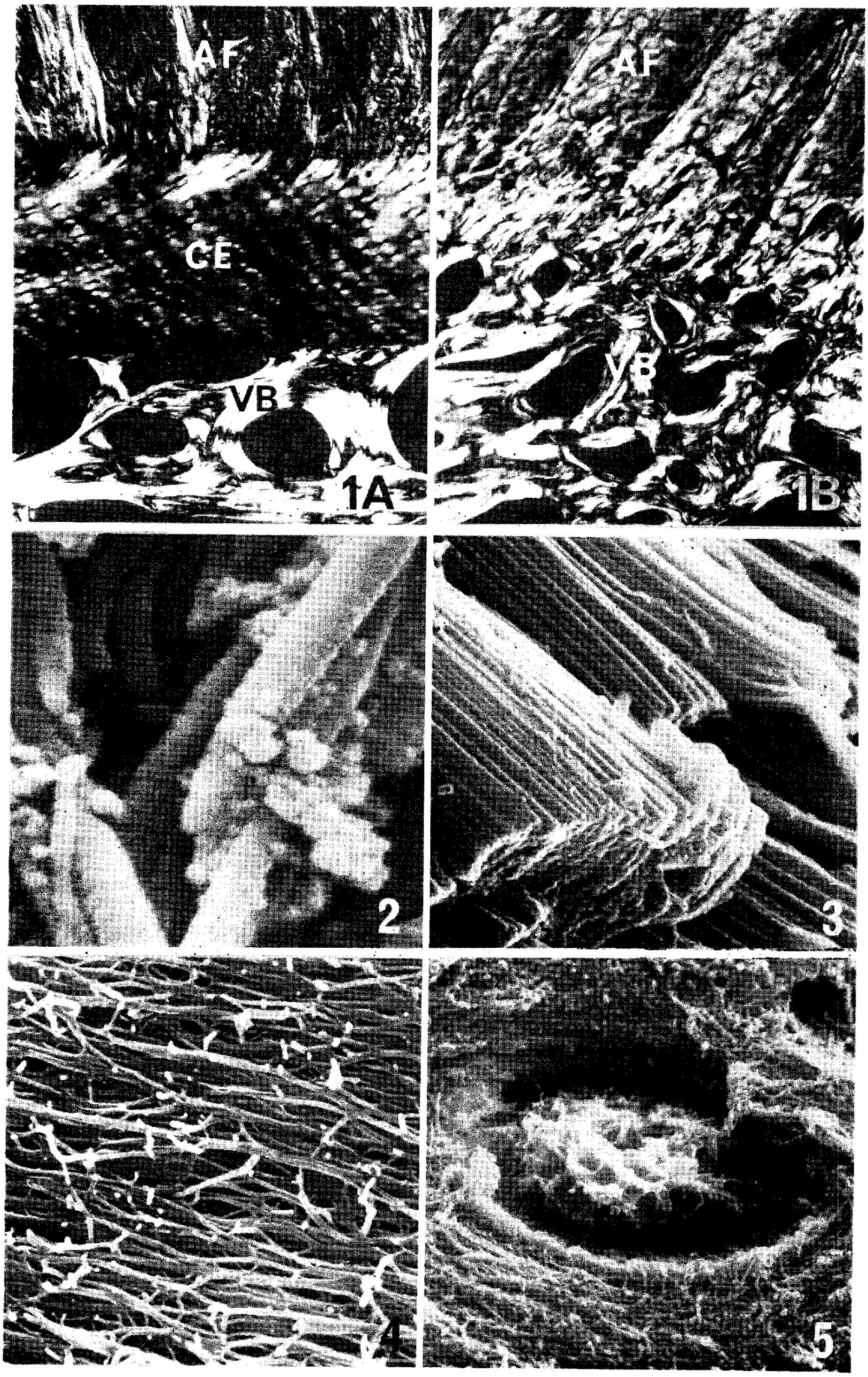
Fig. 14. High powered view showing the junctional area between the annulus and the vertebral rim (VR) firmly anchored with fibrillar bundles. ×6,000

Fig. 15. Polarized light micrograph of sagittally sectioned specimens of fetuses. A: 7 months B: 10 months. ×40

Fig. 16. Lamellar structure of the annulus fibrosus of the 7 months fetus. ×60

Fig. 17. Polarized light micrograph of sagittally sectioned specimen of a full-term fetus. The fibrillar arrangement of the cartilage end-plate (CE), peripheral rim (PR) and annulus fibrosus (AF) are clearly distinguishable. Cartilage cells of the growth plate (GP) show a columnar arrangement. ×40

Fig. 18. Junctional area between the annulus fibrosus (AF) and the peripheral rim (PR), and between the annulus fibrosus and the cartilage end-plate (CE). ×35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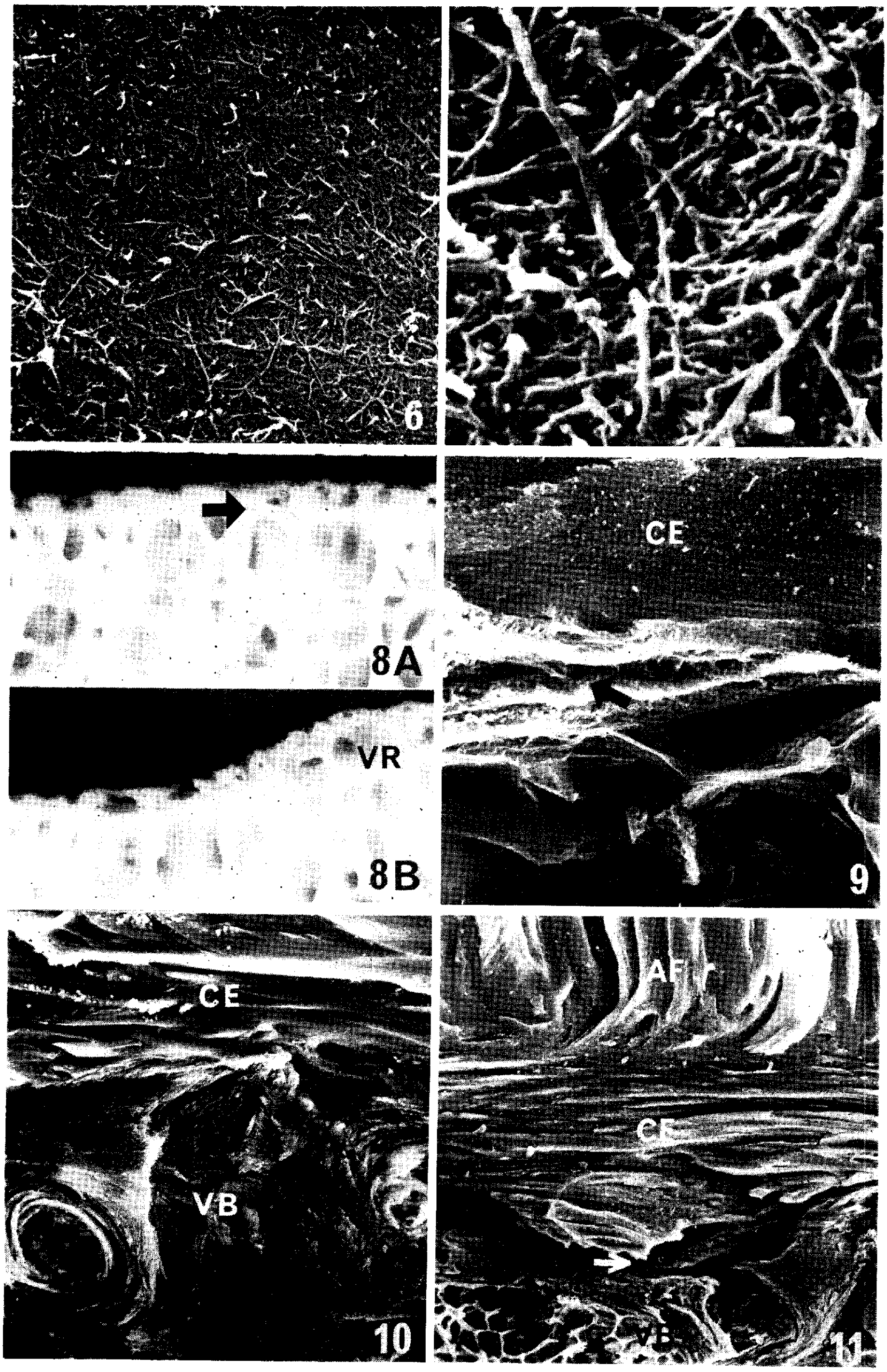
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