Unfortunately, Figs. 5 and 9 have been mixed up.

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THE NUCLEAR ENVELOPE AND THE ORGANIZATION OF THE PORE COMPLEXES

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INTRODUCTION

One of the most distinctive features of eukaryotic cells is a double-membrane layer, the nuclear envelope, which encloses the chromatin thus separating the genome from the cytoplasm. Electron micrographs directly illustrate the efficacy of the nuclear envelope in segregating nuclear and cytoplasmic constitutents. During mitosis, in the absence of the nuclear envelope, cytoplasmic constitutents such as mitochondria, ribosomes, endoplasmic reticulum (ER) and various classes of vesicles occur in the immediate vicinity of the individual chromosomes (Fig. 1a). In contrast, during interphase the nuclear envelope efficiently excludes these cytoplasmic organelles from the nucleoplasm (Fig. 1b). This exclusion principle is seen with particular clarity in oocytes which accumulate large quantities of ribosomes for future embryonic growth and development. An example is provided in Figure 1c. Although assembly of ribosomes takes place in the nucleolus, mature ribosomal particles are recognised exclusively in the cytoplasm (Fig. 1b; see also below).

Clearly, the nuclear envelope acts as a structural barrier between nucleoplasm and cytoplasm. Nonetheless extensive exchange of molecules and larger particles takes place in either direction. The nuclear envelope is uniquely designed to fulfil both functions since inner and outer nuclear membranes are interrupted at numerous sites by pore-like discontinuities representing a multitude of plasmatic channels between both compartments. In fact, Feldherr and colleagues could demonstrate by microinjection of various protein and RNA molecules coupled to gold particles into amphibian oocytes that nucleocytoplasmic transport processes occur through the pore complexes (Feldherr et al., 1984; Dworetzky and Feldherr, 1988; see also the article by Feldherr and Dworetzky in this volume)

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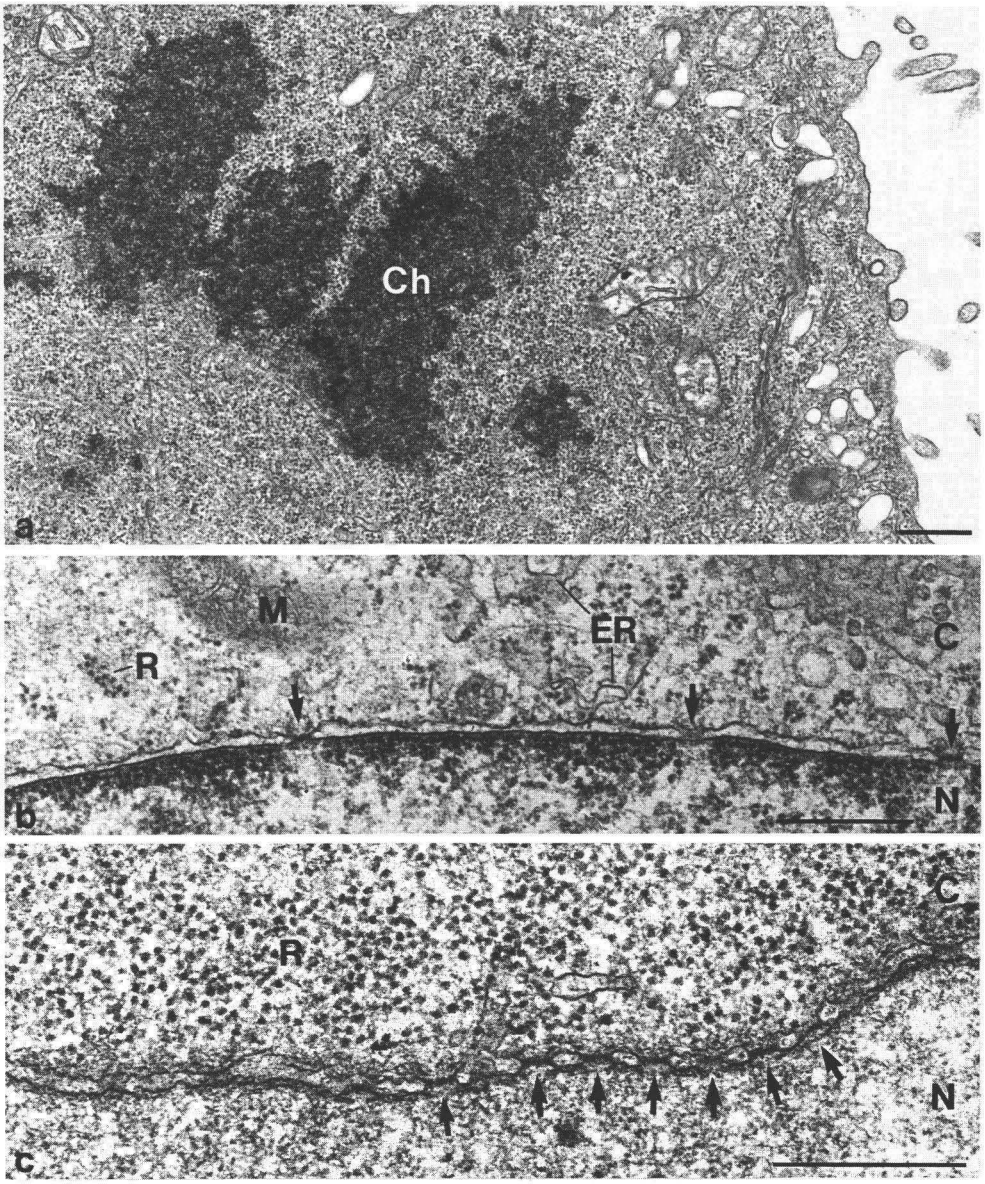

Fig. 1. The nuclear envelope as a barrier between nucleoplasm (N) and cytoplasm (C). During mitosis, in the absence of the nuclear envelope, both compartments are intermingled (a; cultured Xenopus laevis cell; Ch, chromosome). During interphase, however, cytoplasmic components such as ribosomes (R), mitochondria (M) and membranes of the endoplasmic reticulum (ER) are excluded from the nucleus as seen in a cultured rat cell (b) and oocyte of the water beetle Dytiscus marginalis (c). Pore complexes are denoted by arrows in (c). Bars indicate 0.5μm.

However, it should not be overlooked that other mechanisms of nucleocytoplasmic exchange independent of the routes provided by the pores might exist. An example is illustrated in Figure 2. Elements of the nucleolus of a cultured Xenopus cell are apparently extruded into the cytoplasm by a blebbing mechanism. In the final stage of this process the nuclear envelope disintegrates thus exposing the nucleolar material to the cytoplasm (Fig. 2; for literature describing similar phenomena see the review articles by Kessel, 1973; Wischnitzer, 1973; Franke and Scheer, 1974).

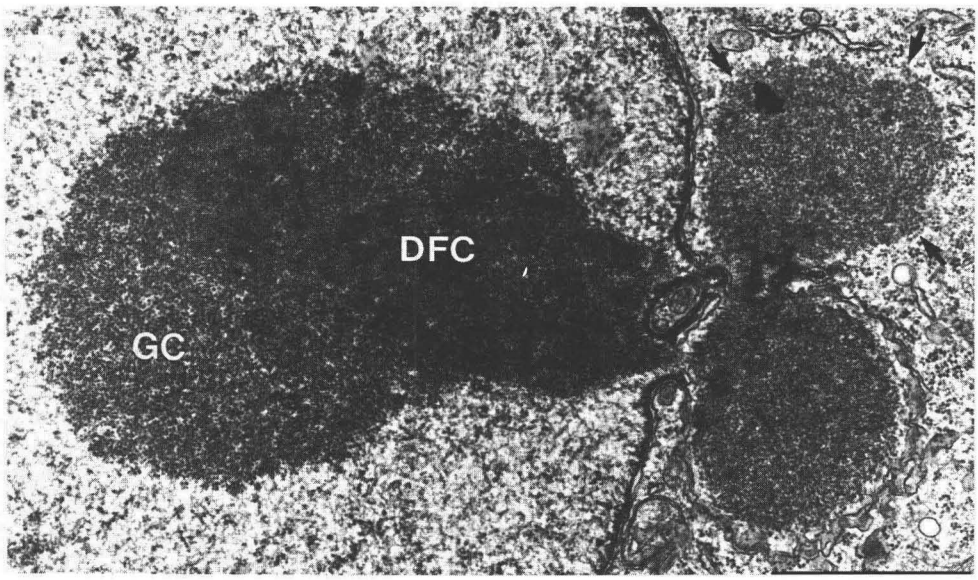

Fig. 2. Extrusion of nucleolar material from the nucleus of a cultured Xenopus laevis (A6) cell by a blebbing mechanism. In later stages of this process the nuclear envelope disappears around the extruded material (arrows). GC, granular component; DFC, dense fibrillar component of the nucleolus. Bar indicates 0.5μm.

INNER AND OUTER NUCLEAR MEMBRANE

The two juxtaposed nuclear membranes enclose an intermembranous space with a luminal width of usually 10-30nm, the perinuclear cisterna (Fig. 3a, b). In contrast to other membrane cisternae such as the ER, the parellel nuclear membranes are joined frequently at specific sites to form circular transcisternal pores (Fig. 3a, b). The outer

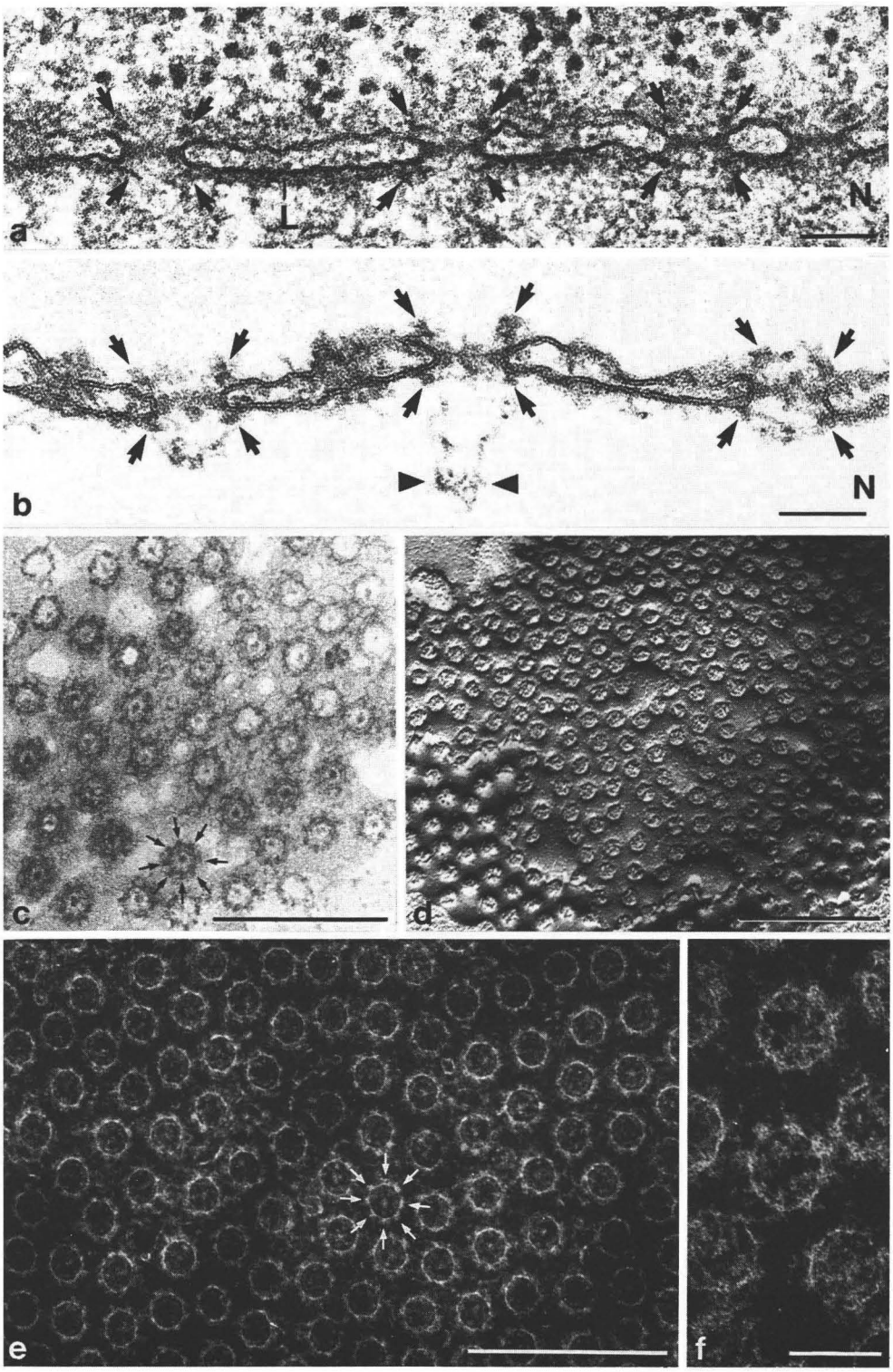
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Fig. 3. Ultrastructure of the nuclear pore complex. Transverse sections through the nuclear periphery of a growing oocyte of Dytiscus marginalis (a) and nuclear envelope isolated from a Xenopus laevis oocyte (b). The annulus subunits on either side of the pores are indicated by arrows (a, b). The inner nuclear membrane in (a) is lined by a distinct layer, the lamina (L). Long fibrils extend from the inner annulus (arrowheads in b). Note the unit membrane aspect of both the inner and outer nuclear membranes (a, b). In sections tangential to the nucleus of a Pleurodeles oocyte the membranous pore perimeter with attached eight subunits (e.g. at the arrows) is recognized as well as central elements (c). Frozen-fractured nuclear envelope of a Xenopus laevis oocyte showing high pore density (d). Negatively stained nuclear envelopes from oocytes of Xenopus laevis (e) and Triturus alpestris (f). Eight symmetrically arranged subunits are associated with the pore margins (e.g. at the arrows in e). The pore lumen is occupied by a central granule (e) and material projecting from the pore wall, often arranged in an octagonal symmetry (f). N, nucleoplasm or nucleoplasmic side, respectively. Bars indicate 0.1μm (a,b,f) and 0.5μm (c-e).

nuclear membrane, facing the cytoplasm, often bears ribosomes and polyribosomes, probably involved in synthesis of secretory proteins, whereas the inner nuclear membrane is intimately associated with a proteinaceous layer, the lamina (see below) which in certain cell types can be directly visualised in situ (Fig. 3a). In view of the frequent continuities of the outer nuclear membrane with membranes of the ER (for example see Franke and Scheer, 1974) it is not surprising that both membrane types share numerous morphological and biochemical properties (for reviews of the biochemical composition and enzyme activities of nuclear membranes in comparison with that of other cellular membranes see Franke, 1974; Kasper, 1974; Harris, 1978). In fact, in certain cell types such as avian erythrocytes which retain only minute amounts of ER during their final stage of differentiation, the nuclear envelope seems to function as a kind of "minimum ER" (see Franke and Scheer, 1974).

THE PORE COMPLEX

a) Structural Organisation

The characteristic components of the nuclear envelope, the pore complexes, have received much attention since the early days of electron microscopy (EM) due to their intriguing symmetrical and highly ordered substructure and in view of

their presumed role for nucleocytoplasmic interactions. The architecture of the pore complexes from a large variety of plant and animal species has been the subject of a number of review articles (e.g. Feldherr, 1972; Kessel, 1973; Wischnitzer, 1973; Franke, 1974; Franke and Scheer, 1974; Maul, 1977; Franke et al., 1981). All these studies suggest that pore complexes are designed according to a universal principle throughout the eukaryotes (see, however, Unwin and Milligan, 1982).

A variety of EM methods such as ultrathin sectioning, freeze-etching and negative staining can be used to study the structure of pore complexes (Fig. 3a-f). The membranous component of the pore forms a cylindrical channel with an inner diameter of 60 to 90nm which traverses the perinuclear cisterna (Fig. 3a,b). The circular pore walls are seen with particular clarity in face-on views of negatively stained isolated nuclear envelopes (Fig. 3e,f). Each membrane channel is associated with a number of nonmembranous structures which give the pore complex its characteristic appearance. The most prominent structures are two rings or annuli situated on either pore margin, each one composed of eight symmetrically arranged subunits with diameters ranging, depending on the specific type of preparation, from 10 to 25nm (Fig. 3a-c, e,f). Cross-sections of isolated nuclear envelopes from amphibian oocytes clearly reveal the presence of annulus subunits on both the cytoplasmic and the nucleoplasmic pore perimeter (Fig. 3b; for further examples see Franke and Scheer, 1974). It has been repeatedly speculated that the annulus subunits might represent ribosomes (Unwin and Milligan, 1982; for earlier literature see Franke and Scheer, 1974). Several lines of evidence strongly argue against this view as discussed in detail (Franke and Scheer, 1974). Furthermore, antibodies to the ribosomal protein S1 which bind to cytoplasmic ribosomes as well as nuclear preribosomal particles (Hugle et al., 1985) do not decorate the annulus subunits (unpublished) and the characteristic ribosomal proteins are not detectable in protein gels of nuclear envelopes isolated from Xenopus laevis oocytes (Fig. 6, lane 3). Inner and outer annulus are not equal since thin fibrils, often forming long hollow cylindrical extensions with transverse fibers, are attached to the annulus facing the nucleoplasm (Fig. 3b, 8a). These inner annulus-attached fibrils are often associated with RNP aggregates (Fig. 5d; 7d). Similar pore fibrils also occur in somatic cells but here they are often obscured by the condensed chromatin in the nuclear periphery (for examples see Franke and Scheer, 1974; Maul, 1977). Fibrils attached to the outer annulus are much

shorter and probably represent fibril-coil transitions of the subunits (e.g. Fig. 3a, b). The pore lumen is filled with eight radially arranged cones or spokes projecting from the pore wall. Frequently, though not always, a particle or rod is located in the pore center (central granule; Fig. 3c,e).

A diagram illustrating the structural components of the pore complex is presented in Figure 4. It should be mentioned that pore complexes of identical architecture are also found in cytoplasmic and nucleoplasmic annulate lamellae with the only exception that they lack the long fibers attached to the inner annulus (for review see Kessel, 1983).

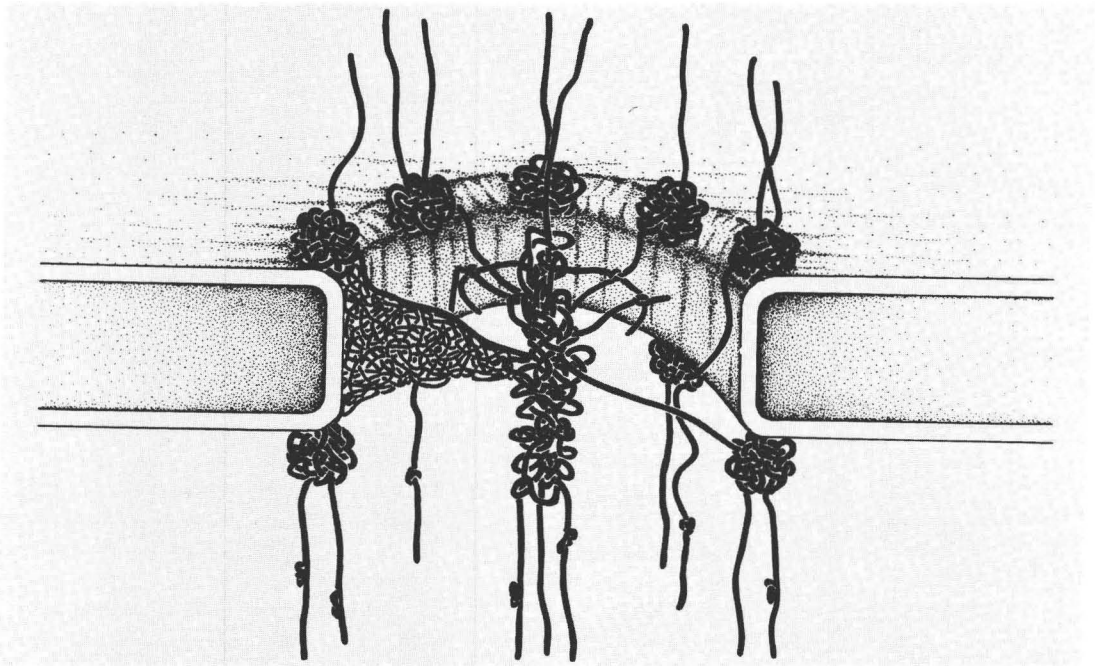

Fig. 4. Model view of the pore complex. For clarity, only one of the cones or spokes projecting from the pore wall into the lumen is shown. The lamina has not been included in this model. From Franke and Scheer (1974).

b) Number and Frequency of Nuclear Pores

The total number and frequency of pore complexes can vary largely in different cell types reflecting to some extent the specific transcriptional activity of a given cell (see Maul, 1977). Thus, the number of pores per square micron nuclear surface ranges from about 3 in mature avian erythrocytes up to 70 in growing amphibian oocytes. The latter values means that

about one quarter of the total nuclear surface is occupied by pores. Total pore numbers vary from a few hundred (avian erythrocytes) to about 50 millions (giant nuclei of amphibian oocytes).

c) Morphological Aspects of Transport Processes Through the Pores

Two experimental approaches allow direct visualisation of transport processes through the pore complexes. Certain gene products such as the RNP granules derived from the Balibiani rings of Chironomus polytene chromosomes can be identified by their characteristic size and shape in ultrathin sections of larval salivary glands (Stevens and Swift, 1966; Skoglund et al., 1983; 1986). When these 50nm large spherical particles approach the pores they unravel into about 15 to 20nm thick rod-like structures and migrate through the very center of the pores (Stevens and Swift, 1966). Massive transfer of particulate material is also observed in growing oocytes of a variety of species (see Kessel, 1973). For instance, in previtellogenic oocytes of Xenopus and other amphibian species numerous large entities occur in the perinuclear zone often in direct structural continuity with the pore complexes (Fig. 5a). This material which seems to be extruded from the nuclei undergoes marked conformational changes during the pore passage (Fig. 5b,c). Such studies directly illustrate that not all of the pore lumen is accessible to transport events but rather a relatively narrow central channel with a diameter of about 20nm, i.e. approximately one third of the diameter of the pore lumen. Frequently aggregates of RNP material are seen in association with the nucleoplasmic pore-fibrils (Fig. 5d; 7d). Such connections appear to be relatively stable as they are retained with isolated nuclear envelopes. It is tempting to compare these fibrils with tentacles of a medusa that fish out RNP complexes from the nucleoplasm thus guiding them to the pores.

Very little is known about the morphological aspects of nucleocytoplasmic transfer of ribosomes. It is generally assumed that the granular component of nucleoli reflects the presence of preribosomal particles in a relatively advanced stage of maturation (Hadjiolov, 1985). However, when the ribosomal particles are released from the nucleolar cortex they apparently unfold into some kind of "transport fibrils" and it is not before their transfer into the cytoplasm that they coil up again into the mature ribosomal particles (Fig. 1b, c; 3a). It is remarkable that this final maturation step which might involve rRNA processing and/or assembly with

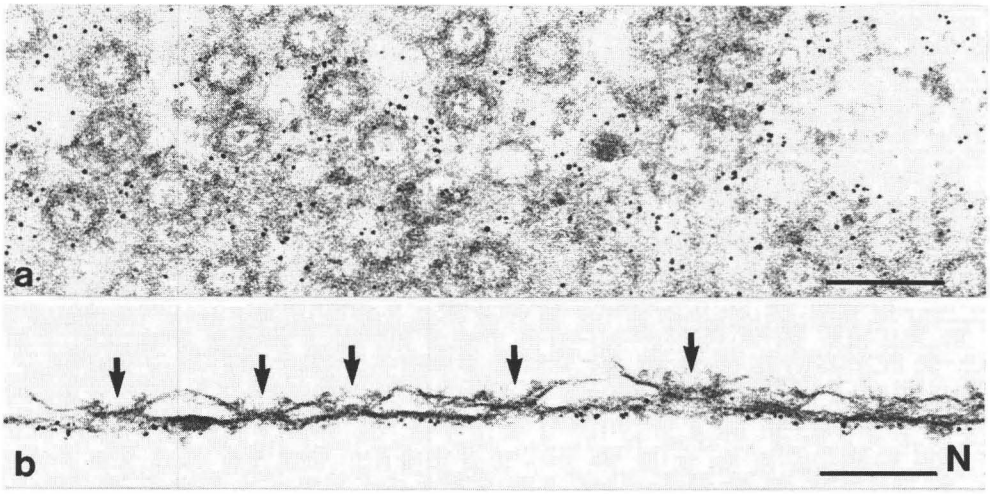

Fig. 5. Morphological aspects of nucleocytoplasmic transport in amphibian oocytes (a, Xenopus laevis; b-d, Triturus alpestris). In previtellogenic oocytes, perinuclear aggregates are often in direct structural continuity with the pores (a). During the pore passage, particulate RNP-material transiently assumes a rod-like conformation with a diameter of 10-15nm (b; the arrows denote the annulus subunits). A similar unfolding process is shown in (c). RNP material bound to the annulus-associated fibrils (arrow) is seen in (d). N, nucleoplasm. Bars indicate 0.5μm (a) and 0.1μm (b-d).

specific ribosomal proteins occurs at some distance from the cytoplasmic face of the pore complexes (Fig. 3a).

The second approach to visualise transport processes is based on the use of electron-dense colloidal tracers. By coating variously sized colloidal gold particles with the karyophilic protein nucleoplasmin or different RNA species, Feldherr and associates could convincingly demonstrate that the trans-pore migration of this material is restricted to a central channel of approximately 20nm in diameter (Feldherr et al., 1984; Dworetzky and Feldherr, 1988; see also the article by Feldherr and Dworetzky in this volume). One of the initial steps in nuclear uptake of proteins might be a transient association with the pore fibrils extending from the outer annulus subunits into the cytoplasm (Richardson et al., 1988).

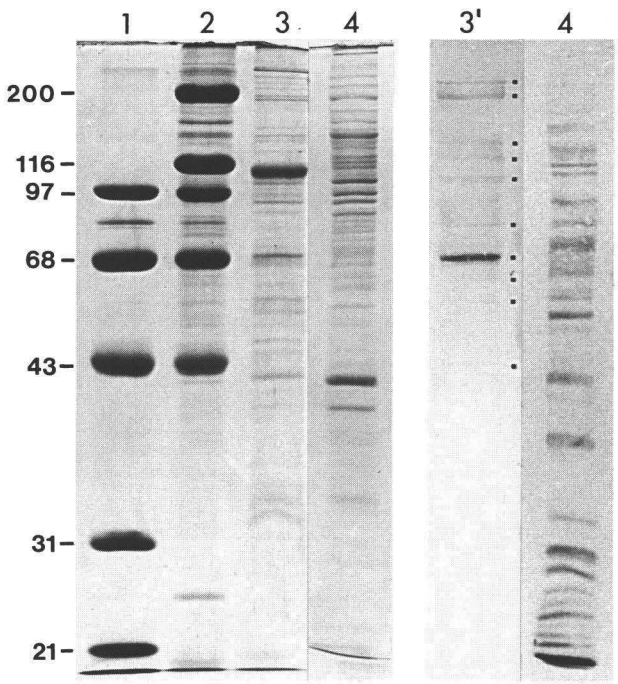

Fig. 6. Gel electrophoretic analysis of nuclear envelope proteins and identification of WGA-binding glycoproteins. Proteins from 200 manually isolated nuclear envelopes from Xenopus laevis oocytes were analyzed by SDS-polyacrylamide gel electrophoresis and Coomassie-Blue staining (lane 3). The most prominent band with a M_r of ca.110 kD represents contaminating yolk protein. For comparison, the polypeptide pattern of the low speed pellet (10 000 g x 5 min) of 80 nuclear contents is shown in lane 4 (Coomassie-Blue staining). Molecular mass markers (M_r values indicated in kD) were run in lanes 1 and 2.
Proteins from gels run in parallel were electrophoretically transferred to nitrocellulose and probed with WGA-peroxidase. WGA-binding proteins were identified using 4-chloro-1-naphtol in the presence of H_2O_2 as substrates. The results are shown in lanes 3′ (400 isolated nuclear envelopes) and 4′ (low speed pellet from 160 nuclear contents). Major glycoprotein bands of the nuclear envelope fraction are denoted by black dots in lane 3′ (apparent molecular weights are, from top to bottom (in kD), 210, 190 (double band), 145, 120, 100, 80, 68, 63, 56, 40). In contrast the glycoprotein pattern of the sedimentable material of the nuclear content is clearly different and much more complex as compared to that of the nuclear envelopes (lane 4′).

d) Changes in Pore Complex Architecture Might be Related to Inhibited Nucleocytoplasmic Transfer

During the terminal differentiation process of avian erythrocytes which involves a progressive inactivation of the genome, the pore complexes undergo extensive structural modifications. In ultrathin sections as well as in negatively stained preparations annulus subunits and pore fibrils are no longer detectable. The only substructure recognized is material inside the pore lumen (see Franke and Scheer, 1974). In hen erythrocytes some residual synthesis of hnRNA is detectable which can be considerably stimulated by incubation of the red blood cells in artificial culture medium (Zentgraf et al., 1975). As shown by light and EM autoradiography the newly synthesized RNA is not transported to the cytoplasm (Zentgraf et al., 1975). It is conceivable that the exclusion of the nuclear RNA from nucleocytoplasmic transport is related to the observed changes of pore complex architecture.

e) Proteins of the Nuclear Pore Complex

Due to the presence of a continuous lamina which tightly interconnects all pores of a given cell nucleus (see below), it has been so far impossible to isolate pore complexes proper. Therefore, identification of a specific protein as a pore constituent requires its positive localization within this structure. Pore complexes are predominantly proteinaceous structures with a molecular mass of ca. 10^8 (Krohne et al., 1978). The protein pattern of manually isolated nuclear envelopes from Xenopus laevis oocytes which are highly enriched in pore complexes (see Fig. 3b, e) is presented in Figure 6 (Lane 3'). The polypeptides with M_r values ranging from 40 to 210 kD are specific for the nuclear envelope (see also Krohne et al., 1978; Franke et al., 1981) and clearly different from those of the separated nuclear content (Fig. 6, lane 4). Some proteins disappear after extraction of the nuclear envelope fraction with Triton X-100 suggesting that they represent integral nuclear membrane proteins. An even more simplified pattern is obtained after sequential extraction of nuclear envelopes with high salt and Triton X-100 (see Fig. 7 in Franke et al., 1981). However, since it is unclear to what extent genuine pore complex proteins are extracted along with membrane proteins (see, e.g. Finlay et al., 1987) this approach is of limited value to relate specific polypeptides to the pore complex.

So far, only a few pore complex proteins have been identified. Gerace and associates (1982) have described a Con A-binding glycoprotein of M_r 190 kD from rat liver (gP190)

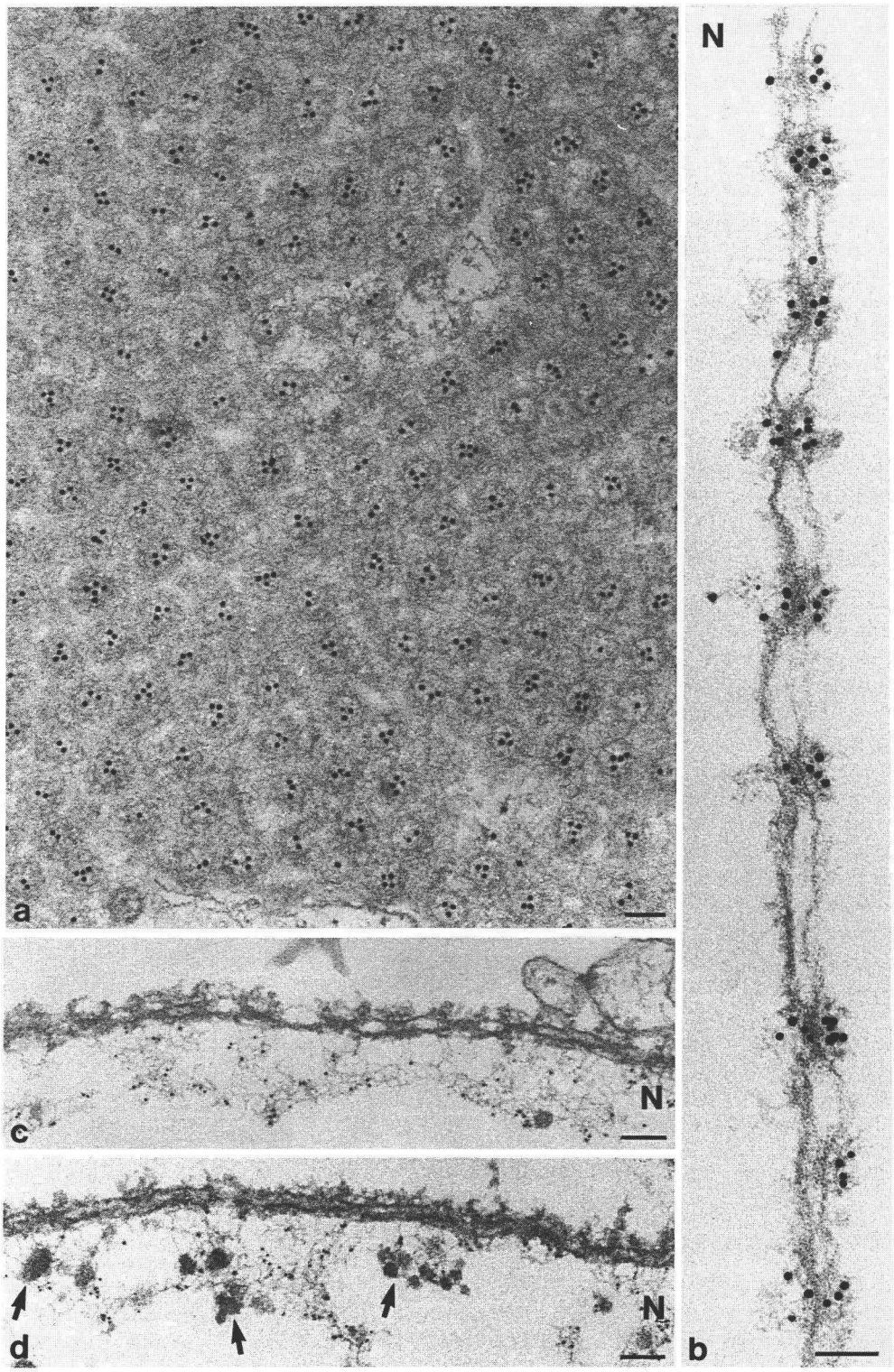
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Fig. 7. Electron microscopic localization of pore complex constituents. Manually isolated nuclear envelopes from Xenopus laevis oocytes were incubated with WGA coupled to 10nm gold, fixed and processed for EM. WGA binds exclusively to the inner pore material as observed in tangential (a) and transverse (b) sections. Control samples prepared in the presence of 250 mM GlcNAc were free of gold particles. A human autoimmune serum of hitherto unknown specificity decorates selectively the inner annulus-attached fibrils (c,d). The bound antibodies were visualised by secondary anti-human antibodies coupled to 5nm gold particles. Note RNP aggregates bound to the pore fibrils (arrows in d). Bars indicate 0.1μm.

which localizes to the nuclear pore complexes. A related protein of M_r 188 kD has recently been isolated from the nuclear matrix-pore complex-lamina fraction of Drosophila melanogaster embryos (Filson et al., 1985). By raising monoclonal antibodies against Triton-extracted rat liver nuclei, Davis and Blobel (1986) have identified another nuclear pore complex glycoprotein of M_r 62 kD (p62; reacting with the lectin WGA but not with Con A). Later these authors noted that p62 is a member of a family of glycoproteins all of which contain terminal O-linked N-acetylglucosamine (GlcNAc) residues (Davis and Blobel, 1987). Glycoproteins with this novel form of GlcNAc-linkage have been shown to be particularly enriched in cytosolic and nuclear envelope fractions (Hold and Hart, 1986). Several monoclonal antibodies have recently been described in the literature which recognize all members of this glycoprotein family from rat liver nuclear envelopes or different subsets therefrom, indicating that the common 0-linked sugar moiety is part of the immunological determinant (Holt et al., 1987; Park et al., 1987). The same protein family was identified when rat liver nuclear envelopes were labelled by galactosyltransferase (Holt et al., 1987) or when total nuclear envelope proteins, after electrophoresis and transfer to nitrocellulose, were probed with the lectin WGA (Hanover et al., 1987; Davis and Blobel, 1987). Definite localization of these glycoproteins termed "nucleoporins" to the plasmatic faces of the nuclear pores was achieved by EM localization methods using either antibodies (Snow et al., 1987; Park et al., 1987) or ferritin-labelled WGA (Hanover et al., 1987; Finlay et al., 1987).

The pattern of WGA-binding proteins of manually isolated nuclear envelopes from Xenopus laevis oocytes is presented in Figure 6 (lane 3′). From a comparison with the corresponding

Coomassie-Blue stained gel (lane 3) it is evident that only a certain subset of the total proteins binds WGA-peroxidase. This pattern is remarkably similar to that of liver nuclear envelopes (e.g. Holt and Hart, 1986; Holt et al., 1987; Hanover et al., 1987). The most prominent WGA-positive band of the Xenopus nuclear envelopes with an apparent M_r of 68 kD (Fig. 6, lane 3') is probably related to the abundant rat liver glycoprotein with M_r values reported from 62 to 67 kD (Holt and Hart, 1986; Finlay et al., 1987; Schindler et al., 1987; Hanover et al., 1987; Davis and Blobel, 1987). The 68 kD glycoprotein must be different from the comigrating lamin L_{III} (L_{III}, the only lamin protein of Xenopus oocytes, has also an apparent M_r value of 68 kD; see Benavente et al., 1985; Krohne and Benavente, 1986) since both proteins show a completely different topological distribution (see below; cf. also Finlay et al., 1987). A by far more complex pattern of WGA-positive glycoproteins is revealed by the sedimentable material of isolated nuclear contents from Xenopus oocytes (Fig. 6, lane 4') indicating that proteins of lampbrush chromosomes, amplified nucleoli, larger RNP particles, etc. are extensively glycosylated.

After incubation of "native" nuclear envelopes from Xenopus oocytes with WGA-gold followed by preparation for EM ("pre-embedding method"), WGA binds exclusively to the inner pore material. This is shown in tangential (Fig. 7a) and transverse (Fig. 7b) sections. Other nuclear pore constituents such as the annulus subunits and the nucleoplasmic pore-attached fibrils appear to be essentially free of gold particles indicating that their protein constituents are not at all or only weakly glycosylated (Fig. 7b). The location of the GlcNAc-linked glycoproteins within the pore lumen suggests that these proteins might be somehow involved in the nucleocytoplasmic traffic. In fact, it has been recently demonstrated that WGA, both *in vivo* and *in vitro*, completely inhibits nuclear protein transport (Finlay et al., 1987; Yoneda et al., 1987; Dabauvalle et al., 1988; Newmeyer and Forbes, 1988).

The resolution of our EM localization provides sufficient sensitivity to locate probes of different specificities to the various pore constituents. For instance, human autoantibodies of hitherto unknown specificity decorate exclusively the inner annulus-attached fibrils which extend deeply into the nucleoplasm and often form a loosely interconnected network with bound RNP particles (Fig. 7c,d).

NUCLEAR LAMINA

Nuclear pore complexes are embedded in the nuclear membranes not as isolated entities but are all interconnected by a fibrillar meshwork of protein filaments which form a layer ("lamina") closely apposed to the nucleocytoplasmic surface of the inner nuclear membrane (for reviews see Gerace, 1986; Krohne and Benavente, 1986). The lamina can be visualized in situ in some specific cell types as a discrete layer lining the inner nuclear membrane (Fig. 1c). Usually, however, isolated nuclear envelopes have to be extracted with high salt solutions and/or non-ionic detergents in order to unveil the lamina. As shown in Figure 8a, the resistant supramolecular assembly consists of pore complexes with their typical architecture and the lamina layer. Face-on views show that the lamina contains a closely packed, in places almost regular, orthogonal network of ca. 10nm thick fibrils (Fig. 8b; see also Aebi et al, 1986). Under mechanical stress this meshwork can be considerably expanded (Fig. 8c). Disruption of the membranes and pore-connecting lamina fibrils as it might occur in spread preparations of amphibian oocyte nuclei ("Miller-spreads") can lead to the release of individual pores (Fig. 8d). The single pore rings are surrounded by numerous short stretches of fibrils, probably representing remnants of the lamina meshwork (Fig. 8d).

The lamina is composed of a small family of related proteins, the lamins (for recent reviews see Gerace, 1986; Krohne and Benavente, 1986). Recently it became clear by sequence analysis of cDNA clones that the lamins share extensive homologies with intermediate filament proteins (for reviews see Gerace, 1986; Franke, 1987; McKeon, 1987). In addition, it has been shown that lamin subunits can assemble in vitro into long filaments of about 10nm thickness which are indistinguishable from the fibrillar constitutents of the lamina (Aebi et al., 1986).

Lamins are not involved in the organisation of the pore complex structure. This is clearly shown by immunogold EM (Figs. 9a,b). When isolated nuclear envelopes from Xenopus oocytes are incubated with antibodies to lamin L III (directed against the only lamina protein in this cell type; cf. Benavente et al., 1985; Krohne and Benavente, 1986) followed by secondary gold-coupled antibodies, the interpore regions are decorated by the gold particles (Fig. 9a). In transverse sections the gold particles are lined up along the nucleoplasmic face of the inner nuclear membrane, i.e. the site of the lamina, but leave out the pore complexes (Fig. 9b).

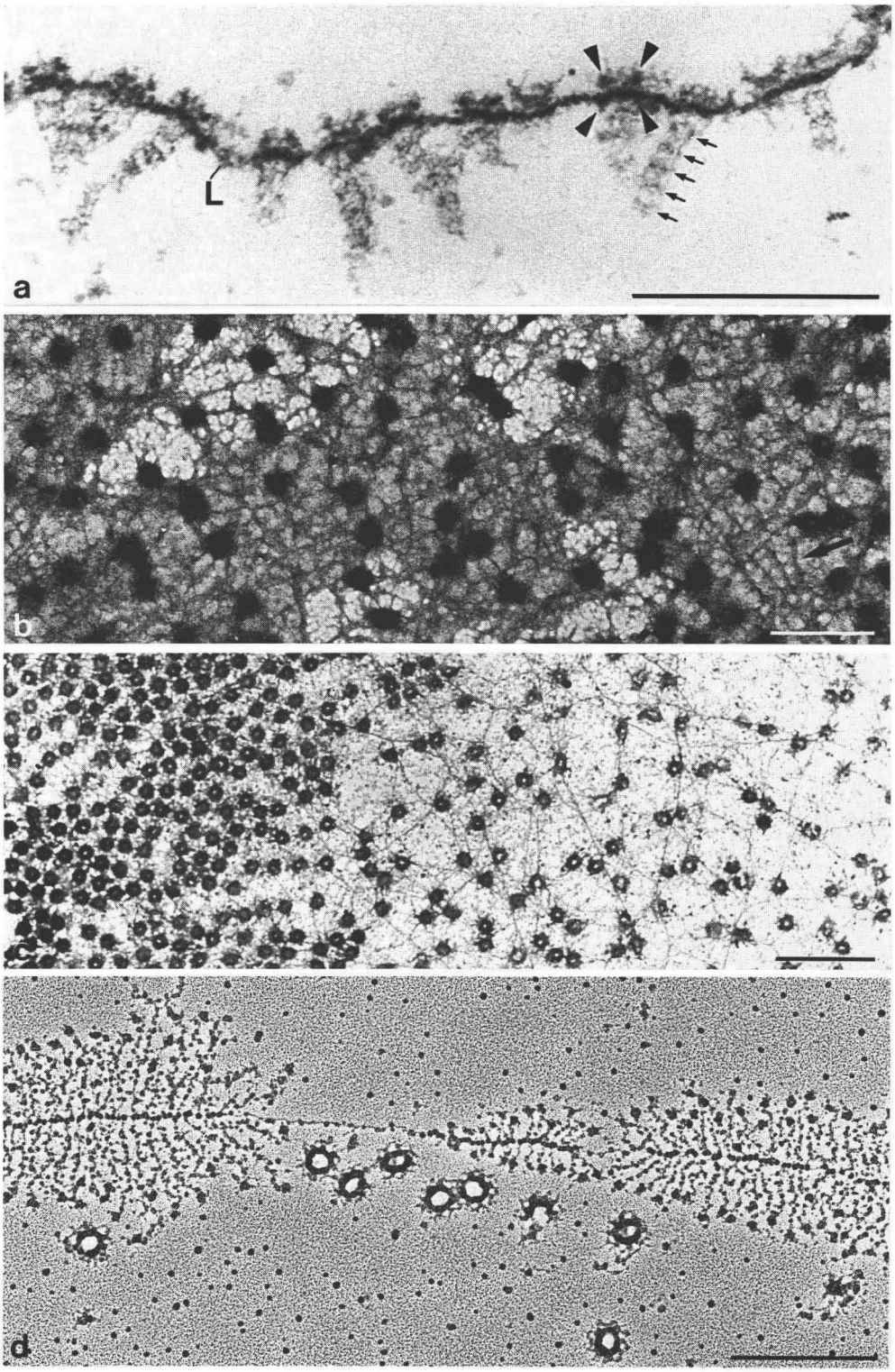
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Fig. 8. The pore complex-lamina assembly. Extraction of isolated nuclear envelopes from Xenopus laevis oocytes with 1% Triton X-100 solubilizes the membranes and uncovers the lamina (L) as shown by thin-sectioning (a). The pore complexes apparently remain intact (a; arrowheads denote subunits of a pore). Note the cylindrical extensions from the inner annulus, occasionally with regularly spaced transverse fibrils (arrows in a). Whole-mount view of a nuclear envelope from a Xenopus oocyte attached to a carbon-coated electron microscopic grid and negatively stained with 2% uranyl acetate. At certain places the interporous lamina meshwork reveals a orthogonal pattern of arrangement (arrow in b). Surface spreading of the nuclear envelope can lead to a considerable extension of the lamina meshwork (c). In Miller-type spread preparations of nuclei from Pleurodeles oocytes, individual pore complexes surrounded by curved arrays of fine fibrils are frequently observed (d). The close association of the individual pores with active rRNA genes (two tandemly arranged transcription units are shown in d) is artifically produced by the centrifugation process. Bars indicate 0.5μm.

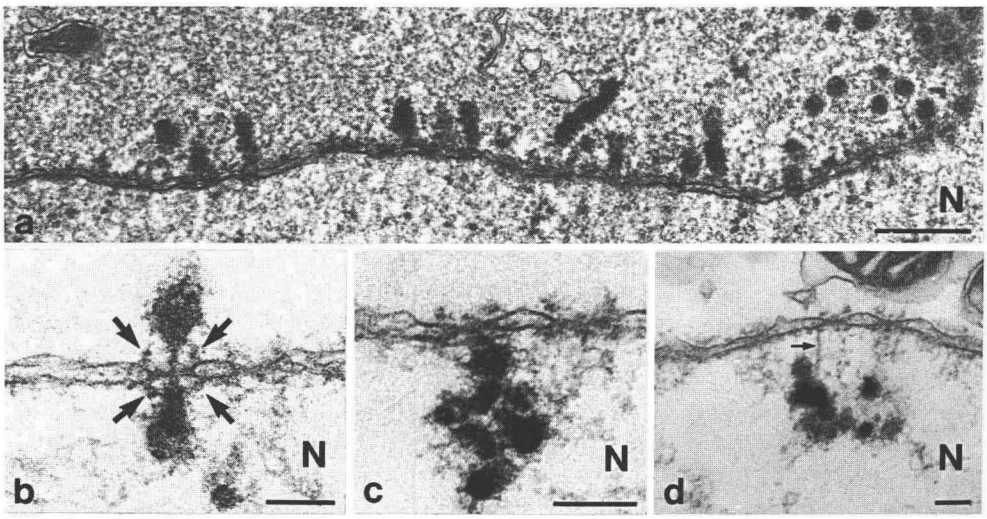

Fig. 9. Localization of lamin L_{III} to isolated nuclear envelopes from Xenopus oocytes. Nuclear envelopes were incubated with monoclonal antibody L_o46F7 followed by secondary antibodies coupled to 5nm gold particles (for details see Benevente et al., 1985). Gold particles occur exclusively in the interporous regions as seen in a tangential section (a). In transverse sections the antibody decorates the lamina but not the pore complexes (b; arrows denote the pores). Bars indicate 0.2μm.

Thus, the nuclear envelope is subdivided into biochemically and morphologically distinct domains with different functions: while the lamina is proposed as playing a role for the specific topological organisation of chromatin in interphase cells (Gerace, 1986; Benavente and Krohne, 1986), the pore complexes act as highly specialised gateways through which active and selective transport processes from the nucleus to the cytoplasm and vice versa take place.

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