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Endothelial cilia in human aortic atherosclerotic lesions*, **

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Summary. "Primary" cilia were present in the endothelial cells of human aortic fatty dots and streaks but not in those of normal intima. They had the features of cilia of the "9+0" axonemal configuration observed in many other cells. A lateral foot process and transitional fibers "anchored" the ciliary basal body in the cytoplasm, but rootlets were not identified in material examined. Ladder-like configurations interconnected the two centrioles (=diplosome) of control endothelium.

The "primary" cilia of endothelium differed from those of the rudimentary type observed in smooth muscle cells in similar lesions of man, but shared many features with cilia of those present in experimental atherosclerosis in rabbit.

Cilia were rarely described in vascular endothelium. It is believed that, to date, they were not reported to occur in normal or pathological arteries in man.

It is being stressed that whereas the significance of these unusual organelles remains uncertain, their widespread occurrence may indicate that their role is more important than was believed previously, and they should cease being a curiosity only.

Key words: "Primary" endothelial cilia – Endothelial centrioles – Human atherosclerosis – Ciliary transitional fibers – Ultrastructure

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** Dedicated to Professor Dr. Gotthard Schettler, Department of Internal Medicine, University of Heidelberg, FRG, on the occasion of his 60 birthday (April, 1987).

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Introduction

In the course of our studies designed to test whether in analogy to experimental atherosclerosis in rabbits (Haust 1984) ciliated smooth muscle cells also occur in human aortic fatty dots and streaks, cilia were found on occasion in electronmicrographs of endothelium of these lesions. Search of the literature disclosed that not many reports are available on ciliated endothelium (Corbett 1961; Vegge 1963; Hogan et al. 1971; Edanaga 1974, 1975; Renard et al. 1976; Gallagher 1980; Yamamoto and Fujimoto 1980), and apparently, none was published on its occurrence in human normal or pathological arteries. Furthermore, ciliated vascular endothelium at other sites in man has been reported only rarely (Vegge 1963; Yamamoto and Fujimoto 1980; see also Wheatley 1982).

Preliminary observations suggested that the mode of formation of the endothelial cilia varied in some aspects from that of similar organelles found in the intimal smooth muscle cells of the same lesions (Haust 1986). It was thought, therefore, of interest to study the morphogenesis of these organelles, and the ultrastructural features of these and related structures. Moreover, the issues relevant to the occurrence, formation and significance of these unusual "single", "solitary", "rudimentary", "primary" or "oligo" – cilia (for review see Ghadially 1975; Wheatley 1982; Pysher and Neustein 1984) remains largely unknown or controversial. Thus, a study regarding their presence in as yet unexplored location and under pathological conditions was considered of value as it might contribute to unravelling of some of the unresolved problems.

The purpose of this communication is to report the findings of an enquiry undertaken with the

above aims, and to discuss the results in the context of the present-day knowledge relating to these unusual cilia and associated organelles.

Material and methods

This enquiry was based on material employed in broader studies concerning the nature and status of cells involved in atherosclerotic lesions, as outlined elsewhere (Haust 1980).

The tissues were processed by standard techniques for light and transmission electron microscopy (TEM). Sections of paraffin-embedded blocks and one-micron-thick sections from plastic-embedded material were examined for identification of lesions (Haust 1971) and normal control tissues (Haust 1983) by established criteria.

Thin sections for TEM were picked up on 300 – mesh copper grids, stained doubly with uranyl acetate and lead citrate, and examined in a Philips-300 electron microscope.

Forty eight electronmicrographs of lesions and adjacent normal intimal areas showing endothelial cells with either centrioles or cilia, and selected from randomly photographed thin sections, constituted the basis for the present enquiry. The present study was not designed to assess the incidence of cilia and related structures in the endothelial cells of either the normal or atherosclerotic intima.

Results

In control tissues, the centrioles seen in endothelial cells were usually present as a pair (a diplosome) in the region between the nucleus and the cytoplasmic portion resting upon the basement membrane (Fig. 1). The longitudinal axes of the two centrioles were either perpendicular or slightly oblique to each other. In most instances a prominent Golgi complex and a variable number of cytoplasmic microtubules were in close vicinity to one or both centrioles. On occasion, two or three electron-opaque ladder-like arrangements were observed between the two organelle (Fig. 1 and Fig. 1-inset). The rungs of the ladder varied in thickness and width, and appeared to be connected to each other and to the centrioles by fine filaments. The tubular nature of the peripheral region and a moderately electron-lucid core were apparent in most centrioles. However, the images of suitably cross-cut centrioles, necessary for identification of their peripherally arranged, nine triplet-microtubules and some (known) components of the core (see in Wheatley 1982), were not available for examination. The cytoplasmic area bearing the centriolar pair (and associated structures or material) was more electron-lucid than were other regions of the cytoplasm (Fig. 1). No cilia were observed in the electronmicrographs examined.

In lesions, the appearance of endothelial cells containing the organelles under discussion, varied. It also differed from one area of the lesion to another. For example, in a well developed fatty streak, measuring 0.7 cm in length, the endothelium at the "advancing" pole (Fig. 2) and that of the centre (Fig. 3) often had different ultrastructural features. In the latter region, containing numerous, granulo-membranous, electron-opaque lipid-associated extracellular precipitates, the endothelial cells also showed electron-opaque inclusions which varied in number, size, shape and density (Fig. 4A). Usually, numerous dilated profiles of rough-surface endoplasmic reticulum (containing a finely fibrillar substance) was evident in such endothelium. Centrioles, when seen, appeared not as a pair but as single organelles at either pole of the nucleus and in the vicinity of endothelial surface. Often, only one centriole was present in a given electronmicrograph; it was not possible to determine whether the second organelle was truly absent or not visualized. The centrioles were – again – associated with a prominent Golgi complexes (Figs. 4A and B).

Similar features of centrioles (and related organelles) were apparent in smaller lesions (fatty dots) and at the advancing pole of a large fatty streak (Fig. 2). Here, the extracellular fat-complexes (see above; Figs. 3 and 4A), were absent or few, and fat droplets were present largely in the native intimal smooth muscle cells (Fig. 5). Again, when both centrioles were visualized each was present at either pole of the nucleus and was "directed" towards the luminal plasma membrane. On occasion, one centriole gave rise to a "primary" cilium, whose shaft and the apex of the enclosing vacuole pointed to the surface of the cell (Figs. 5 and 6). In some sections the identity of a cilium could be only surmised on the basis of the presence of two segments varying in the degree of electron-opacity; the less opaque pole, directed towards the surface of the cell was accompanied on either side by a large vacuole (Fig. 7 and Fig. 7-inset). Since on closer inspection there was a suggestion of transitional fibers extending from the distal end of the darker segment (i.e., the basal body) to the base of the vacuoles, semiserial sections were cut from the appropriate blocks to follow the course and identity of these structures. In some instances the semiserial sections showed that the two vacuoles fused with each other (accommodating an emerging albeit often short ciliary shaft) and ultimately "opened" into the lumen by fusing with the attenuating plasma membrane (Fig. 8). The cilium now was intraluminal. The transitional fibers, tenuously present in the foregoing sections (Fig. 7 and Fig. 7-inset) and a lateral foot process became readily visible (Fig. 8 and Fig. 8-inset).

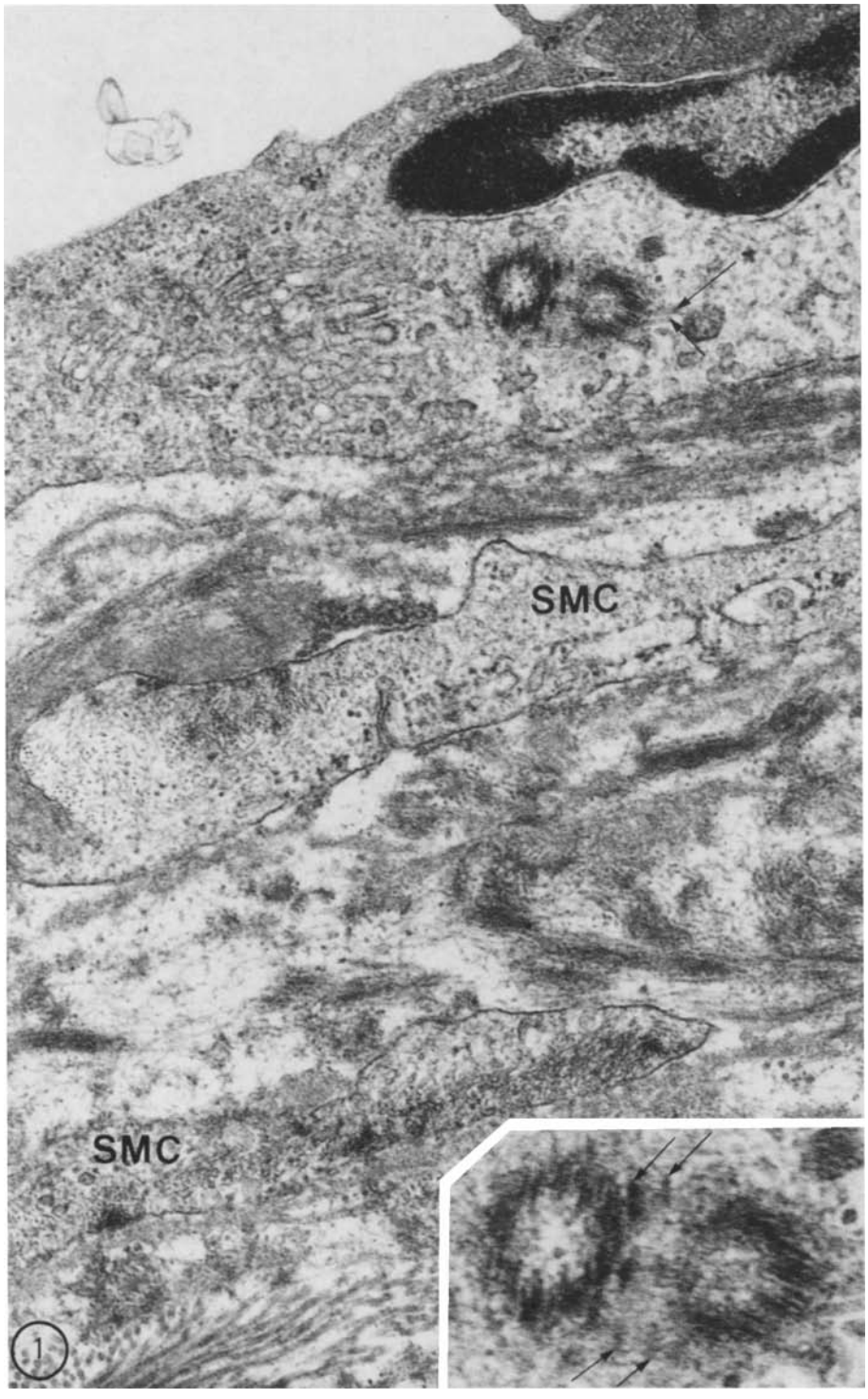


Fig. 1. Electronmicrograph of endothelium of normal aortic intima. The diplosome (two centrioles) is situated in a cytoplasmic area between the nucleus and the basement membrane. Prominent Golgi complex is seen to the left and a few short cytoplasmic microtubules to the right of the centrioles (*arrows*). Note that the intimal smooth muscle cells (*SMC*) are free of fat. Magnification = × 42,000. (*inset*) Higher magnification of centrioles shows their tubular nature. *Arrows* indicate the rungs of the ladder-like arrangement spanning between the centrioles. Magnification = × 86,500

The "primary" cilium, when fully visualized, showed in all instances its characteristic features in keeping with the definition and appearance as delineated by Sorokin (1962, 1968). It consisted of a shaft and a basal body. The basal body, situated and "anchored" in the cytoplasm by a lateral foot process (Figs. 5, 6 and 8) and other less consistently described structures (transitional fibers) (Figs. 5–8) (Bessis et al. 1958; Dahl 1963; Gallagher 1980), was derived and had an internal structure indistinguishable from that of a centriole. It continued as a shaft which was wrapped in plas-

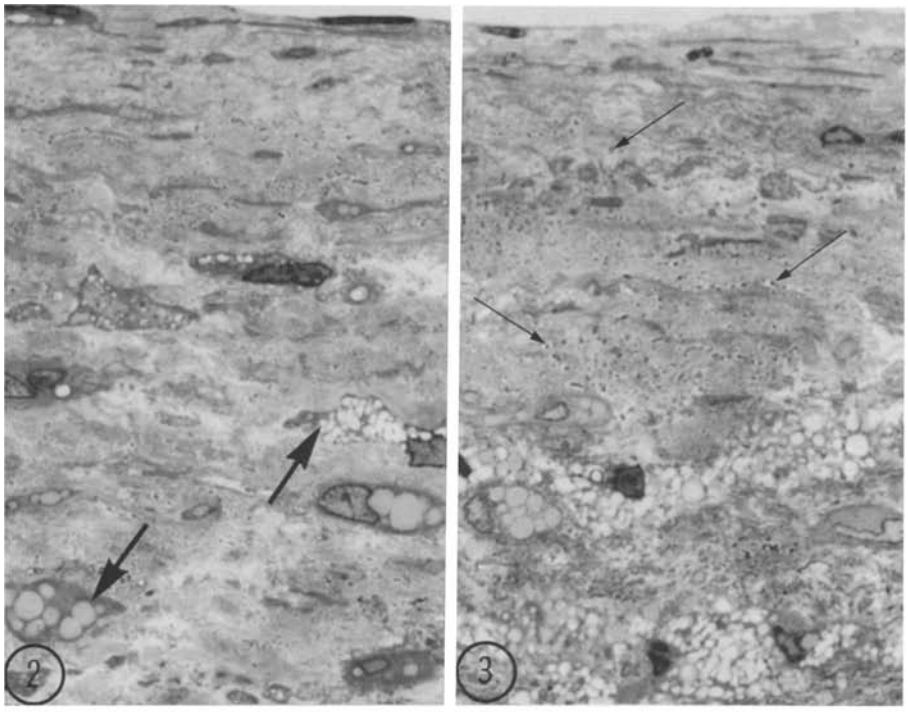


Fig. 2. Light microscopy of an advancing pole of a fatty streak with features similar to those of a fatty dot. Note that fat is largely confined to intimal smooth muscle cells (*arrows*) with little extracellular fat-containing granular material present (*lower half of photograph*). Magnification = × 950

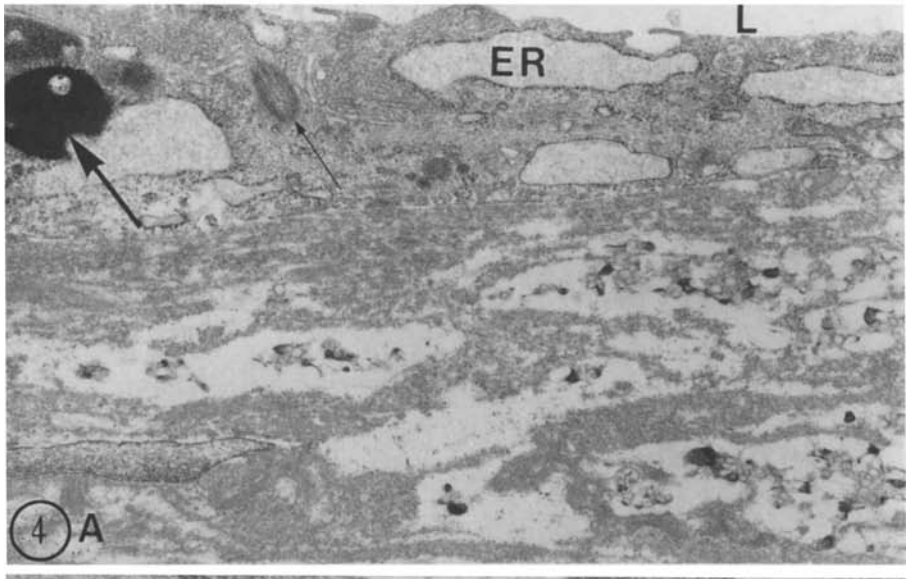


Fig. 3. Light microscopy of a center of a large fatty streak. Fat droplets distend the intimal cells deep in the lesion. The extracellular fat-containing granular material is present in the superficial areas (mid-area of the photograph; few indicated by *arrows*). Magnification = × 950

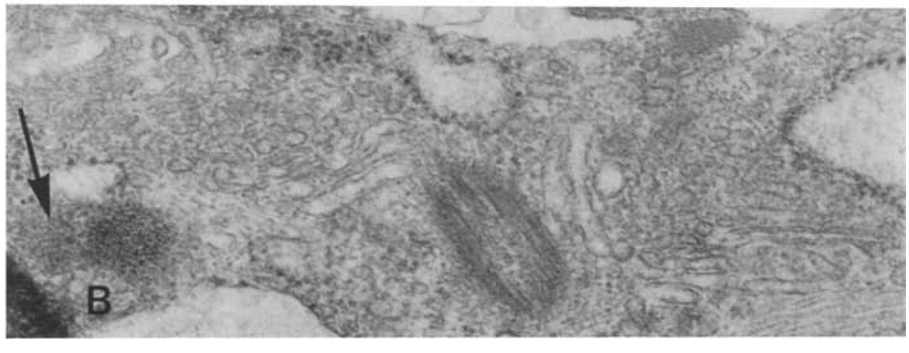
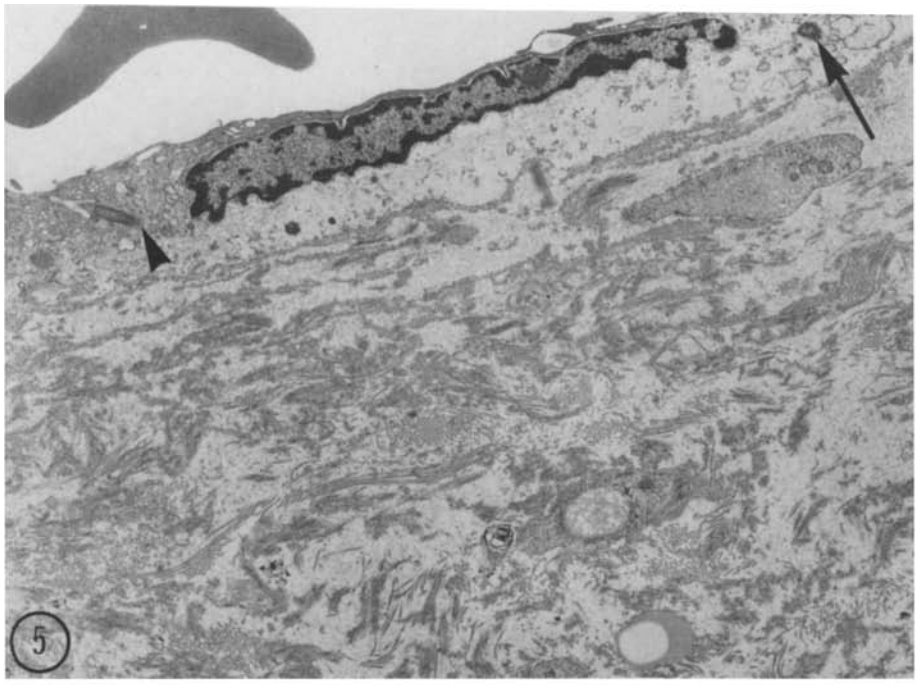


Fig. 4A. Electronmicrograph of superficial layers of a lesion illustrated in Fig. 3. Interstitial spaces contain granular, electron-opaque fat precipitates. The endothelial cell adjacent to lumen (*L*) contains an electron-opaque inclusion (*large arrow*), dilated profiles of endoplasmic reticulum (*ER*) and a centriole (small arrow) surrounded by a prominent Golgi complex. Magnification = × 21,000

Fig. 4B. Details of centriolar region depicted in Fig. 4A. It is uncertain whether the structure with the slight indication of tubular nature (*arrow*) represents a second centriole. Magnification = × 57,000



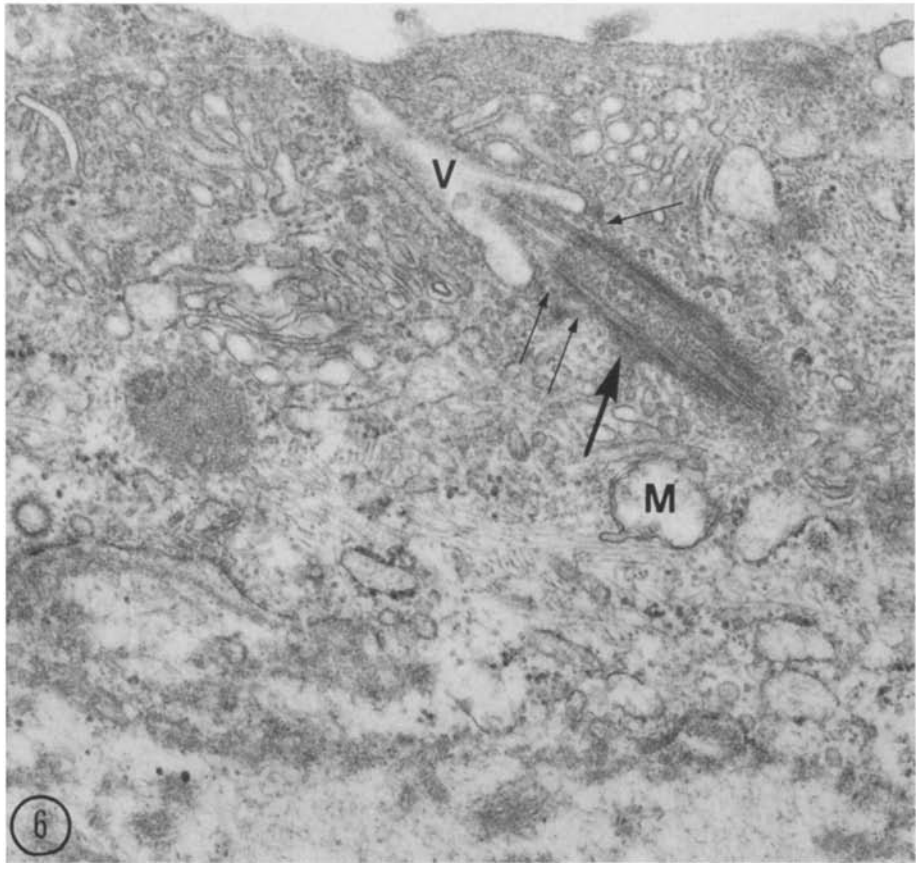


Fig. 5. Electronmicrograph of a lesion shows an endothelial cell with one centriole to the right of the nucleus (*arrow*) and the other, giving rise to a primary cilium, on the left (*arrowhead*). Magnification = ×7,500

Fig. 6. Details of the primary cilium indicated by an arrowhead in Fig. 5. A lateral foot process projects from the mid-portion of the basal body (large arrow). The microtubular nature of the basal body and ciliary shaft (in vacuole = *V*) is evident. Small arrows indicate transitional fibers. Mitochondria (*M*) are not well preserved. Magnification = ×45,000

ma membrane and projected either into an intracytoplasmic vacuole or into the arterial lumen. The shaft was surrounded at its base by a plasmalemmal reflection which formed a recess; the reflected plasma membrane in this area displayed features similar to those of "coated" vesicles or Porter pits (Fig. 6 and Fig. 7-inset). The transitional fibers extended from the invagination to the distal part of

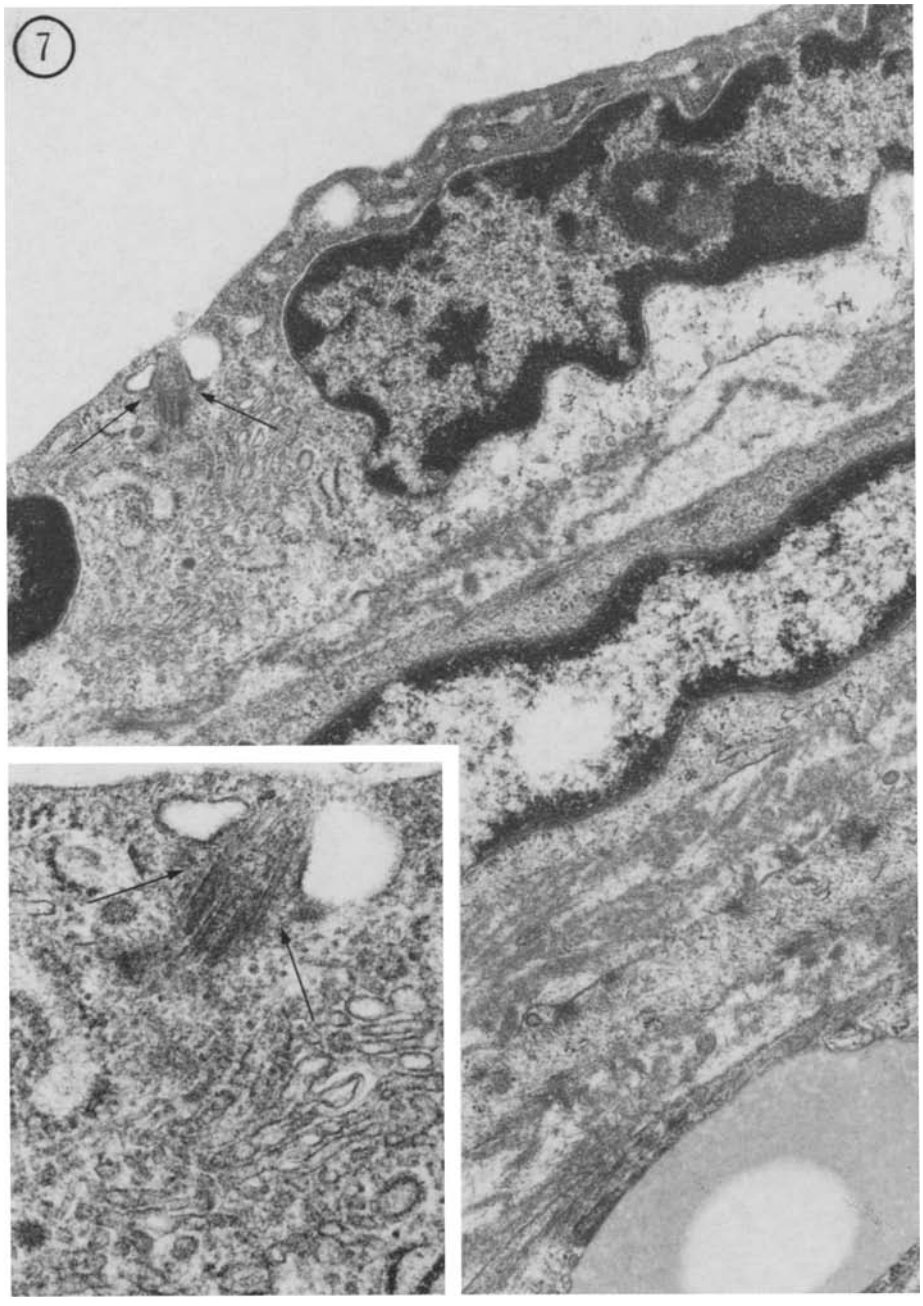


Fig. 7. Electronmicrograph of a lesion shows a "forming" primary cilium between two nuclei. The centriole is surrounded by two large vacuoles in the immediate vicinity of plasma membrane. Note the transitional fibers (*arrows*). Magnification = × 23,000. (*inset*) Higher magnification of the forming primary cilium and its vicinity seen in Figure 7. There is differential staining of microtubules of the proximal segment (*darker*) and that of the distal part (*lighter*) indicating an initiated formation of the latter to a ciliary shaft. Note the transitional fibers (*arrows*). Magnification = × 47,000

the basal body (Figs. 6–8). One triangular foot process projected with its apical part laterally into the cytoplasm from the surface of a more proximal segment of the basal body (Figs. 5, 6 and 8). The basal body was more electron opaque than the ciliary shaft, and microtubular structures parallel to its longitudinal axis, were well visualized. These were in continuity with those of the shaft, but in the latter were less prominent and in some segments, ill-defined. Oblique sections of either part of the cilia showed no central tubules, but on occasion images of "median longitudinal section" (Dingle and Fulton 1966) conveyed the impression that these were present. None of the electronmicrographs examined showed an appropriate transverse section through the shaft of the cilium suitable for the determination of the internal structure, but the assessment of all sections suggested that it was "9+0", i.e., the axoneme characterizing the "primary" cilia rather than the "9+2" axoneme of the classicial cilia (for review see Wheatley 1982).

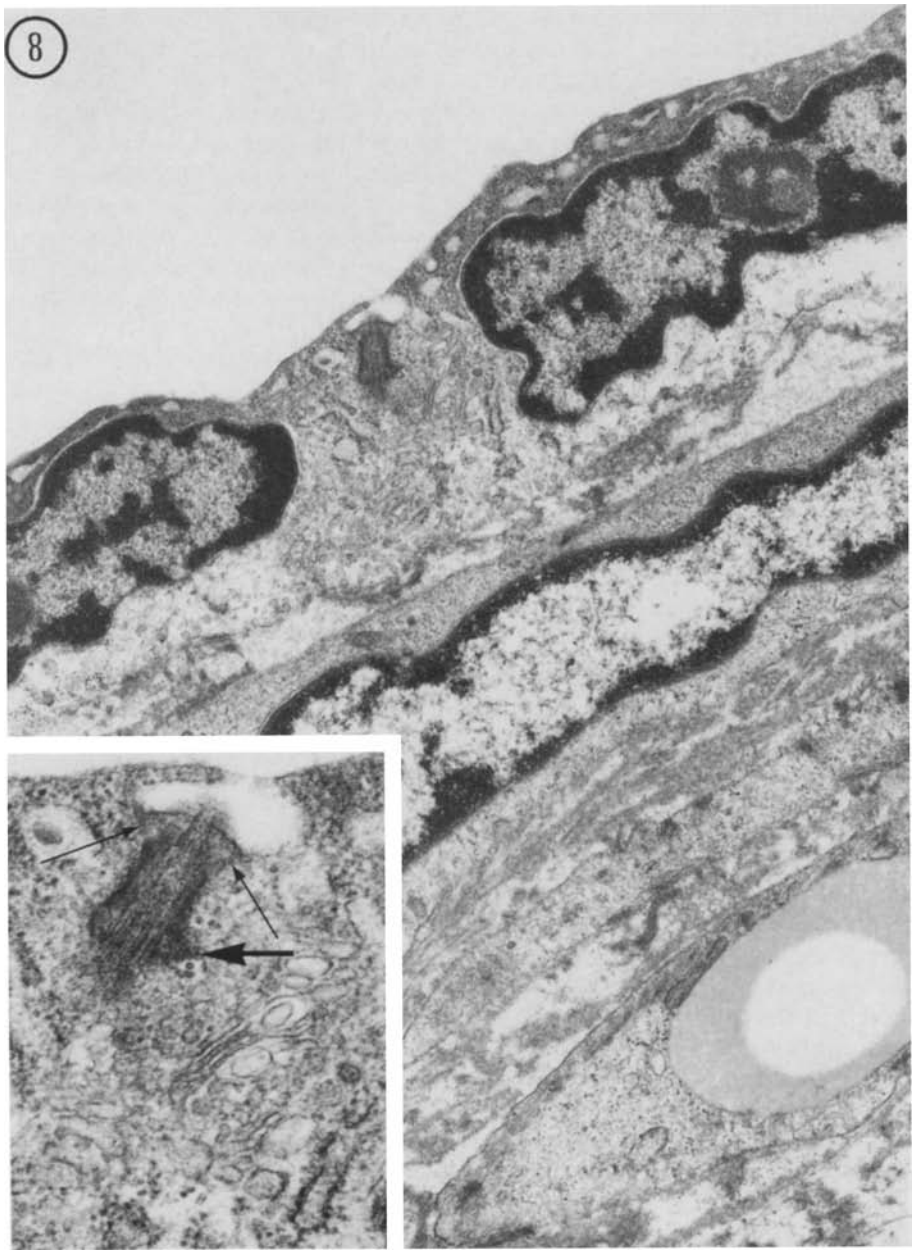


Fig. 8. Electronmicrograph representing a semi-serial section of that depicted in Fig. 7. The two lateral vacuoles (seen in Fig. 7 on either side of the forming primary cilium) fused with each other and with the plasma membrane of which only a thin discontinuous layer remains. The short ciliary shaft projects now into the lumen. Magnification = ×17,500. (*inset*) Details of the primary cilium illustrated in Figure 8. Note the slight transverse periodicity of the short shaft; the lateral foot process (*large arrow*) and transitional fibers (*small arrows*) originate from the basal body. Magnification = ×47,000

Discussion

Present studies show that the endothelial cells of early aortic atherosclerotic lesions (fatty dots and streaks) of young and middle-aged adults contain cilia. Whenever observed, only one cilium was present in a given cell and consisted of a basal body and ciliary shaft. A nearby associated centriole was not visualized, but its occurrence cannot be ruled out. The shaft was either surrounded by dilated cytoplasmic vacuoles (Figs. 7 and 7-inset), contained within one large vacuole (Figs. 5 and 6), or was accompanied at its emergence into the lumen by vestiges of the vacuolar membranes fused with the plasma membrane (Figs. 8 and 8-inset). Thus, the shaft emerged from the main body of the cell in a "recessed" pit (Fig. 8). Structures interpreted as transitional fibers (Figs. 6–8) (Dahl 1963) extended from the pit (or the ivaginated plasma membrane) to the junction of the shaft with the basal body. In the material examined only one, clearly identifiable, lateral foot process projected from the surface of the basal body into the cytoplasm (Figs. 5, 6 and 8). Rootlets extending from

the proximal pole of the basal body into the cytoplasm were not observed, but this does not preclude their presence. The microtubular structure of the ciliary shaft and the basal body were well visualized. Whereas images of transversally-cut shafts were not available for examination, those of the longitudinally-cut cilia were compatible with the "9+0" axonemal structure (for reviews see: Ghadially 1975; Wheatley 1982; Pysher and Neustein 1984).

Most of the ciliary features observed in the present enquiry are in keeping with the characteristics of the "primary" cilia as defined by Sorokin (1962, 1968), and resemble those reported to occur in the endothelia of diverse nature and site. The available information concerning the endothelial cilia is derived largely from studies of the trabeculum (Vegge 1963; Wickham and Worthen 1976) or the cornea (Hogan et al. 1971; Renard et al. 1976; Gallagher 1980) of the eye. At these sites the endothelium may be considered to be specialized as it is not of the ("channeled") vascular type. The vascular ciliated endothelial cells were described in the aorta (Edanaga 1974) and endocardium (Edanaga 1975) of normal rabbits, and in a human capillary of the pineal gland (Yamamoto and Fujimoto 1980). Also, ciliated endothelium was observed in the course of ultrastructural studies of canine muscular and elastic arteries (Corbett 1961).

The minor structural differences between the cilia described in the ocular endothelium (trabecular and corneal) and those observed in the aortic lesions in the present study may be either true and relate to the differences of site and function, or be only apparent. This concerns particularly the presence of lateral extensions from the basal body: four cross-striated arms were present in the corneal endothelium (Gallagher 1980), but only one unstructured (foot) process was observed in the present study. Striated (3–5) "arms" were reported to occur in other "primary" (non-endothelial) cilia (Bessis et al. 1958; Sorokin 1968) but similarly, single lateral foot processes were observed to project from the basal body on numerous other occasions (see for review: Wheatley 1982; Laschi and Baccetti 1983; Sturgess and Turner 1984; Pysher and Neustein 1984).

It is uncertain whether the transitional fibers (Figs. 5–8) (Bessis et al. 1958; Dahl 1963; Gallagher 1980) and the alar sheets (Anderson 1972), both being nine structures extending from the distal end of the basal body to the plasma membrane, are in fact two different terms for the same structures. The definition of the former implies the presence of a cellular invagination (a "pit") which is not always a feature of "single", "solitary" or "rudimentary" cilia.

Cilia were not found in the endothelial cells of the control, normal intimal areas, but their presence cannot be entirely ruled out. Since the diplosomes (a pair of centrioles) were present in the cells in their usual position (adjacent to the nucleus and placed usually in the cytoplasm facing the basement membrane), there was no indication that these were involved in the "preparatory" stages of cilia-formation. This contrasted with the features of centrioles in many endothelial cells overlying the lesions; here, the centrioles (when both visualized) were widely separated, each being present at the opposite poles of the nucleus, or one already "converted" to the basal body of a primary cilium (Figs. 5 and 6).

The striated structures extending between the two centrioles were observed rarely, but only in the normal control endothelium (Fig. 1). Similar structures were reported to occur occasionally in the endothelium (cornea in rabbit, Gallagher 1980) and other cells (choroid in rabbit, Radnot et al. 1970; human myoblasts, Myklebust et al. 1977).

It was suggested on the basis of reconstruction of semiserial sections that in the two to three ladder-like arrangements of the electron-opaque substance (Fig. 1), the rungs of the ladder actually represented oval discs measuring 40×80 nm. These discs were connected to each other and to both centrioles by thin short filaments, and the ladders formed a barrel (Gallagher 1980).

It may be noted that the "primary" cilia of the endothelium in the fatty dots and streaks of human aorta differed in several aspects from cilia observed in the smooth muscle cells (SMCs) of similar lesions (Haust 1986). In the SMCs these organelles were of the "rudimentary" (Gardiner and Rieger 1980) variety, and not "primary" cilia. Since more than one basal body (with or without a visible shaft) was encountered in the SMCs, it was concluded that a given SMC in human lesions contained more than one cilium. As in the herein reported endothelial cells, the cilia in the SMCs were in most instances not accompanied by a nearby centriole. With the exception of the last feature, the endothelial cilia of human aortic fatty dots and streaks resembled more those present in the SMCs of similar, experimentally produced, lesions in the rabbit (Haust 1984) than those of man (Haust 1986).

It is difficult to reconcile the above differences in appearance of cilia in the endothelium and SMCs of the same or similar lesions. Perhaps rele-

vant to this problem are the experiments carried out on corneal endothelium (Gallagher 1980) where, – depending on the physiological state of the endothelial cell layer –, cilia appeared to project from the cell surface at a preferred angle. In fresh tissue maintaining its normal thickness the angle between the cilium and the endothelial surface had a mean value of $23.2° \pm 5.4°$. When corneal swelling followed injury, the angle changed to $45.8° \pm 5.9°$; now, a few basal bodies were perpendicular to the surface and the ciliary shaft emerged directly from the surface of the cell rather than originating from the depth of a "pit", i.e., within a plasmalemmal invagination (Gallagher 1980). On that basis one might speculate that the SMCs of human atherosclerotic lesions are more edematous than are the overlying endothelial cells and the SMCs under the conditions of a short-term (4 weeks) experimentation (Haust 1984). Alternatively, the presence of "primary" cilia in some cells and largely "rudimentary" forms in another cell type in the same lesions may reflect a difference in cellular activity or response to injury. It has been proposed that ciliary formation results from a stimulation of centriolar reproduction without subsequent mitosis (Milhaud and Pappas 1968), and that there is an inverse relation between the disappearance of centrioles and formation of the (non-classical) cilia (Rash et al. 1969). Might the difference between the cilia in endothelium and SMCs imply that in the diseased intima the rate of mitotic activity of the SMCs is greater than that of the endothelia? It is conceivable that the process of ciliogenesis via the intracytoplasmic vacuole-formation (primary cilia) is slower than that "directing" the centrioles to the cell membrane for rudimentary cilia formation. This highly speculative possibility would also have to apply to the rate of SMCs-proliferation in experimental lesions of rabbits.

Whereas some work supports the inverse relation between mitosis and formation of the non-classical cilia in many types of cells, other data do not. Cilia were shown to be present in rapidly dividing cells (Fonte et al. 1971), and ciliated centrioles were found in quiescent cells arrested in G1 (Tucker and Pardee 1979). These centrioles lost their cilia upon stimulation to enter DNA-synthesis. The cilia regenerated within 6–8 h, but were lost again with the onset of DNA-synthesis at 12–24 h. The results of the above study suggested to some investigators that many centrioles form cilia during G1, possibly utilizing prior to mitosis, the microtubules for formation of the spindle apparatus. However, the observation that primary cilia were resorbed in the early phases of mitosis (Rieder et al. 1979), and that there was simultaneous presence of the microtubules and the mitotic spindle, probably invalidate the latter hypothesis.

Of the several theories postulating that these unusual cilia have a chemoreceptor (Munger 1958) or pressure sensory (Barnes 1961) function, or that they represent evolutionary remnants (Latta et al. 1961), none explains satisfactorily all the characteristics of these organelles, and all were refuted (Milhaud and Pappa 1968).

It has become apparent only recently that the non-classical cilia are not an incidental finding but rather are widespread, occurring in a great variety of tissues, and are more numerous in a given tissue than believed previously. For example, a primary cilium is present in each corneal endothelial cell (Gallagher 1980). It must be surmised, therefore, that they may have a more significant function than was realized to date, and they should cease to be considered as a curiosity only.

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