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THE STRUCTURE OF THE TUBULIN HETERODIMER IN ZINC-INDUCED SHEETS

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The structure of negatively stained zinc-induced tubulin sheets has been studied in projection by minimum beam microscopy (1,2) and image processing. Figure (a) shows a typical sheet image, displaying the characteristic and prominent protofilament structure. The bar represents 500 nm. Figure (b) is an enlargement of part of (a).

Optical diffraction patterns (Figure c) reveal an orthogonal unit cell lattice of about 9.7 nm X 8.2 nm. The 8.2 nm repeat arises from the arrangement of heterodimers in the protofilaments, and is the first observation of such a repeat in sheet aggregates. It is only observed consistently in diffraction patterns from images recorded by minimum beam methods (1,000-2,000 e/nm^2) and arises from small, but reproducible, structural differences between two similar subunits (3,4) believed to represent the two chemical species of tubulin monomer (55,000 M.W.). At higher electron doses (10,000-20,000 e/nm^2), the additional information is lost or very much reduced, and only a repeat of 4.1 nm is observed, owing to the loss of distinction between adjacent monomers in the protofilaments.

The apparent mm symmetry in the reflections and their intensities, and the systematic absence of reflections along the equator (h axis) indicate the presence of a dyad-screw axis normal to the protofilament axes and in the plane of the sheet. This is confirmed by the phase relationships between the h,k and -h,k reflections, and is clearly revealed in the reconstructed images (Figures d & e).

Reconstructions were computed from areas, containing 650 unit cells (box, Figure a), of four separate sheet images. After shifting to a common phase origin, these data were averaged. The reconstruction in Figure (d) is at the same magnification and orientation as Figure (b). The sheets are composed of 4.9 nm wide, polar protofilaments, similar to those observed in microtubules, however, the interprotofilament packing completely differs in the two structures. Whereas in opened out microtubules all protofilaments point and face in the same direction, in the zinc-induced sheets adjacent protofilaments point and face in opposite directions; i.e. they are related by dyad-screw axes. Thus, the sheets are crystals of space group $P2_1$, containing one tubulin heterodimer per asymmetric unit.

One cell is outlined in Figure (e), with the screw axes indicated by the broken lines with half-arrows. Each protofilament contains two distinct monomer shapes, arbitrarily labeled α and β. Subunits of adjacent protofilaments are clearly related, even though no symmetry constraints were imposed on the reconstructions. The subunits within each protofilament apparently pair to form heterodimers, as indicated by the labeling scheme. The intraprotofilament density between members of a pair is significantly higher than between different pairs. The probable contact regions between adjacent protofilaments are labeled P, Q, R, P', Q' and R' in Figure (e). They appear much weaker than the intraprotofilament connections.

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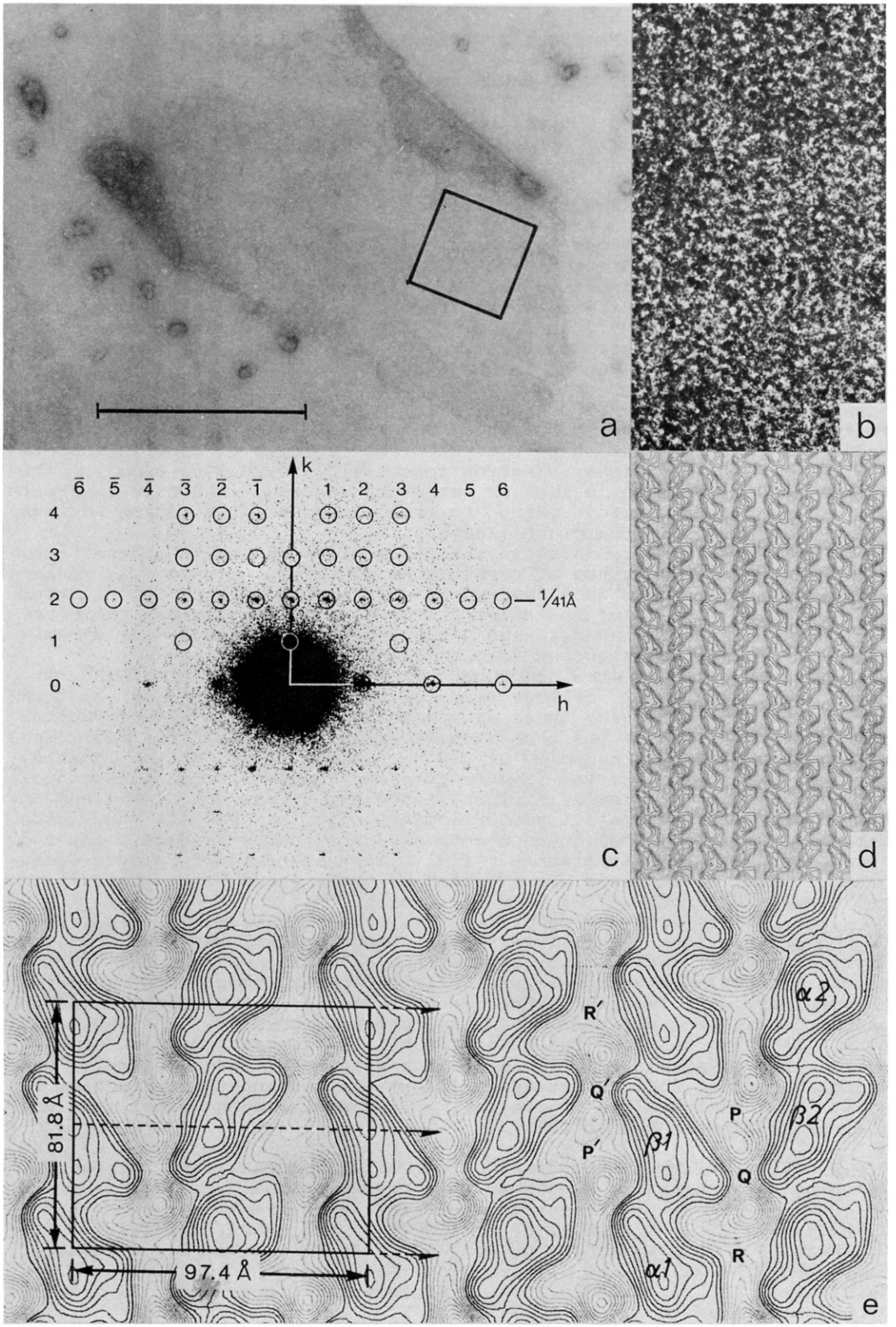
a
b
k
h
1/41Å
c
d
81.8 Å
97.4 Å
R′
Q′
P′
P
Q
R
α2
β2
β1
α1
e