

## ULTRASTRUCTURE OF FELINE ARTICULAR CARTILAGE IN THE POSTNATAL PERIOD

D. HORKÝ and F. TICHÝ

Department of Histology and Embryology, Faculty of Medicine, Masaryk University, 602 00 Brno  
Department of Histology and Embryology, University of Veterinary and Pharmaceutical Sciences, 612 42 Brno

Received September 18, 1994

Accepted March 30, 1995

### Abstract

Horký D., F. Tichý: *Ultrastructure of Feline Articular Cartilage in the Postnatal Period*. Acta vet. Brno, 1995, 64: 63-70.

Articular cartilage was investigated in five cats of both sexes, aged 1, 21 and 43 days, and in two adult cats aged 5 years. Samples for transmission electron microscopy were collected from femoral heads and processed using conventional techniques. The object of the investigations was cellular structures and intercellular matrix of the superficial, middle and deep layers, but not those of transition cells and the tide-mark region.

In the superficial layer of the samples collected from 1-, 21- and 43-day old kittens, chondrocytes were found mostly in pairs sharing a common lacuna surrounded with well formed pericellular matrix. Reticular-type nucleoli were usually present in nuclei, and scarce small mitochondria, dilated GER (granular endoplasmic reticulum) cisternae and transport vacuoles were observed in cytoplasm. Towards the middle layer, cell membranes of chondrocytes contacted the intercellular matrix. The surface of the articular cartilage was covered by a continuous and well formed chondrosynovial membrane. Areas with various appearances can be distinguished in the cartilages of adult cats. Continuous chondrosynovial membrane covered a thick layer of intercellular matrix with scarce chondrocytes in undamaged areas, while other areas showed signs of various degrees of damage.

No differences in the structure of the middle layer were found among the various age groups. Oval or spherical chondrocytes contain large nuclei and cytoplasm contains numerous GER cisternae, mitochondria, Golgi's complex, numerous smooth vesicles, sporadic lysosomes and rare centrioles and lipid droplets. Pericellular matrix had almost disappeared and cell membrane contacted closely the intercellular matrix.

The deep layer of the articular cartilage of 1-, 21- and 43-day-old kittens contained lacunae harbouring either single chondrocytes or pairs thereof arranged perpendicularly to the surface. The spindle-shaped cells were smaller and contained a lesser amount of organelles than their counterparts in the middle and the surface layers. The pattern of the intercellular matrix was similar to that of the middle layer. In addition to intact chondrocytes with a normal structure of cytoplasm and nucleus, the deep layer of the adult cartilage contained degenerated cells with large lipid droplets, glycogen deposits, disintegrated mitochondria and pyknotic nuclei.

*Cat, cartilage, articular, ultrastructure*

The first description of the submicroscopical structure of the articular cartilage (Zelander 1959) was followed by extensive studies covering almost all mammalian and several avian species. The structure has been described in rabbits (Davies et al. 1962), mice (Sillberger et al. 1976), rats (Mark et al. 1989), dogs (Wiltberger and Lust 1975), cattle (Franzén 1981; Horký 1980, 1991a, b), swine (Nakano et al. 1979; Hattnagar et al. 1981; Horký 1989, 1991c, 1993a, b) and goats (Horký 1994b).

The hyaline articular cartilage develops from mesenchyme during skeletal ontogenesis as a component of cartilaginous blastema of the bone rudiment which changes into bone tissue during ossification. The pre-formed bone rudiment is reduced during this process which, however, does not involve the articular cartilage. Towards the joint cavity, this tissue is preserved and undergoes a series of changes during the subsequent ontogeny (Bonucci 1967; Hanoka 1976). The structural development of the articular cartilage is mostly controlled by pulling forces of muscles and ligaments and perhaps by the first fetal movements during the prenatal period, and by pressure forces associated with locomotion after birth. Another important factor is the age (see a review by Horký 1991a).

The function of the articular cartilage is predominantly mechanical and the tissue must meet the following two essential requirements to ensure correct activity: a) resist pressures, and b) provide good sliding properties of the areas of contact. The resistance to pressures results from the structure of the cartilage and arrangement of both components of the intercellular matrix (B l o e b a u m and W i l s o n 1980; H o r k ý 1980; C l a r k 1980). Chondrocytes are of negligible importance in the mechanics of articular motion, but play a key role in the synthesis of intercellular matrix which is responsible for the mechanical properties of the cartilage (B u c k w a l t e r et al. 1989 and others). Much attention has been paid to the surface layer which plays the major role in providing good sliding properties of the areas of contact (W o l f 1975; H o r k ý 1980; G i l e s 1992).

Although the published data indicate that the structure of the articular cartilage has been studied in almost all mammalian species, we have not found any description of the feline cartilage and therefore we decided to complete at least partly the existing data on its morphology.

### Materials and Methods

Samples of the articular cartilage for transmission electron microscopy were collected from five kittens aged 1, 21 and 43 days and from two adult, 5-year-old cats. The sampling site was the area between ligamentum capitis femoris and trochanter major of the femoral head. Strips 1 x 1 x 3 mm were cut from the samples for further processing. The strips were immediately fixed in 400 mmol/L glutaraldehyde dissolved in 0.1 M phosphate buffer, pH 7.4. Then the tissue was decalcified twice for 60 min in 0.1 M EDTA dissolved in 400 mmol/L glutaraldehyde, pH 7.2 and subsequently left in the decalcifying solution overnight. After four 30-min washings in 0.1 M phosphate buffer, pH 7.4, the strips were fixed twice in 40 mmol/L OsO<sub>4</sub> in phosphate buffer, pH 7.4. Conventional methods were used for dehydration, immersion and embedding into Durcupan ACM. Semithin sections were prepared from the embedded samples and stained with methylene blue and Azur II for light microscopy. Ultrathin sections for electron microscopy were prepared using the ultramicrotome LKB Nova and stained with lead citrate and uranyl acetate, or with lead citrate alone. The sections were viewed and photographed with the electron microscope Tesla BS 500.

### Results

Superficial, middle and deep layers were clearly distinguishable in the articular cartilage. Attention was paid to cell types in the layers, but not to transition types of chondrocytes and to the tide-mark area owing to their considerable multiformity.

#### Submicroscopical structure of the superficial layer

In day-old kittens, the superficial layer of the articular cartilage was formed by single chondrocytes or pairs thereof sharing a common lacuna near the surface ( Plate XXIII, Fig. 1). The single chondrocytes were markedly spindle-shaped, while those of the isogenous pairs were irregularly oval in shape. Most of the nuclei with a diameter of up to 4  $\mu$ m were spherical. Chromatin was arranged in a relatively thin layer close to the nuclear membrane and in several karyosomes that can be seen in the cross-sections of the nuclei. Reticular-type nucleoli with adjacent chromatin were usually present in the nuclei. Cytoplasm contained scarce small mitochondria, transport vacuoles filled with a finely granular mass, or large, dark granules (Fig. 1). Granular endoplasmic reticulum (GER) has the appearance of dilated cisternae often communicating with the perinuclear space. Numerous short cytoplasmic projections extend into the pericellular matrix. Numerous pinocytotic vesicles can be seen near the cell membrane, particularly on the side facing towards the surface (Fig. 1). No intermediary filaments were observed.

Pericellular and intercellular matrices are distinguishable in the intercellular matter. The pericellular matrix is markedly formed in the area of chondrocyte nests facing towards the surface. The matrix is formed by abundant amorphous ground substance in which aperiodic

collagen fibrils and solitary collagen fibrils are recognisable (Fig. 1). The pericellular matrix is missing on the reverse side of chondrocytes which is contiguous to the intercellular matrix containing collagen fibrils. The latter are arranged in parallel with the chondrocyte nests, but are scattered in a random pattern below them. The layer over the chondrocytes is covered by a thin layer of intercellular matrix formed by a small amount of collagen fibrils running in parallel with the surface, and by a  $0.5 \mu\text{m}$ -thick chondrosynovial membrane formed by aperiodic fibrils and terminations of typical collagen fibrils inserted into it.

No differences in the submicroscopical structure of the superficial layer of the articular cartilage were found between the 21- and the 43-day-old kittens and therefore it will be described in common.

Spindle-shaped and elongated chondrocytes are situated somewhat deeper in the intercellular matrix than in the day-old kittens, occurring almost exclusively as single cells forming indistinct cell nests (Fig. 2). The long axes of the spindle-shaped chondrocytes run in parallel to the surface. Light nuclei are relatively large, the arrangement of chromatin is similar to that found in the day-old kittens and cytoplasm forms only a narrow border around the nucleus. Most of mitochondria are elongated with the usual appearance and size. Numerous narrow and often branched GER cisternae contain moderately osmiophilic granular substance. Short cytoplasmic projections extend towards the surface of cartilage, but the reverse side, facing to the middle layer, is rather smooth (Fig. 2). Scarcely, autophagic vacuoles, containing glycogen and pseudomyelin formations, were seen in the cytoplasm of chondrocytes of the middle layer.

The pericellular matrix is formed only partly and most of the chondrocytes lack it entirely. Cell membranes of the majority of chondrocytes contact closely the intercellular matrix (Fig. 2). Unlike the findings in day-old kittens, the pericellular matrix forms a dense network of crossing collagen fibres running in parallel with the surface. It is only in the between-cell space, which is usually divided by a partition, where the fibrils are arched. The chondrosynovial membrane, covering the articular cartilage, has the same structure and thickness as that of the day-old kittens.

Areas with various structures can be observed in the superficial layer of the articular cartilage in the 5-year-old cats. Most of the surface is covered by a well developed chondrosynovial membrane (Plate XXIV., Fig. 3). Up to  $0.1 \mu\text{m}$ -thick collagen fibres, scattered in the amorphous ground substance in a random pattern and forming a dense and irregular network, predominate in the underlying, several  $\mu\text{m}$ -thick layer of the intercellular matrix. Electronoptically dense corpuscular deposits can be observed among the collagen fibres down to the depth of  $1.5 \mu\text{m}$ .

The appearance of the rest of the surface is quite different (Fig. 4). Collagen fibres, running in parallel with the surface, are surrounded with only a small amount of the amorphous ground substance. The chondrosynovial membrane is damaged and disintegrates as do collagenous fibrils which become exposed and protrude into the articular cavity. Thus the pattern of arthrotic cartilage develops (Fig. 4). At deeper levels, the collagen fibres run in parallel with the surface.

#### Submicroscopical structure of the middle layer

In day-old kittens, the middle layer of the articular cartilage consists of single chondrocytes or pairs thereof situated in the intercellular matter (Plate XXV., Fig. 5). The oval chondrocytes in size of  $10 \times 7 \mu\text{m}$  contain oval nuclei in which chromatin accumulates into several karyosomes in a close vicinity of the nuclear membrane. Cytoplasm contains numerous giant mitochondria with the usual structure and size and GER cisterns filled with finely granular and moderately osmiophilic substance. Agranular endoplasmatic reticulum is present in the form of minute vesicles. A common finding is transport vacuoles containing a matter with

various densities. Short cytoplasmic projections extend into the pericellular matrix. The relatively narrow cell nests are free of fibrils and contain only the amorphous ground matter (Fig. 5). In some areas, however, the fibrils extend into the proximity of cell membrane coming into a close contact with them.

In the 21- to 43-day old kittens, the submicroscopic structure of the middle layer does not differ significantly from that of day-old kits (Plate XXV., Fig. 6). The appearance and size of chondrocytes, as well as the arrangement of chromatin in the nucleus are similar to those described in the day-old kittens. Cytoplasm shows an amplification of Golgi's complex structures (Fig. 6) and smooth vesicles. Centrioles, situated typically in the proximity of nuclei, were observed frequently.

The arrangement of the intercellular matter is different. The pericellular matrix has almost disappeared and both aperiodic and collagen fibres come into contact with cell membrane (Fig. 6).

The middle layer of the articular cartilage of adult cats contains single chondrocytes or groups of 3 to 4 isogenous chondrocytes arranged perpendicularly to the surface of articular cartilage. These are 8- to 9- $\mu\text{m}$ -long chondrocytes, oval or spindle-shaped with their long axes oriented perpendicular to the surface. The nuclear shape is adjusted to that of the cells. Chromatin is arranged into several small clusters (Plate XXVI., Fig. 7). Cytoplasm contains GER cisternae, mitochondria with the usual appearance, dark corpuscles and lipid droplets. The arrangement of cell membrane does not differ from that observed in the previous stage. Owing to the absence of lacunae, the pericellular matrix has disappeared and cell membrane is in a close contact to the intercellular matrix (Fig. 7).

#### Submicroscopical structure of the deep layer

No differences in the appearance of the deep layer of the articular cartilage were observed among the 1-, 21- and 43-day-old kittens. The size of the irregularly spindle-shaped chondrocytes, occurring alone or in pairs, is 10 x 5 - 6  $\mu\text{m}$  and their axes are directed towards the surface (Plate XXVI., Fig. 8). Nuclei are relatively small and hyperchromatic, and contain a continuous layer of chromatin adjacent to the inner nuclear membrane. Cytoplasm contains numerous short GER cisternae, Golgi apparatus, mostly round-shaped mitochondria and numerous small smooth vesicles. Lysosomes are rather scarce (Fig. 8). The surface of cell membrane is mostly smooth with the exception of the poles where few projections extend into the pericellular matrix. The major part of the cell membrane contacts closely the intercellular matrix in which periodic collagen fibres are apparent.

The deep layer of the articular cartilage of adult cats contains a smaller number of chondrocytes varying in their appearance (Plate XXVII., Fig. 9,10). Besides cells with a structure essentially identical with that described in kittens, cells showing various degrees of damage are present (Fig. 10). Cytoplasm of the degenerated cells contains clusters of glycogen and large lipid vacuoles, and signs of nuclear damage are also evident (Fig. 10). No pericellular matrix was seen around the undamaged cells (Fig. 9). The intercellular matrix extends to the cell membrane and some collagen fibres were seen between cell membrane projections. Some pericellular matrix, containing granular substance, is present in the proximity of the cell membrane, while the appearance of the intercellular matrix is unchanged (Fig. 10).

#### Discussion

Similar to other mammalian species (P a l f r e y and D a v i e s 1966; H o r k ý 1987, 1994ab, and others) three layers were clearly distinguishable in the feline articular cartilage in the period under study. Our findings correspond to those published by M o d l et al. (1991) as a result of a series of examinations by magnetic resonance. The definition of the three lay-

ers in the articular cartilage conforms with our findings obtained by transmission electron microscopy (see reviews by B o z d ě c h et al. 1990 and H o r k ý et al. 1994ab).

The results of the investigations of the prenatal chondrosynovial membrane in cats (H o r k ý 1994a) and of the same tissue in other mammalian species in the postnatal period (cf. H o r k ý) conform with the observations published by W o l f (1975) and M c C o n a i l l (1951). Similar conclusions were arrived at by G i l e s (1992) and K a m a l a n a t h a n and B r o o m (1993). Our repeated observations let us assume that bundles of aperiodic filaments, situated on or immediately below the surface cartilage, are involved in the formation of this structure without polymerization of the filaments into typical collagen fibres. Thus, a relatively thick layer develops as soon as in the prenatal period. The layer runs lower with the advancing age and provides primarily good sliding properties of the articular surfaces (S w a n n et al. 1984).

The maturation is associated with an increase of the proportion of collagen fibres in the intercellular matrix. The fibrils are largely responsible for elasticity and resistance to pressure inherent to proteoglycans of the amorphous ground substance. This view has been fully confirmed by our finding of an increased number of collagen fibrils in the superficial layer, observed also in bovine and caprine cartilages, e.g. (H o r k ý 1994b). Our description of the pattern of the collagen fibrils in the superficial layer of the caprine articular cartilage corresponds very well to the observations published by B l o e b a u m and W i l s o n (1980) and C l a r k (1990). In cats, the bundles were not as thick as in goats (H o r k ý 1994b). They are situated at various depths underneath the surface, or below the uppermost row of chondrocytes. Their structure has also been the object of interest of other authors, because it plays an important role in the formation of the fibrous component of the cartilage (B r o o m 1986; C l a r k 1990; H e d l u n g et al. 1993) - a view which we share, too.

Here and there, fibrils of the superficial layer loosen and lesions typical of arthrosis develop (B o z d ě c h et al. 1990). This is no unusual finding, as such damage was described, among others, by W i l t b e r g e r and L u s t (1975) and G r o n d a l e n (1974a, b) in a series of papers on canine and porcine cartilages. These authors investigated the development of the damage under various conditions including experimental surgical interventions. Recently, B i b b and R o b i n s o n (1993) described similar lesions in the articular cartilage after the reparation of an artificial damage in primates.

The middle layer of the feline articular cartilage does not substantially differ from that of other mammals of comparable age. However, the intercellular matter is arranged in a somewhat different pattern. The pericellular matrix is not distinctly developed in newborn kittens. It is particularly on the side facing towards the deep layer, where the intercellular matrix contacts closely the cell membrane of chondrocytes. The basket-like structures of collagen fibres, surrounding chondrocytes, which are typical of the bovine (H o r k ý 1983) or human (H o r k ý 1980) cartilages, were not seen in feline material.

No differences in the arrangement of the deep layer were recognisable among the age groups (1, 21, 43 days, 5 years) under study. The structure of this layer is identical with that described in other mammalian species at similar phases of ontogeny (H o r k ý 1980, 1983, 1987, 1991ab, 1993, 1994ab).

The differences in the structure between young and adult individuals, so-called sprinters, and, e.g., the corresponding age groups of cattle are evident when compared with the descriptions of the superficial and the middle layers published earlier (H o r k ý 1983, 1987).

### **Ultrastruktura kloubní chrupavky kočky v postnatálním období**

Byla studována kloubní chrupavka 5 jedinců kočky obojího pohlaví v období 1,21,43 dnů po narození a 2 jedinců stáří 5 roků. Vzorky chrupavky byly odebrány pro transmisní elek-

tronovou mikroskopii vždy z hlavice kyčelního kloubu a chrupavka byla zpracována obvyklým způsobem.

Bylo zjištěno, že v povrchové vrstvě chrupavky věkových kategorií 1, 21 a 43 dnů po narození jsou chondrocyty uloženy nejčastěji ve dvojicích ve společné lakuně a pericelulární matrix je dobře vytvořena směrem k povrchu chrupavky. Intercelulární matrix směrem ke střední vrstvě je v kontaktu s buněčnými membránami chondrocytů. Na povrchu artikulární chrupavky je souvislá, zřetelně vytvořená chondrosynoviální membrána. U dospělých jedinců má povrch chrupavky rozdílný vzhled. Buďto je neporušen a je kryt souvislou chondrosynoviální membránou, pod níž se vyskytuje mohutná vrstva mezibuněčné hmoty s řídce uloženými chondrocyty, nebo se objevují typické známky artrozy.

Střední vrstva u všech věkových kategorií má prakticky shodnou stavbu. Chondrocyty jsou oválného nebo okrouhlého tvaru s velkým jádrem, v cytoplasmě obsahují četné cisterny GER, mitochondrie, Golgiho komplex, četné hladké váčky a ojediněle lysosomy a vzácně lze pozorovat centrioly a tukové kapénky. Pericelulární matrix téměř vymizela a buněčná membrána je v těsném kontaktu s matrix intercelulární. V hluboké vrstvě kloubní chrupavky 1., 21. a 43. dne po narození jsou chondrocyty uloženy jednotlivě v lakunách, které jsou seřazeny do sloupců kolmo k povrchu chrupavky. Buňky jsou většinou protáhlé, menších rozměrů než v předchozích vrstvách. Mezbuněčná hmota má podobné uspořádání jako ve vrstvě střední. U dospělých jedinců kromě intaktních chondrocytů s obvyklou strukturou cytoplasmy a jádra se vyskytují degenerované buňky, které obsahují velké tukové kapénky, depozita glykogenu, desintegrované mitochondrie a jádra se zřetelnými známkami pyknosy chromatinu.

#### References

- BHATNAGAR R., CHRISTIAN R. G., NAKANO T., AHERNE F. X., THOMPSON J. R. 1981: Age related changes and osteochondrosis in swine articular and epiphyseal cartilage: light and electron microscopy. *Can. J. Comp. Med.* **45**:188-195
- BIBB C. A., ROBINSON P. D. 1993: Histologic study of articular cartilage repair in the marmoset condyle. *J. Oral Maxillofac. Surg.* **USA 51/10**:1088-1095
- BLOEBAUM R. D., WILSON A. S. 1980: The morphology of the surface of articular cartilage in adult rats. *J. Anat.* **131/2**:333-346
- BONUCCI E. 1967: Fine structure of early cartilage calcification. *J. Ultrastruct. Res.* **20**:33-45
- BOYD J. S. 1977: Patterns of ossification in the feline foetus: a study of the foetal development of the skeleton of the feline using comparative methods. Index-to-Theses. 25:2-73. PhD Thesis, Glasgow University
- BOZDĚCH Z., HORKÝ D., JANEČEK M. 1990: Chrupavka a synoviální tkáň lidského kloubu. *Acta fak. med. Univ. Masaryk. Brunensis* 1-150.
- BROOM N. D. 1986: The collagenous architecture of articular cartilage - a synthesis of ultrastructure and mechanical function. *J. Rheumatol.* **13**:142-152
- BUCKWALTER J. A., SMITH K. C., KAZARIEN L. E., ROSENBERG L. C., UNGAR R. 1989: Articular cartilage and intervertebral disc proteoglycans differ in structure: an electron microscopic study. *J. Orthop. Res.*, **7/1**:146-151
- CLARK J. M. 1990: The organization of collagen fibrils in the superficial zones of articular cartilage. *J. Anat.* **171**:117-130
- DAVIES D. V., BARNETT C. H., COCHRANE W., PALFREY A. J. 1962: Electron microscopy of articular cartilage in the young adult rabbit. *Ann. rheum. Dis.* **21**:11-22
- FRANZEN A. 1981: Variations in the composition of bovine hip articular cartilage with distance from articular surface. *Biochem. J.* **195**:535-543
- FREEMAN M. A. R., KEMPSON G. E. 1973: Load carriage. Adult articular cartilage. In: M. A. R. Freeman, Alden Press, Oxford, Great Britain pp. 228-246
- GARDNER E., O'RAHILLY R. 1968: The early development of the knee joint in staged human embryos. *J. Anat. London* **102**:289-299
- GHADIALLY F. N., ROY S. 1969: Ultrastructure of synovial joints in health and disease. Butterworths, London pp. 30-80
- GHADIALLY F. N. 1982: Ultrastructural pathology of the cell and matrix. Butterworths, London, pp. 20-45
- GHADIALLY F. N. 1983: Fine structure of synovial joints. Butterworths, London pp. 42-80
- GILES L. G. F. 1992: The surface lamina of the articular cartilage of human zygoapophyseal joint. *Anat. Rec.* **233**:350-356

- GRONDALEN T. 1974a: Osteochondrosis and arthrosis in pigs. I. Incidence in animals up to 120 kg live weight. *Acta Vet. Scand.* **15**:1-25
- GRONDALEN T. 1974b: Osteochondrosis and arthrosis in pigs. II. Incidence in breeding animals. *Acta Vet. Scand.* **15**:26-42
- GRONDALEN T. 1974c: Osteochondrosis and arthrosis in pigs. III. A comparison of the incidence in young animals of the Norwegian Landrace and Yorkshire breeds. *Acta Vet. Scand.* **15**:43-52
- GRONDALEN T. 1974d: Osteochondrosis and arthrosis in pigs. VI. Relationship to feed level and calcium, phosphorus and protein levels in the ration. *Acta Vet. Scand.* **15**:147-169
- GRONDALEN, T. 1974e: Osteochondrosis and arthrosis in pigs. VII. Relationship to joint shape and exterior conformation. *Acta Vet. Scand.* **15**, (Suppl. 46):1-32
- HANAOKA H. 1976: The fate of hypertrophic chondrocytes of the epiphyseal plate. An electron microscopic study. *J. Bone Jt Surg* **58**: 226-229
- HEDLUNG H., MENGARELLI-WIDHOLM S., REINHOLT F. P., SVENSSON O. 1993: Stereologic studies on collagen in bovine articular cartilage. *APMIS, DNK* **101**/2:133-140
- HILLS B. A. 1990: Oligolamellar nature of the articular surface. *J. Rheumatol.* **170**: 340-356
- HILLS B. A. 1989: Oligolamellar lubrication of joints by surface active phospholipid. *J. Rheumatol.* **16**: 82-91
- HORKÝ D. 1980: Submicroscopic structure of the human joint cartilage. *Acta vet. Brno*, **49**:145-176
- HORKÝ D. 1983: Ontogenic development of the ultrastructure of bovine joint cartilage. *Acta vet. Brno*, **52**:103-130
- HORKÝ D. 1986: Ultrastructure of bovine articular cartilage between weeks 8 and 23 of prenatal development. *Acta vet. Brno*, **55**:227-246
- HORKÝ D. 1987: Submicroscopic structure of bovine articular cartilage in prenatal and early postnatal period. *Acta vet. Brno*, **56**:3-18
- HORKÝ D. 1989: The ultrastructure of articular cartilage in the prenatal pig. *Acta vet. Brno*, **58**:143-174
- HORKÝ D. 1991a: Submicroscopic structure of articular cartilage in human embryos six to eleven weeks old. *Acta vet. Brno*, **60**: 15-30
- HORKÝ D. 1991b: Submicroscopic structure of human articular cartilage in the period between 19 to 38 weeks after fertilization. *Acta vet. Brno*, **60**:111-126
- HORKÝ D. 1991c: The submicroscopic structure of articular cartilage in swine in the early postnatal period. *Acta vet. Brno*, **60**: 323-334
- HORKÝ D. 1993a: The submicroscopic structure of articular cartilage in the adult pig. *Acta vet. Brno*, **62**:9-18
- HORKÝ D. 1993b: The ultrastructure of articular cartilage in the prenatal domestic cat. *Acta vet. Brno*, **62**:115-120
- HORKÝ D. 1994a: Feline articular cartilage in the prenatal and early postnatal periods. A scanning electron microscopic study. *Acta vet. Brno*, **63**:33-39
- HORKÝ D. 1994b: The submicroscopic structure of caprine articular cartilage in ontogeny. *Acta vet. Brno*, **63**:41-48
- HORVATH A. 1983: Radiographical investigation of postnatal development of the hindlimb skeleton of the cat. Inaugural Dissertation, Tierärztliche Fakultät, Ludwig-Maximilians-Universität München, 70 p.
- HORVATH I. 1983: Radiographical study of the postnatal development of the forelimb skeleton of the cat. Inaugural Dissertation, Tierärztliche Fakultät, Ludwig-Maximilians-Universität München, 67 p.
- CHAPPUIS J., SHERMAN I. A., NEUMANN A. W. 1983: Surface tension of animal cartilage as it relates to function in joints. *Ann. Biomed. Eng.* **11**: 435-451
- JEFFERY A. K., BLUNN G. W., ARCHER C. W., BENTLEY G. 1991: Three-dimensional collagen architecture in bovine articular cartilage. *J. Bone Jt. Surg. B.*, **73**:795-801
- KAMALANATHAN S., BROOM N. D. 1993: The biomechanical ambiguity of the articular surface. *J. Anat.* **183**/3: 567-578
- KIEFER G. N., SUNDBY K., McALLISTER D., HRIVE N. G., FRANK C. B., LAM T., SCHACHAR N. S. 1989: The effect of cryopreservation on the biomechanical behavior of bovine articular cartilage. *J. Orthop. Res.* **7**:494-502
- LUST G., PRONSKY W., SHERMAN D. 1972: Biochemical and ultrastructural observation in normal and degenerative canine articular cartilage. *Am. J. Vet. Res.* **33**:2429-2440
- MARK M. P., BUTLER W. T., RUCH J. V. 1989: Transient expression of a chondroitin sulfate-related epitope during cartilage histomorphogenesis in the axial skeleton of fetal rats. *Develop. Biol.* **133**:475-489
- MAROUDAS A. 1973: Physico-chemical properties of articular cartilage. In: *Adult articular cartilage*. Ed.: M. A. R. Freeman, Alden Press, Oxford, pp. 131-170
- McCONAILL M. A. 1951: The movements of bones and joints. The mechanical structure of articulating cartilage. *J. Bone Jt. Surg.* **33 B1**:251-257
- McCUTCHEEN C. W. 1966: Boundary lubrication by synovial fluid: demonstration and possible osmotic explanation. *Fed. Proc.* **25**:1061
- MEACHIM G., STOCKWELL R. A. 1973: Adult articular cartilage. In: *Adult articular cartilage*. Ed.: M. A. R. Freeman, Alden Press, Oxford, pp. 20-129
- MODL J. M., SERHER L. A., HAUGHTON V. M., KNEELAND J. B. 1991: Articular cartilage: Correlation of histologic zones with signal intensity at mr imaging. *Radiology, USA.* **181**/3:853-855

- NAKANO T., AHERNE F. X., THOMPSON J. R. 1979: Changes in swine knee articular during growth. *Can.J.Anim.Sci.* **59**:167-179
- NEAME P.J., CHOI H. U., ROSENBERG L. C. 1989: The primary structure of the core protein of the small, leucine-rich proteoglycan (PG I) from bovine articular cartilage. *J. Biol. Chem.* **264**: 8646-8653
- PALFREY A. J., DAVIES D. V. 1966: The fine structure of chondrocytes. *Amer. J. Anat.* **100**:213-228
- PALMOSKI M. J., BRANDT K. D. 1984: Effects of static and cyclic compressive loading on articular cartilage plugs in vitro. *Arthritis Rheum.* **27**:675-682
- PERRIN W. R., AHERNE F. X., BOWLAND J. P., HARDIN R. T. 1978: Effects of age, breed and floor type on the incidence of articular cartilage lesions in pigs. *Can. J. Anim. Sci.* **58**: 129-138
- POOLE C. A., WOTTON S. F., DUANCE V. C. 1988: Localization of type XI collagen in chondrons isolated from porcine articular cartilage and rat chondrosarcoma. *Histochem. J.* **20**/10:567-574
- SHELDON H., KIMBALL F. B. 1962: Studies on cartilage III. The occurrence of collagen within vacuoles of the Golgi apparatus. *J. Cell Biol.* **12**:559-613
- SCHERFT J. P., DAEMS W. Th. 1967: Single cilia in chondrocytes. *J. Ultrastruct. Res.* **19**:546-555
- SILBERGER R., SILBERGER M., VOGEL A., WETTSTEIN W. 1961: Ultrastructure of articular cartilage of mice of various ages. *Am. J. Anat.* **109**: 251-275
- SILBERGER R., HASLER M., LESKER P. 1976: Ultrastructure of articular cartilage of achondroplastic mice. *Acta Anat. (Basel)* **96**:162-175
- STOCKWELL R. A., MEACHIM G. 1979: The chondrocytes. In: *Adult articular cartilage*. 2nd edition. Ed.: M.A.R. Freeman, London, Pittman Medical
- SWANN D. A., SILVER F. H., SLAYTER H. S. 1985: The molecular structure and lubricating activity of lubricin isolated from bovine and human synovial fluids. *Biochem.J.* **225**:195-201
- WEISS C., ROSENBERG L., HELFET A. J. 1968: An ultrastructural study of normal young adult human articular cartilage. *J. Bone Jt Surg.* **50A**:663-674
- WILSMAN N. J., FARNUM C. E., HILLEY H. D., CARLSEN C. S. 1981: Ultrastructural evidence of a functional heterogeneity among physical chondrocytes in growing swine. *Am. J. Vet. Res.* **42**: 1547-1553
- WILTBERGER H., LUST G. 1975: Ultrastructure of canine articular cartilage: comparison of normal and degenerative (osteoarthritic) hip joints. *Am. J. Vet. Res.* **365**:727-740
- WOLF, J. 1975: Function of chondral membrane on surface of articular cartilage from point of view of its mechanical resistance. *Folia Morphol. (Prague)* **23**:77-87
- ZELANDER T. 1959: Ultrastructure of articular cartilage. *Z. Zellforsch.* **49**: 720-738



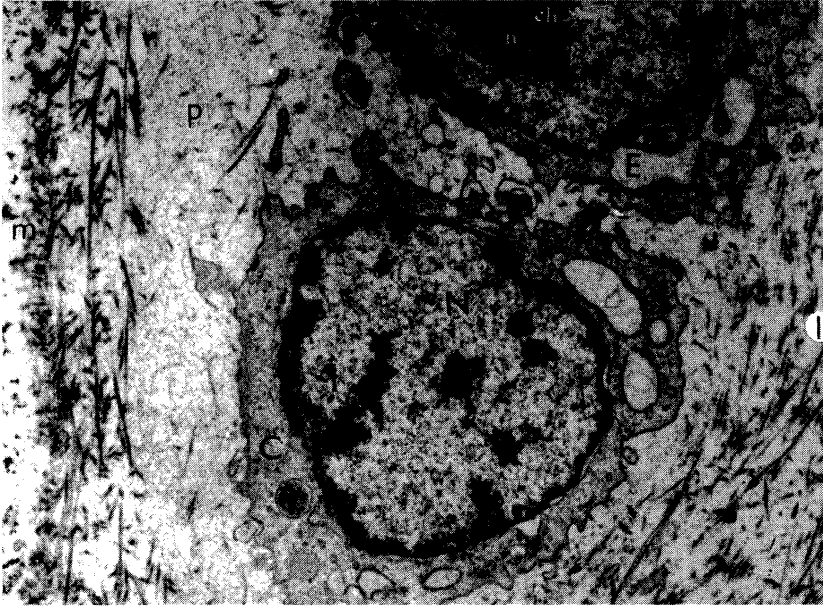


Fig. 1. Superficial layer of articular cartilage of a day-old kitten. A pair of chondrocytes (C) in a common lacuna. Nucleus (N), nucleolus (n), perinucleolar chromatin (ch). Transport vacuoles (V), GER (E). Pericellular matrix (p), intercellular matrix (I). Chondrosynovial membrane (m). x 12,000

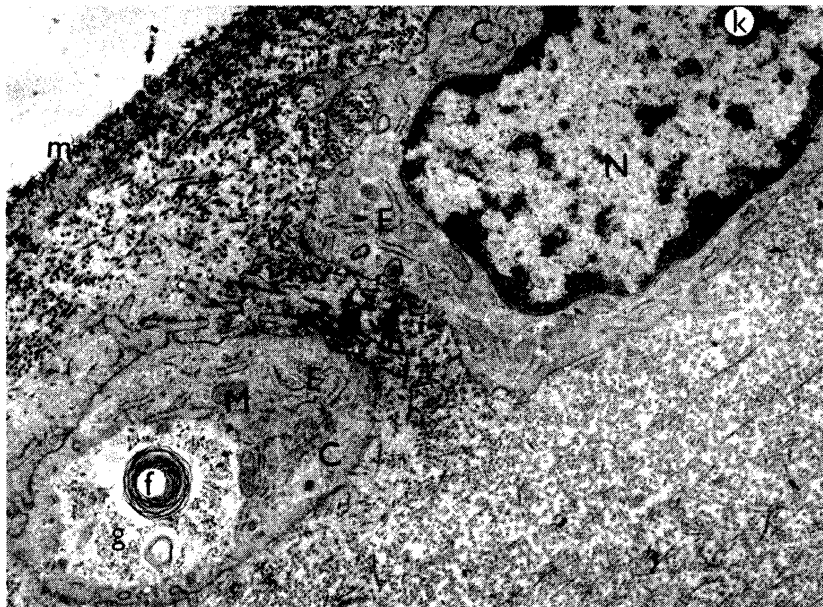


Fig. 2. Superficial layer of articular cartilage of a 43-day-old cat. Chondrocytes (C) separated by intercellular matrix (I). Nucleus (N), karyosomes (k), mitochondria (M), GER (E), autophagic vacuole containing glycogen (g), and a pseudomyelin formation (f). Thick chondrosynovial membrane (m). x 12,000



Fig. 3. Intact surface of articular cartilage of a 5-year-old cat. The superficial layer is thick and contains a small number of cells. Chondrosynovial membrane (m) is thin and covers intercellular matrix containing coarse periodic collagen fibres (c). Some of the thinner fibrils point to the surface (arrow). x 16,000



Fig. 4. Arthrotic lesions in the superficial layer of articular cartilage in a 5-year-old cat. Disintegrated chondrosynovial membrane (m), undulated collagenous fibrils, some of which are exposed (arrow). x 12,000

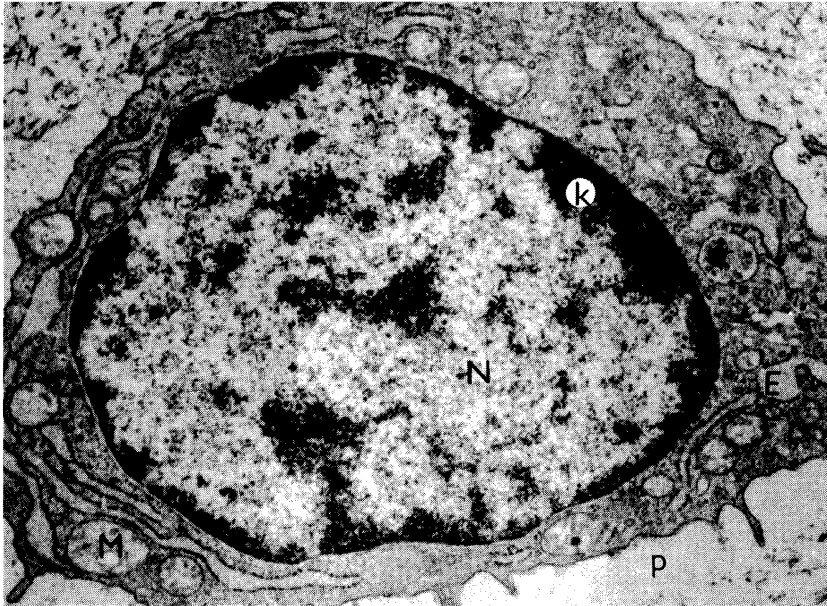


Fig. 5. Middle layer of articular cartilage of a day-old cat. Chondrocyte with a typical shape and size. Nucleus (N), karyosomes (k), mitochondria (M), transport vacuoles (V), GER cisternae (E), Golgi apparatus (G). Pericellular matrix (p) is well formed only towards the neighbouring cell in the lacuna and the middle layer. x 16,000

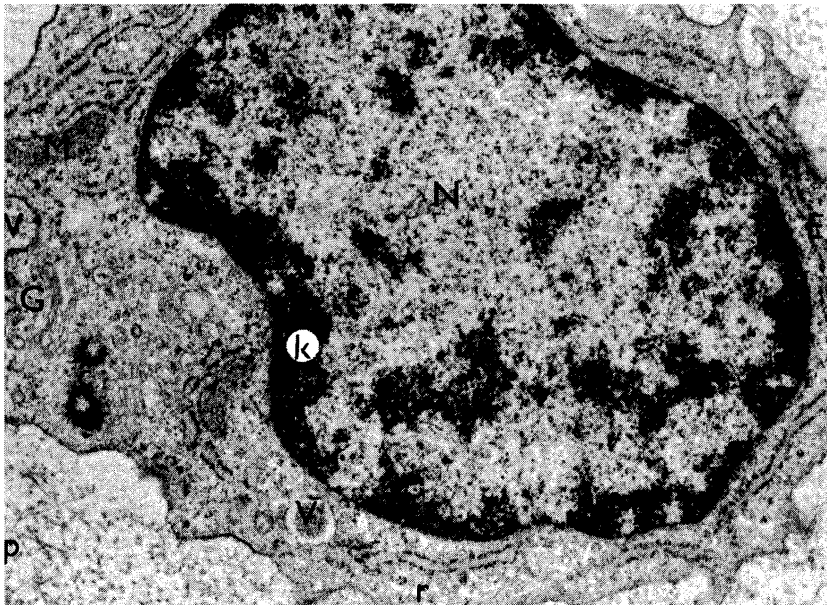


Fig. 6. Chondrocyte of the middle layer of articular cartilage of a 43-day-old cat. Nucleus (N), karyosomes (k). Mitochondria (M), transport vacuoles (V), GER (E), polysomes (r), Golgi apparatus (G), centrioles (C). Indistinct pericellular matrix (p). x 16,000

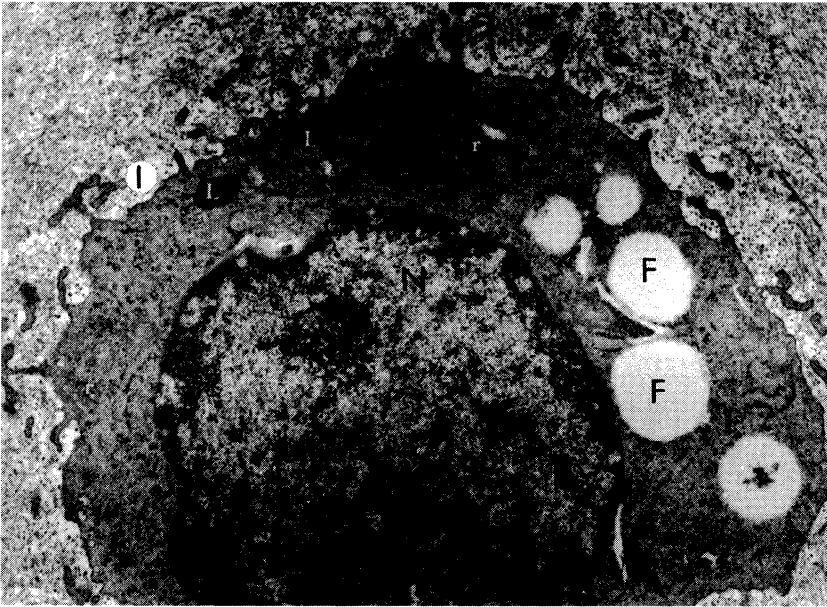


Fig. 7. Chondrocyte of the middle layer of articular cartilage of a 5-year-old cat. Nucleus (N), GER cisternae (E), dark bodies (L), ribosomes (r), lipid droplets (F). Intercellular matrix contacts closely cell membrane. x 16,000

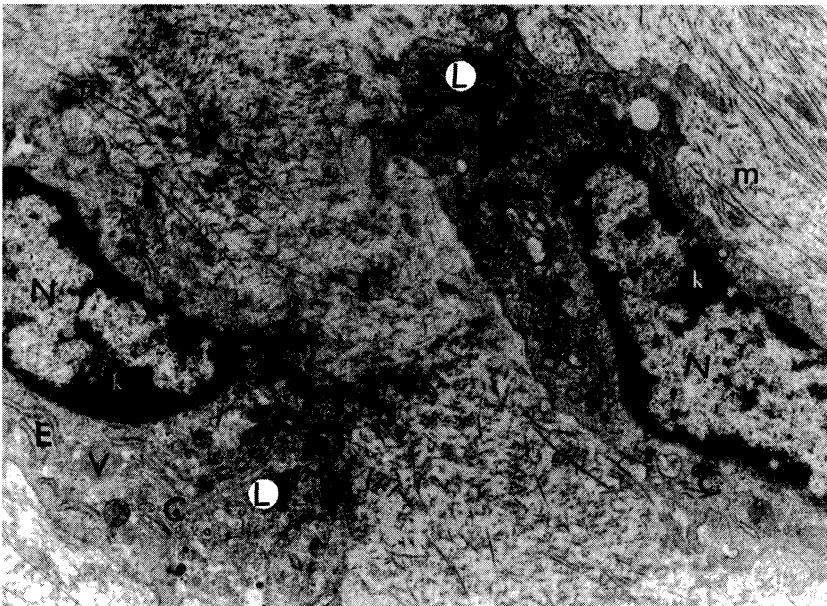


Fig. 8. Deep layer of articular cartilage of a 21-day-old cat. Single chondrocytes are arranged in columns pointing to the surface. Nucleus (N), karyosomes (k). Cytoplasm contains Golgi apparatus (G), GER (E), lysosomes (L) and transport vacuoles (V). Cell membrane contacts closely intercellular matrix. x 12,000



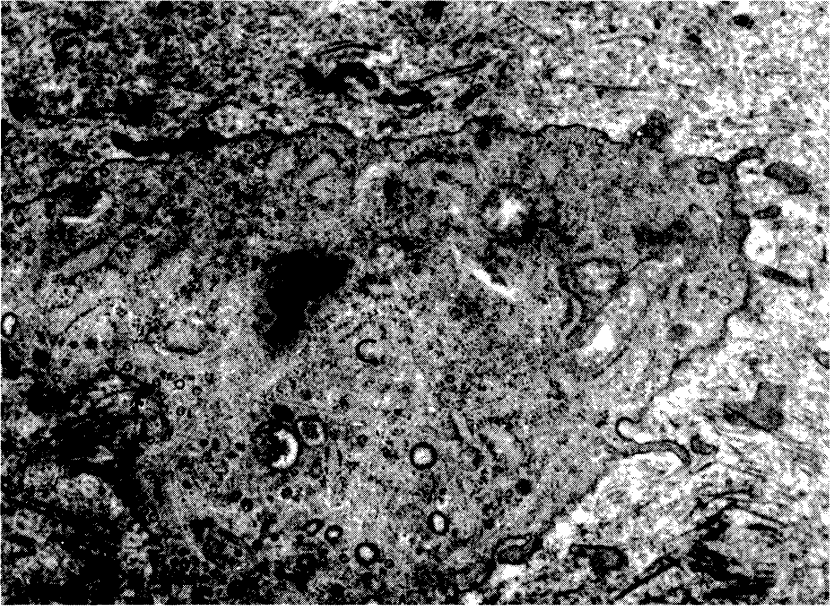


Fig. 9. Deep layer of articular cartilage of a 5-year-old cat. Chondrocyte (C) showing all signs of synthetic activity. Cytoplasm contains the usual organelles. In one of its folds, collagen fibres penetrate cell membrane into intercellular matrix (arrow). x 16,000

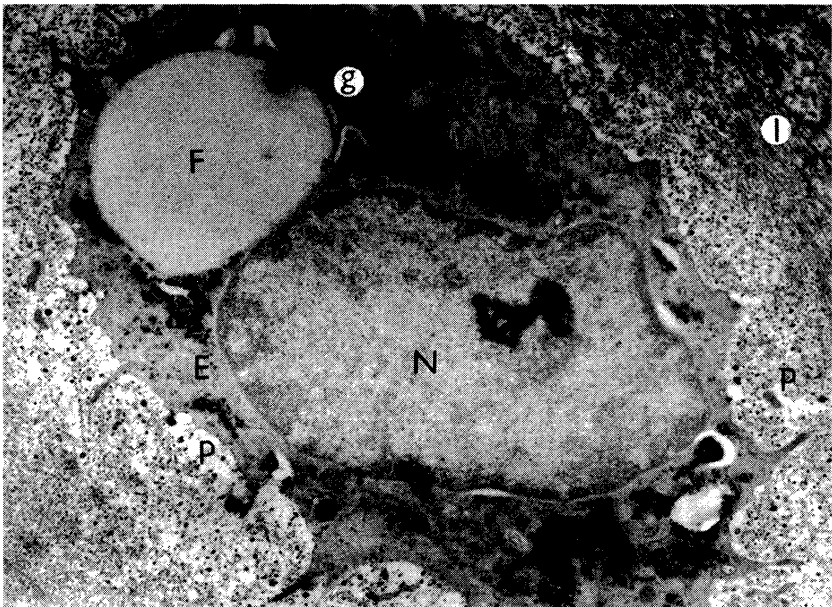


Fig. 10. Deep layer of articular cartilage of a 5-year-old cat. Chondrocyte with signs of degeneration. Nucleus (N), glycogen deposits (g) and a large lipid vacuole (F) in cytoplasm. Rests of GER cisternae (E). Glycoprotein precipitates in pericellular matrix (p) and collagen fibrils (k) in intercellular matrix. x 12,000