

A fine structural study of coronal and root dentinogenesis in the mouse: observations on the so-called 'von Korff fibres' and their contribution to mantle dentine

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INTRODUCTION

Although earlier reports exist, von Korff (1905) is credited with the first detailed description of what appear to be coarse bundles of collagen fibres arising from the dental pulp, passing between the odontoblasts, and fanning out to form the fibrous matrix of the dentine of the tooth. These 'fibres' stain black with silver and are referred to as the argyrophilic fibres of von Korff.

Soon after von Korff's description of these fibres debate began as to their significance in dentine formation, and the details of this have been well reviewed by Lester & Boyde (1968) and Moss (1974). Essentially the dispute centred on whether or not von Korff fibres were present throughout the entire period of dentinogenesis, and thus whether or not they formed the sole source of dentinal collagen. This dispute seemed to be settled when Weidenreich (1925) distinguished 'mantle dentine' (the first formed dentine) from 'circumpulpal dentine' (the remaining dentine which constitutes the bulk of the tooth). It was suggested that the collagen of mantle dentine was derived from von Korff fibres arising in the pulp whilst that of the circumpulpal dentine was derived from the secretion of the odontoblasts.

Von Korff fibres were considered to be aligned perpendicular to the enamel-dentine junction in mantle dentine, whereas in circumpulpal dentine the collagen fibres of the matrix were considered to lie at right angles to the dentinal tubules. However, this description of the orientation of von Korff fibres in mantle dentine is disputed. Bradford (1967) wrote: "These fibres were first noted by von Korff as running in bundles towards the forming dentine surface parallel to the long axes of the odontoblasts. There is still controversy about the direction of the fibres in this region as there is *no doubt that at the dentinal end of the odontoblast these fibres are already aligned parallel to the dentine surface at right angles to the long axes of the odontoblasts.*" Moss (1974), however, concluded that mantle dentine can only be defined on a topographical basis since there is no consistency in the orientation of fibres in mantle dentine in different mammalian species.

With the advent of the transmission and scanning electron microscopes it might have been thought that the problem of von Korff fibres and their contribution to the matrix of the dentine would easily be resolved. Unfortunately, this has not been the case and, if anything, the debate has intensified.

Lester & Boyde (1968) described, with the aid of the scanning electron microscope, what they termed 'von Korff fibres' in several mammalian dentines. However, they appear to have studied the ordinary collagen fibres within the dentine matrix. Ten Cate *et al.* (1970) concluded that the controversy concerning von Korff fibres resulted from a misinterpretation of silver-based stains at the light microscope level.

They proposed that silver stains visualized the reducing sugars in an extensive extracellular compartment between widely separated pre-odontoblasts, giving with the light microscope a spurious appearance of black argyrophilic fibres. On this basis, with continued hypertrophy of the odontoblasts, and the exclusion of this extracellular compartment, the well-recognized reduction in the number of the so-called von Korff fibres during circumpulpal dentinogenesis was explicable.

Their contention seemed to be supported by Nalbandian (1968), who thought staining of ground substance occurs, and also by Yoshiki & Kurahashi (1971), who described apparent von Korff fibres in silver-stained sections of rat tooth germs examined with the light microscope but, in corresponding electron micrographs, could not find collagen fibres between odontoblasts. These later interpretations were challenged by Whittaker & Adams (1972), who believed they had demonstrated classical von Korff fibres: this has prompted the present re-examination of early dentinogenesis and a review of previously published electron micrographs purporting to demonstrate von Korff fibres, in an attempt to resolve the nature of these fibres and their contribution to the structure of dentine.

MATERIAL AND METHODS

The bulk of the material used for this investigation consisted of mouse molar teeth from animals of varying ages from birth to 42 days prepared for other studies. They had all been processed using conventional techniques for electron microscopy involving fixation with 4% glutaraldehyde, demineralization in ethylenediaminetetraacetic acid (E.D.T.A.), post-fixation with osmium tetroxide, embedding in Epon and staining with uranyl acetate and lead citrate.

In addition, mouse first molar tooth germs were dissected from the jaws and treated as follows. Some were processed for conventional electron microscopy as described above. Others, after fixation in 4% glutaraldehyde, were washed for 24 hours in a large volume (600 ml) of 0.2 M sodium cacodylate-sucrose at pH 7.4. After washing, the tooth germs were frozen in liquid nitrogen and then sectioned at 45 μm on a cryostat. The sections were then stained by the silver impregnation method used by us and fully detailed in our previous study (Ten Cate *et al.* 1970). Some sections were selected as controls and exposed for 6 hours at 22 °C to 16 ml acetic anhydride in 24 ml of dry pyridine to block reducing sugars. Following this treatment these sections were then exposed to the silver impregnation technique. After impregnation, the 45 μm sections were blocked in Epon and fine sections cut for examination in the electron microscope.

RESULTS

Dentine formation in the root

Root dentinogenesis begins with the differentiation of odontoblasts from the cells of the dental papilla, differentiation being induced by the epithelial cells of Hertwig's root sheath. At this stage (Fig. 1) the root sheath consists of epithelial cells lying between distinct basal laminae on its follicular and papillary surfaces. The epithelial cells are joined to each other by means of desmosomal attachments and their cytoplasm contains many free ribosomes and mitochondria, some Golgi profiles and considerable amounts of rough endoplasmic reticulum. Tonofilaments are not a prominent feature.

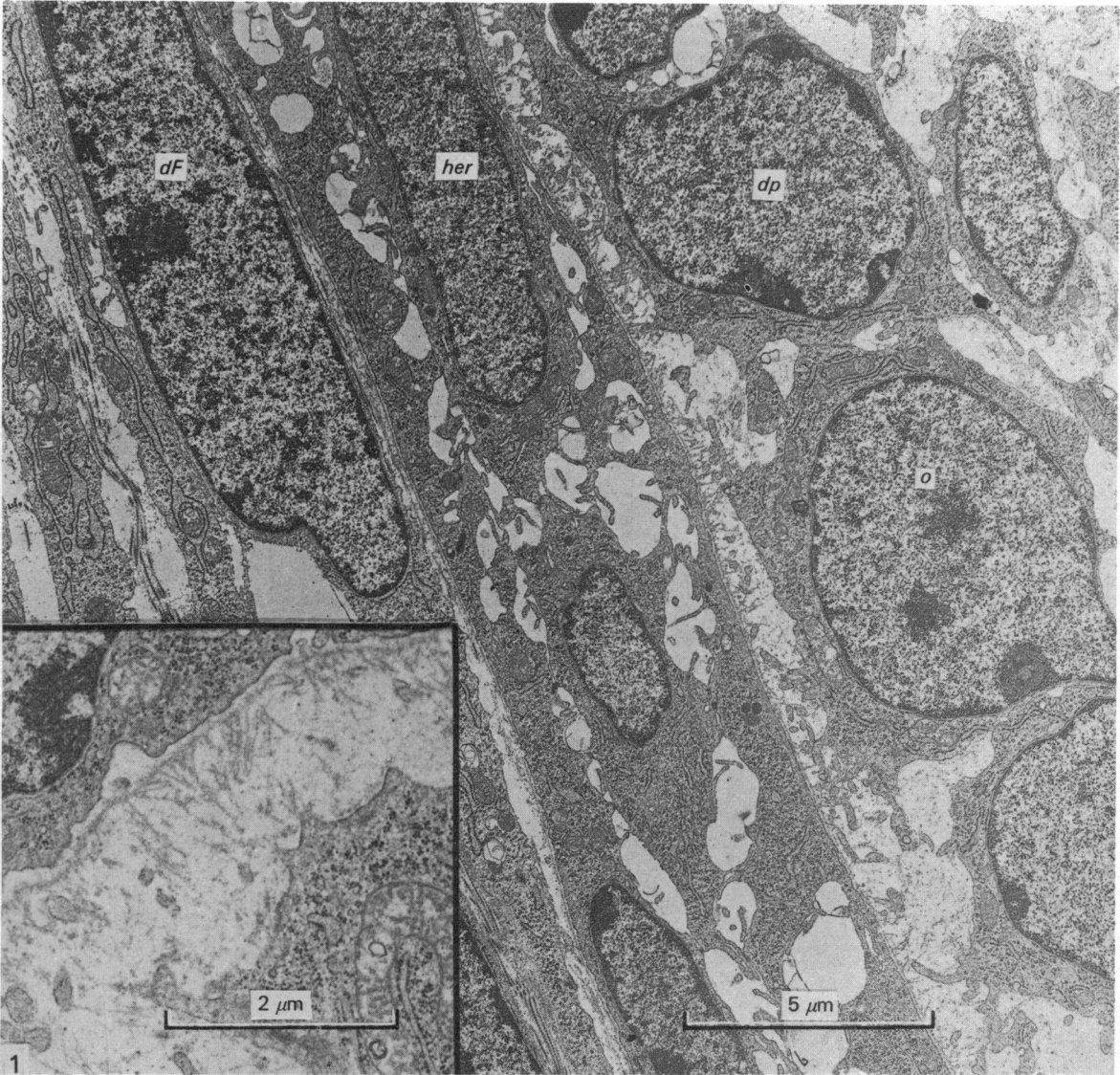
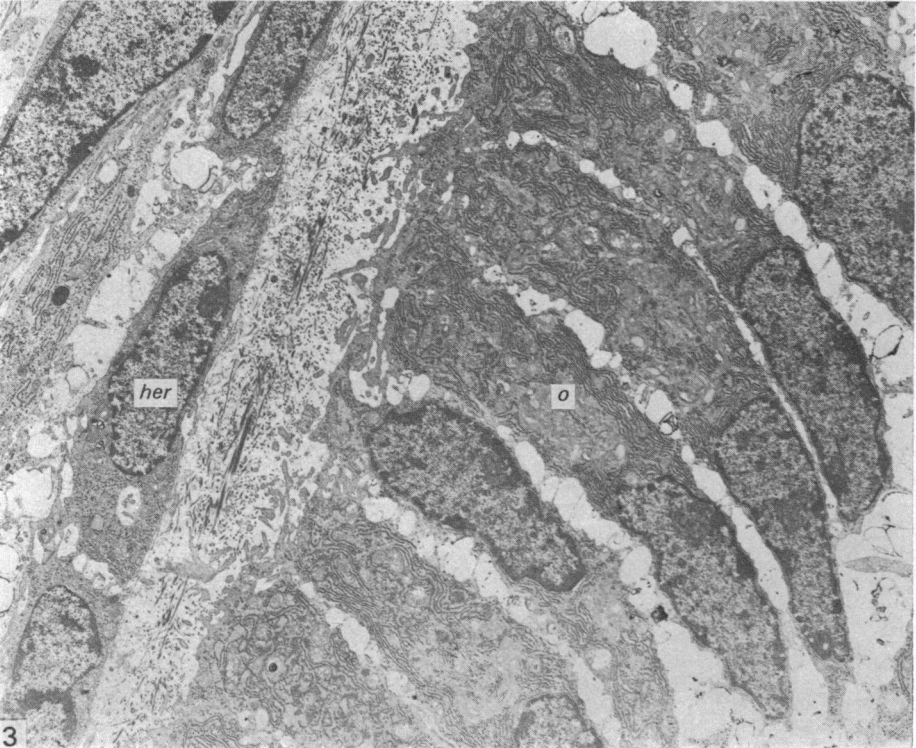
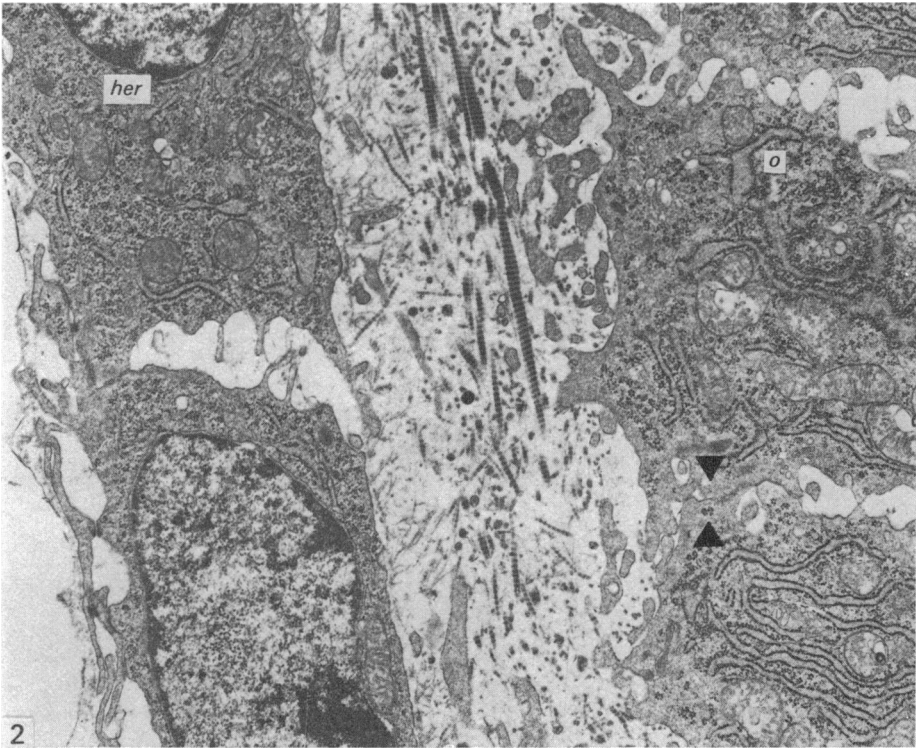


Fig. 1. Electron micrograph illustrating, from left to right, the dental follicle (*dF*), Hertwig's epithelial root sheath (*her*) and the dental papilla (*dp*). Note that the newly differentiated odontoblast (*o*) is surrounded by a collagen-free extracellular compartment. The inset illustrates the aperiodic fibrils dependent from the basal lamina supporting the epithelial root sheath. 12 day mouse first molar. $\times 6800$ (insert $\times 16700$).

The milieu in which odontoblasts differentiate consists of numerous aperiodic fibrils which depend from the basement lamina of the root sheath and which separate the epithelial cells from a collagen fibril-free ground substance. The newly differentiated odontoblasts rapidly develop the characteristics of secretory cells and establish junctional complexes between themselves. The first banded collagen fibrils of the dentine matrix are found in the extracellular compartment bounded by the newly differentiated odontoblasts and the basement lamina of the root sheath. These fibrils



are of large diameter and are aligned parallel to the basement lamina (Fig. 2). No banded collagen fibrils are seen between the newly differentiated odontoblasts or, for that matter, between the cells of the sub-odontoblast layer. The absence of collagen fibrils in this situation is clearly demonstrated in some of the material where shrinkage of odontoblasts has occurred (Fig. 3).

As the development of root dentine was followed further, loss of the basal lamina on both the follicular and papillal surfaces of the root sheath was seen. With this loss of basal lamina, pseudopodial extensions of the epithelial cells were found in the forming dentine matrix. Follicular fibroblasts were also found interposed between the root sheath cells, which still contained significant amounts of rough endoplasmic reticulum.

Also at this time there was a progressive increase in the number of large collagen fibrils within the forming dentine matrix. These fibrils eventually formed a distinct band lying parallel to the root sheath. This band, lying first in close proximity to the root sheath, gradually became located further away from the cells of the root sheath up to a maximum distance of $1.25 \mu\text{m}$, with the intervening gap between filled with a granular material and a few fine collagen fibrils (Fig. 4). There were still no banded collagen fibrils between either the odontoblasts or the cells of the sub-odontoblastic zone.

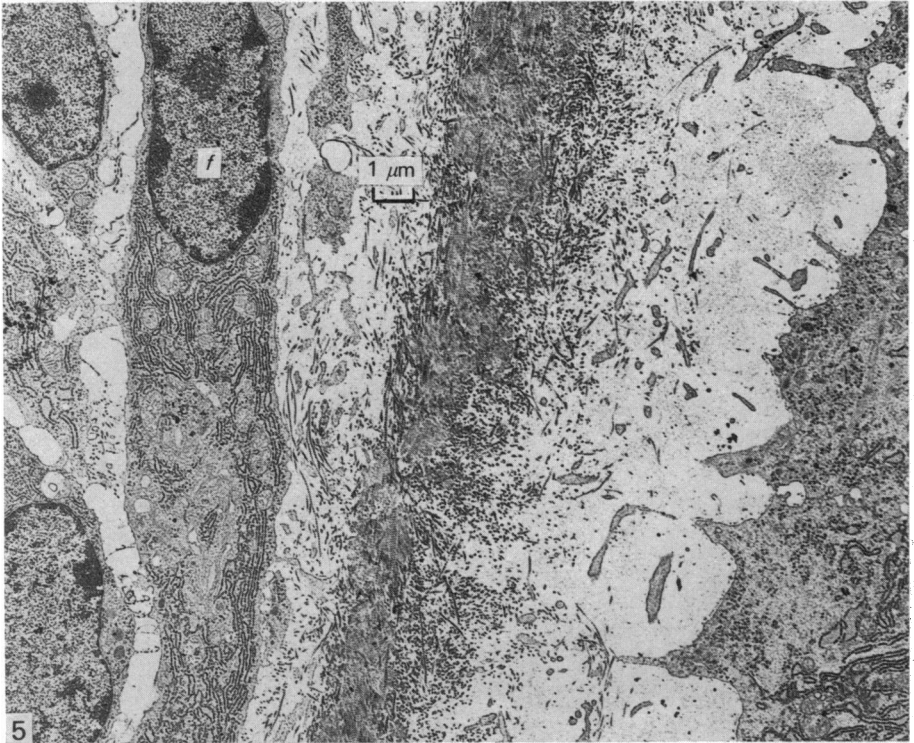
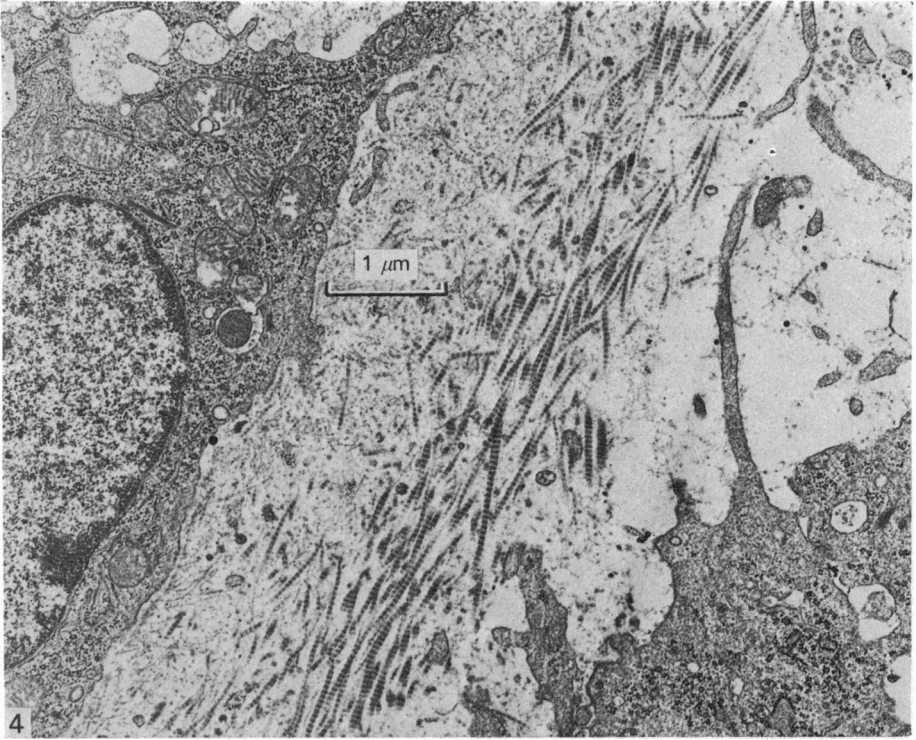
As root dentinogenesis progressed a change occurred in the pattern of collagen deposition in the forming dentine matrix. Instead of 'coarse' fibrils being deposited and aligned parallel to the root surface, much finer collagen fibrils were now observed, mainly cut in cross section (Fig. 6). After the onset of mineralization within the dentine, and also in erupted functional teeth, it was still possible to distinguish the band of coarse collagen fibril bundles running parallel to the root surface. This layer was always covered by the layer of indistinct composition approximately $1 \mu\text{m}$ thick (mentioned previously), which with further development was covered eventually by cement (Figs. 6, 7, 8).

Dentine formation in the crown region

Dentine formation in the crown region was essentially similar to that in the root except for one key difference. This difference concerned the first appearance of collagen fibrils in the presumptive dentine matrix. As in root dentinogenesis, such fibrils first appeared in the extracellular compartment between the basal lamina of the internal dental epithelium and the newly differentiated odontoblasts, but their orientation was at right angles to, and not parallel with, the basement lamina as in the root (Figs. 9, 10). Again, no banded collagen fibrils were found in the extracellular compartment between odontoblasts (Fig. 11).

Fig. 2. Illustrates the first appearance of large banded collagen fibrils in the presumptive dentine matrix. At this stage the cells of the root sheath still contain many cytoplasmic organelles but its supporting basement lamina is disrupting. Note the early development of junctional complexes between the odontoblasts (arrowed) and the orientation of the collagen fibrils parallel to the root sheath. *her*, root sheath; *o*, odontoblasts. 12 day mouse first molar $\times 12400$.

Fig. 3. This electron micrograph illustrates the disposition of the first formed collagen fibrils in root mantle dentine and the absence of collagen fibrils between odontoblasts and from the sub-odontoblast region. In this specimen some shrinkage of the odontoblasts has occurred thereby enhancing the intercellular spaces. *her*, root sheath; *o*, odontoblasts. 12 day mouse first molar. $\times 4000$.



Finally, in the silver-stained materials of coronal dentinogenesis the silver was mainly deposited in the extracellular compartment between the odontoblasts. In the controls, such silver deposition was not present (Figs. 12, 13).

DISCUSSION

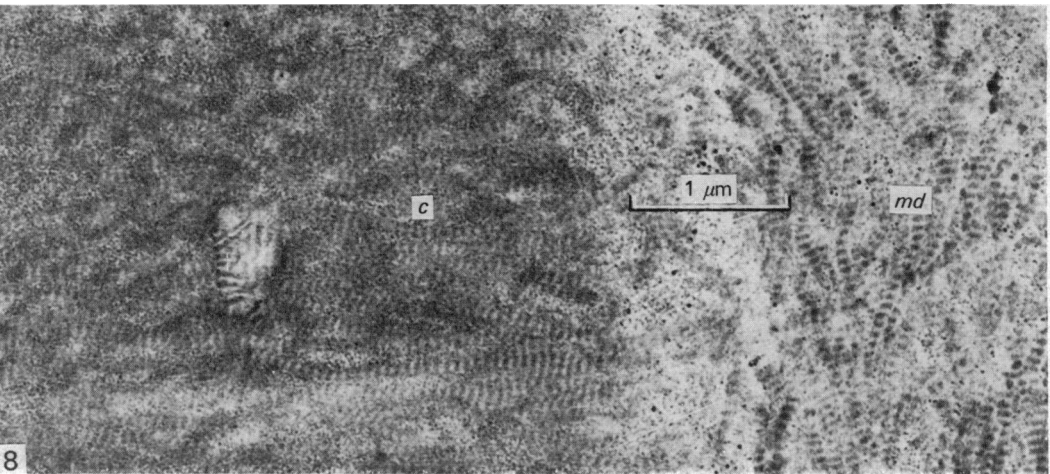
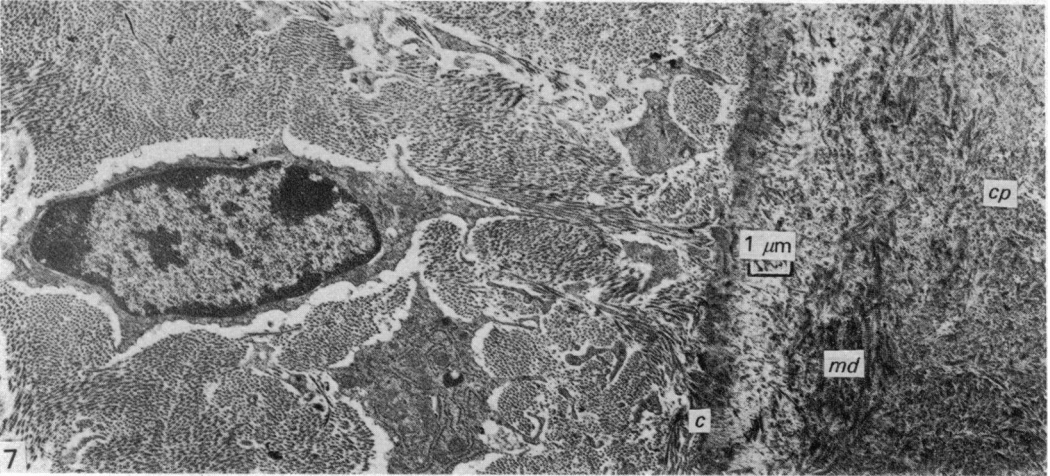
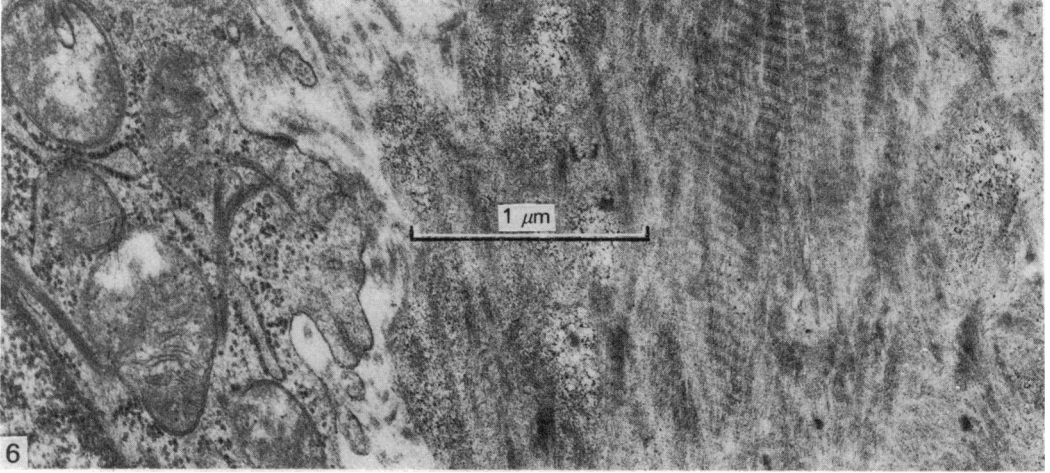
It is first necessary to define very precisely the term 'von Korff fibres'. The term should be confined to silver-staining 'fibre bundles', presumed to be collagenous, seen with the light microscope, and which seem to *arise* from the sub-odontoblast zone of the dental papilla, pass *between* the odontoblasts, and fan out to form the fibrous matrix of the first formed, or mantle, dentine. The terms collagen fibril and collagen fibre need also to be defined. The term fibril is used to describe characteristically banded collagen elements resolvable only with the electron microscope. These fibrils may be gathered into bundles. If the bundles are of greater diameter than 0.2 μm they are resolvable in the light microscope, and are then termed collagen fibres. Thus 'fibres' are collagen visible with the light microscope. In this study of dentinogenesis in the mouse molar it has not been possible to demonstrate collagen fibrils arising from the pulp and ascending between the odontoblasts at any stage of development examined. It can therefore be stated unequivocally that 'collagenous von Korff fibres' in the accepted sense do not exist in the developing teeth of the mouse. The apparent occurrence of such 'fibres' in tooth germs after silver staining and examination with the light microscope has already been explained (Ten Cate *et al.* 1970), and confirmed again in this study. Moreover, the absence of any silver deposition after blocking the reducing sugars further supports the contention that the classical von Korff fibre is an artefact of light microscopy created by the deposition of silver in the extracellular compartment.

If this interpretation is correct, can the reports by some workers of von Korff fibres demonstrable at the ultrastructural level be explained? In many instances it is the collagen fibrils in the pre-dentine which such workers have called von Korff fibres. This is admitted by Sisca & Provenza (1972) in their paper on initial dentine formation in human deciduous teeth when they state that 'while von Korff fibre bundles were often in close proximity to the interfaces of adjacent odontoblastic processes they were not found in the intercellular spaces of the odontoblast cell bodies'. Other studies of human dentinogenesis (Johansen & Parks, 1962; Frank, 1966) illustrate large collagen fibrils in pre-dentine, labelling them as von Korff fibres.

Obliquity of section may be the explanation for the apparent demonstration of collagen fibrils between odontoblasts. It is well established (see for example, Garant, Zabo & Nalbandian, 1968) that, at the neck of the odontoblast, in the region of the junctional complexes, there is a marked diminution in the number of cytoplasmic

Fig. 4. An electron micrograph of the first formed dentine of the root illustrating the nature of the matrix between the root sheath and the distinctive band of collagen fibrils. This matrix is approximately 1.25 μm wide (see bar) and consists of a few fine fibrils scattered in a granular background. This granular material also occurs between the epithelial cells. Notice also the numerous organelles within the epithelial cells. 13 day mouse first molar. $\times 10800$.

Fig. 5. An electron micrograph illustrating the transition from mantle dentinogenesis to circum-pulpal dentinogenesis in the root. The root sheath is now absent and follicular fibroblasts (*f*) lie adjacent to the forming root surface. The gap between the follicular cells and the distinctive band of collagen fibrils is still approximately 1 μm (1 μm bar). Fine collagen fibrils are now being deposited in the dentine matrix on the pulpal aspect of the coarse fibre bundles lying parallel to the root surface. 13 day mouse molar. $\times 5000$.



organelles within its cytoplasm with the result that its process is practically devoid of most major cell organelles. Any figure claiming to demonstrate von Korff fibres between odontoblast cell *bodies* must show that the odontoblast cytoplasm contains a full complement of cytoplasmic organelles. If cytoplasmic organelles are sparse it is most likely that the fibres are in fact situated on the pre-dentinal side of the junctional complexes.

Examination of Johansen & Parks' (1962) and Frank's (1966) illustrations of human coronal dentinogenesis which purport to show von Korff fibres between odontoblasts makes it clear that the fibres lie between cell profiles devoid of cytoplasmic organelles. Furseth's (1971) illustrations of human circumpulpal dentinogenesis in the root also label von Korff fibres between odontoblast profiles which have a paucity of organelles within the cytoplasm. The major evidence for the involvement of von Korff fibres in rat dentinogenesis comes from Reith's (1968) study, and his findings therefore warrant careful consideration. He states that "although von Korff's fibres are present in large numbers at the very onset of dentinogenesis, they become less numerous shortly thereafter and ultimately are hardly to be seen". Reference is made to two figures, one of which can be dismissed, as it labels, as von Korff fibres, collagen clearly situated in pre-dentine. In the other figure the von Korff fibres are depicted very close to the junction of the odontoblast cell body with its process, and they could very well be situated on the pre-dentinal face of the junctional complex.

The only really convincing evidence for the presence of von Korff fibres between odontoblasts during dentinogenesis comes from two sources. The first is a single electron microscope (Fig. 4) in Whittaker & Adams' (1972) communication on human dentinogenesis. Even here there is evidence that obliquity of sectioning may be confusing the issue. The bundles of collagen fibrils actually labelled as von Korff fibres are most likely within pre-dentine. Only a few, very fine, collagen fibrils towards the bottom of the picture are inexplicable on the basis of obliquity of section, and seem truly to lie between odontoblasts. The second is from a study of dentinogenesis in the cat (Silva & Kailis, 1972). In their Figure 6, collagen fibres are demonstrated between odontoblast cell bodies with a full complement of cytoplasmic organelles. However, they occur only at the dentinal end of the intercellular space, and cannot be traced into the papilla. Thus, apart from the above examples, the bulk of the evidence indicates an absence of classical collagenous von Korff fibres during dentinogenesis. Neither has scanning electron microscopy provided evidence for the existence of classical von Korff fibres. Lester & Boyde (1968) examined only the surfaces of mature and developing dentine. Because the cells had been removed it was not possible to determine whether von Korff fibres were situated between odonto-

Fig. 6. An electron micrograph depicting the root surface just after mineralization has begun (this is a demineralized section). The root surface is still covered by an epithelial cell in which mitochondria and profiles of rough endoplasmic reticulum are evident. The coarse banded collagen fibrils of mantle dentine are evident as is the layer between it and the epithelial cell (1 μm bar marker). 13 day mouse first molar. $\times 31\,750$.

Fig. 7. A low power electron micrograph of the root and periodontal ligament of an erupted and functional molar tooth. To the right is circumpulpal dentine (*cp*). The mantle dentine (*md*) can be recognized and so can cement (*c*). A less electron-dense layer of 1 μm in thickness (1 μm bar) intervenes between the mantle dentine and cement. 28 day mouse first molar. $\times 5300$.

Fig. 8. A higher power electron micrograph from another specimen illustrating mantle dentine (*md*), cement (*c*) and the intervening layer (1 μm bar). 42 day mouse first molar. $\times 23\,700$.

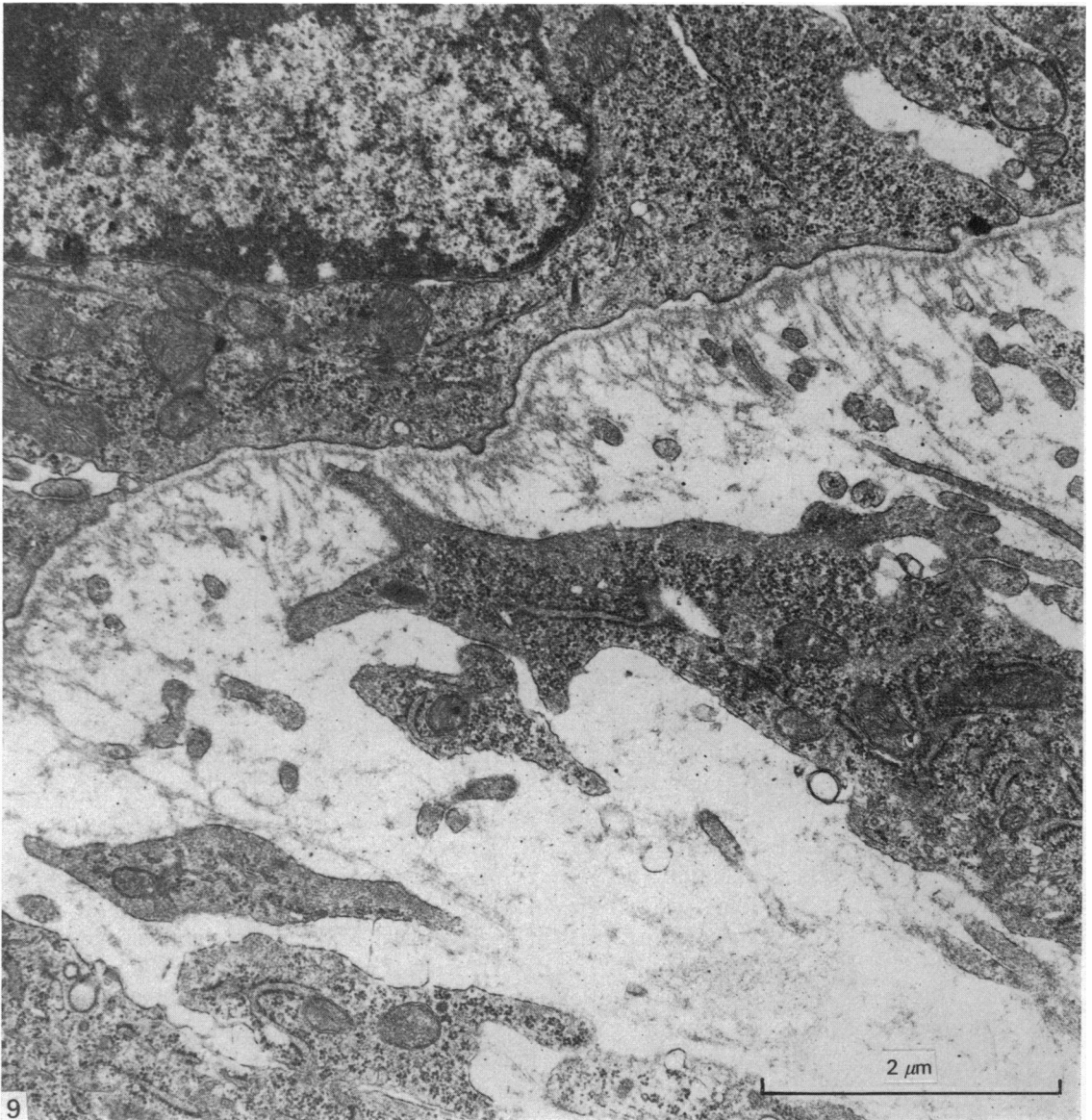


Fig. 9. An electron micrograph illustrating the milieu in which coronal dentine matrix first forms. Note the basement lamina with its dependent aperiodic fibrils which supports the epithelial cells of the internal enamel epithelium. Note also the absence of any banded collagen fibrils in this electron micrograph. Compare with Figure 1. 1 day mouse first molar. $\times 20400$.

blasts. The structures they describe, therefore, are the large collagen fibrils found in the first formed dentine.

Thus, at the fine structural level, there is no substantive evidence for the real existence in mammalian dentinogenesis of von Korff fibres as previously defined in this article. This is in agreement with the conclusions reached by Moss (1974) in his study of mantle dentine. He felt that, "on balance, the available data strongly suggest the non-existence of these fibrils *in-vivo*". He then pointed out that, if von Korff fibres

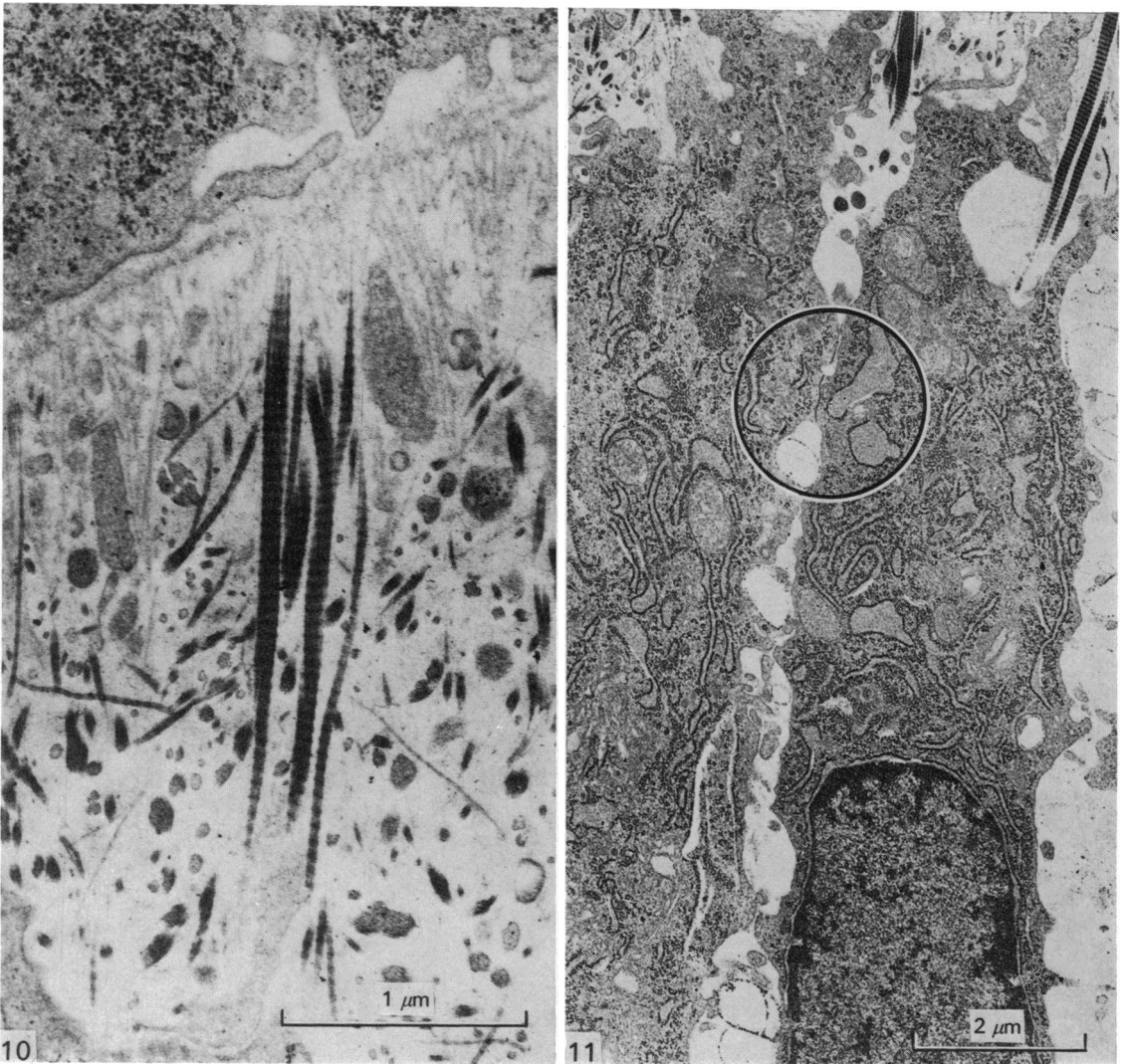


Fig. 10. A slightly later stage of coronal mantle dentinogenesis than shown in Figure 9. Coarse collagen fibrils are clearly seen lying at right angles to the basement lamina supporting the internal enamel epithelium and interposed with the aperiodic filaments. This figure should be compared with Figure 2. 2 day mouse first molar. $\times 31300$.

Fig. 11. An electron micrograph of odontoblasts associated with coronal mantle dentinogenesis. Note the prominent junctional complex (circled) and the absence of banded collagen fibrils from the intercellular spaces. 2 day mouse first molar. $\times 10800$.

do not exist, this would not imply the non-reality of mantle dentine; such a layer does exist, but is definable by other parameters.

It must be emphasized that the conclusion reached in this study is that classical collagenous von Korff fibres do not exist. The presence of large diameter collagen fibrils in mantle dentine is not denied. Indeed, a key observation of this study is that the orientation of these fibres differs depending upon whether root or coronal dentinogenesis is being studied. Whether or not it is worth retaining the term von Korff fibres (in a new sense) for these large diameter fibres in dentine is another

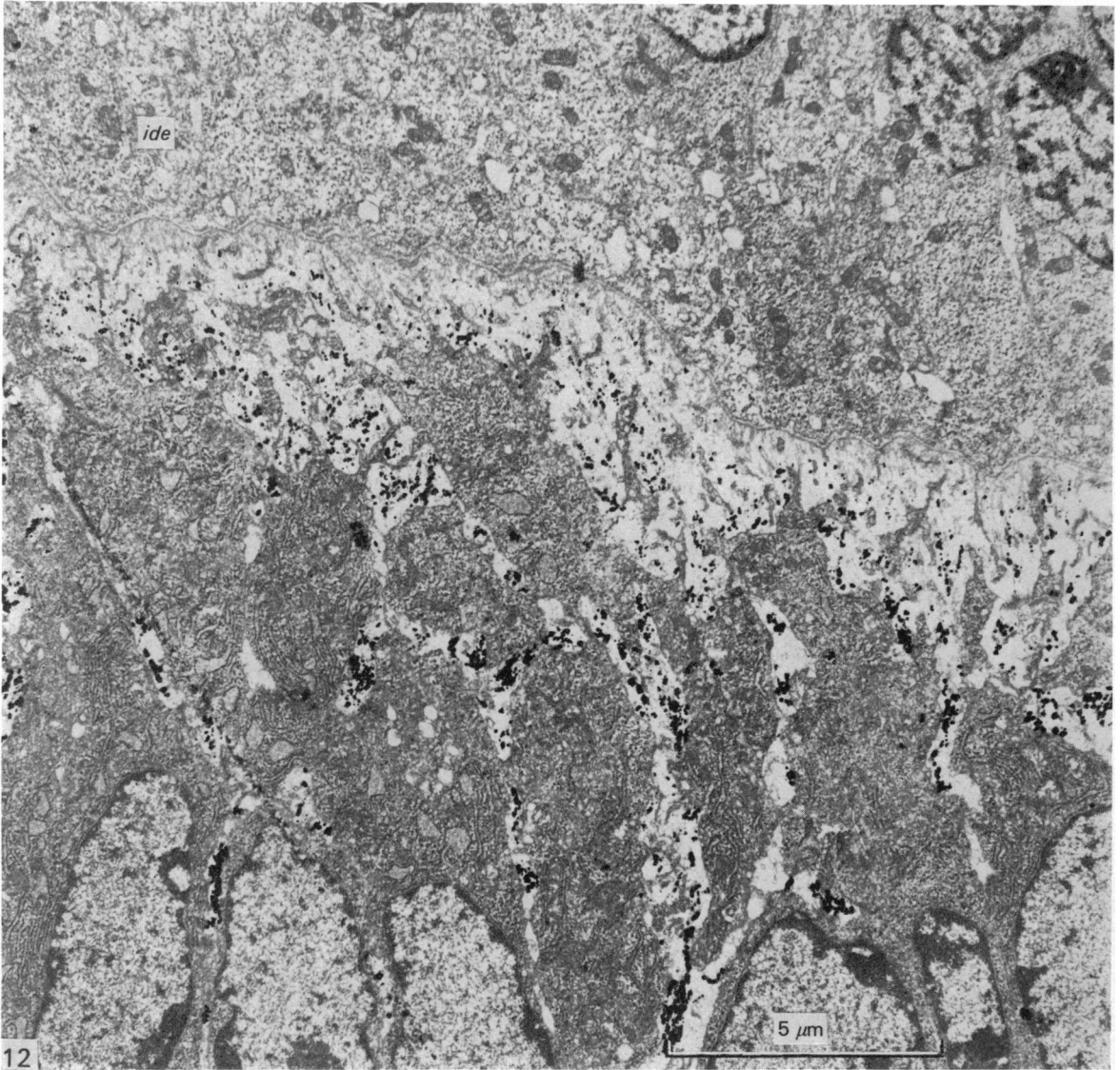


Fig. 12. Silver stained section showing coronal mantle dentinogenesis. Because of the silver staining technique cytoplasmic organelles are somewhat distorted. The basement lamina separating the internal dental epithelium (*ide*) from dental pulp is clearly visible. Silver grains are located in the extracellular compartment between odontoblasts. 2 day mouse first molar. $\times 7200$.

matter: probably not, as this term has for many years been associated with the concept of a dual origin of dentinal collagen, whereas more recent evidence suggests that all dentinal collagen is the product of odontoblastic activity.

The observation that the disposition of these large collagen fibrils differs in mouse coronal and root mantle dentine may, if the same is true for other mammalian dentines, explain the confusion exemplified in the quotation of Bradford (1967) already given, and also the call for further studies on mantle dentine by Moss (1974) to explain its structure.

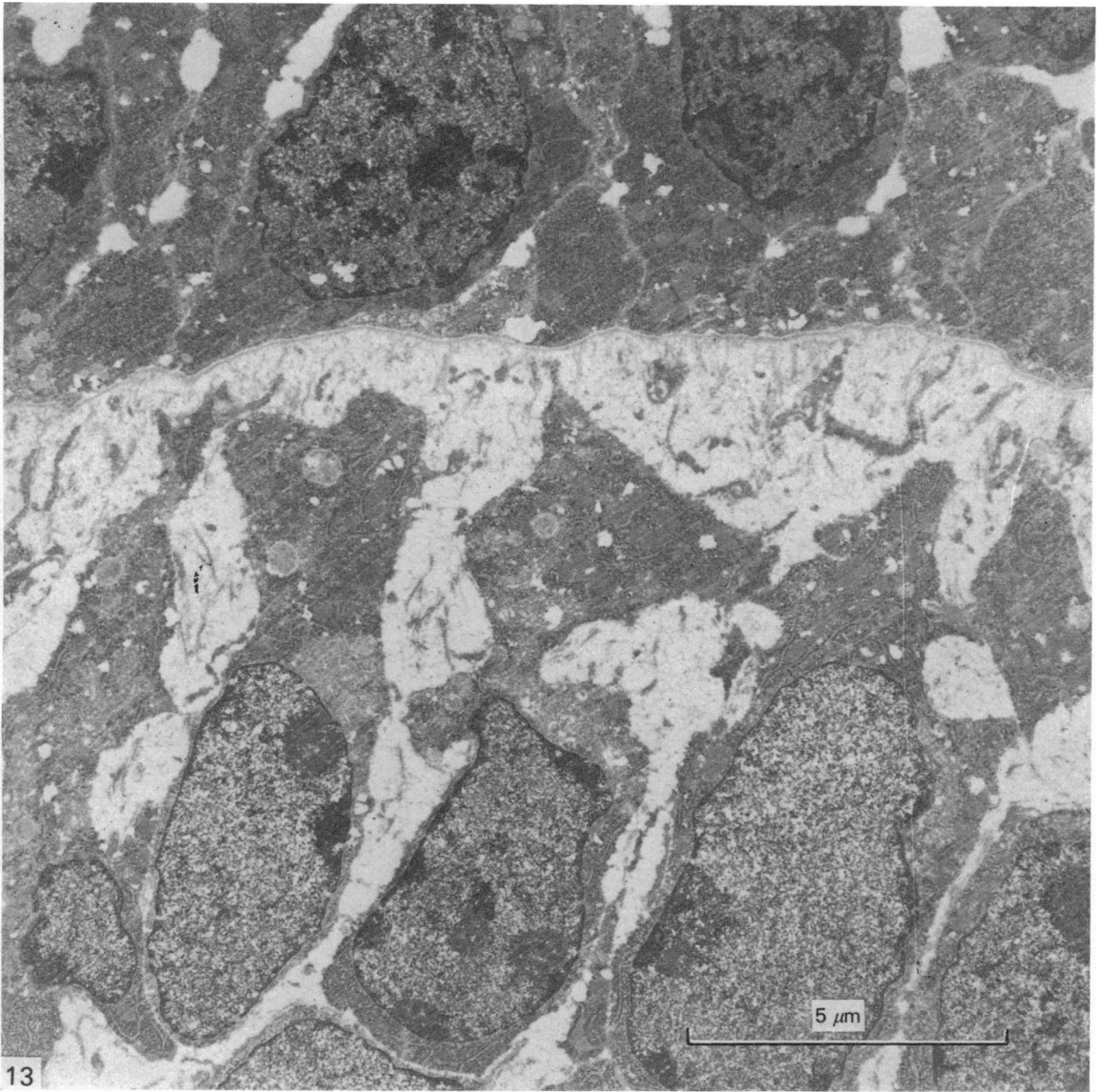


Fig. 13. Electron micrograph of a field similar to that illustrated in Figure 12. This section was treated with acetic anhydride to block reducing sugars and then stained with silver. 2 day mouse first molar. $\times 8500$.

The disposition of the large collagen fibres in pre-dentine during coronal mantle dentinogenesis seems to follow a consistent pattern in all species studied. Thus in man (Sisca & Provenza, 1972), cat (Silva & Kailis, 1972), rabbit (Slavkin *et al.* 1972) and rat (Reith, 1968) these fibres are arranged at right angles to the basement lamina of the internal dental epithelium. Unfortunately, root mantle dentinogenesis has not been documented so well. The studies of Noble, Carmicheal & Rankine (1962) and Furseth (1971) on human root dentinogenesis describe only circumpulpal dentinogenesis. However, Kramer (1951), in a light microscopic study of human

dentine, noted that the fibre orientation in the mantle dentine of the crown seemed to differ from that of the root.

Lester (1969) has described root formation in the rat, and his electron micrographs illustrating initial dentine formation show large collagen fibrils lying parallel to the basement lamina. There is, therefore, some evidence of species variation in the orientation of fibres in the mantle dentine of the root and crown and this should be kept in mind in any future study of mantle dentine.

Finally, a brief comment may be made about the layer approximately 1 μm thick between mantle dentine and root sheath. This layer is possibly the homologue in the mouse of the hyaline layer of Hopewell-Smith (1903) found in human teeth, which has been extensively studied by Owens (1972, 1973, 1974). The present author's fine-structural study of root dentinogenesis leads to the conclusion that both epithelial cells and odontoblasts may be involved in the synthesis of this layer because both kinds of cell at this stage possess organelle complements (including rough endoplasmic reticulum) characteristic of secretory cells. Stahl & Slavkin (1972) reported that the first formed layer of *cement* consists of two thirds collagen and one third epithelium-derived matrix. However, this is a different matter: for Owens has shown that Hopewell-Smith's layer (when present) is *dentine*, not cement.

SUMMARY

The fine structure of mantle dentine formation has been studied in the mouse molar. No evidence was found for the presence of collagenous von Korff fibres arising from the dental papilla, passing between odontoblasts and fanning out to form the collagenous matrix of mantle dentine. Instead, large collagen fibrils were first demonstrable in the matrix peripheral to the dentinal aspect of an extensive junctional complex system occurring at the necks of the odontoblasts. The orientation of the fibres was at right angles to the future amelo-dentinal junction in coronal dentinogenesis, but parallel to the root surface in radicular dentinogenesis. These large collagen fibrils formed the mantle dentine. It is concluded that von Korff fibres, as strictly defined, are artefacts. Photographs in the literature purporting to show von Korff fibres are attributable to obliquity of section. Also, it is suggested that the difference in fibril orientation in coronal and root mantle dentine is the reason for the conflicting opinions on the pattern of fibril orientation in this tissue.

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