

THE GEOMETRY OF TRIPLETS IN CILIARY BASAL BODIES FROM PRIMATE OVIDUCTS

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Anderson (3) has recently developed a pleasing reconstruction of the basal body from primate oviducts. A reexamination of some of the details, however, suggests a few modifications. The present writer finds the following four points open to doubt: (*a*) the tubules constituting the nine triplets are helical in a left-handed sense; (*b*) the tubules make an angle of 10° – 15° with the axis of the basal body; (*c*) each triplet twists towards the lumen of the basal body about the axis of the A (inner) tubule of the triplet as one passes from the proximal to the distal end; (*d*) the external diameter of the basal body decreases from the proximal to the distal end by the amount indicated by Anderson's theoretical formulation (Fig. 17 of reference 3). Each of these points is discussed in turn below. Other points are also mentioned. Finally, suggestions are offered for a modified reconstruction of the basal body.

THE HELICAL SENSE OF THE TRIPLETS

There can be little doubt that the tubules making up the triplets in basal bodies and centrioles are often approximately helical. André (5) and many other authors (7, 8) have noted that the appearance of sections not precisely perpendicular to the axis of the basal body or centriole is typical of a family of helical filaments. The sense of the helix, however, appears not to have been determined.

The basis of Anderson's (1–3) conclusion that the helix is left-handed is an experiment on a cross section of a basal body (Fig. 7 of reference 3). He observes and compares the changes in appearance of the section and a section of a model when the two are tilted. Noting that the two show a similar response to tilting, he concludes that the two have the same sense (i.e., both helices are left-handed). However, examination of details in the electron

micrographs (Fig. 7 of reference 3) and the model (Fig. 8 of reference 3) shows an important difference. The innermost tubule (the A tubule) of each triplet consistently appears clearest with the C tubule fuzziest in the case of the model. This is not true of the cross section of the basal body. If there is any gradation in clarity at all, it is in the opposite direction with the C tubule clearest. This is perhaps most apparent in Fig. 6 of reference 3.

From this, one can conclude that the axes of the A, B, and C tubules make very nearly the same angle with the axis of the basal body. If there is any difference, then the angle probably decreases from A to C. In Anderson's reconstruction (see Figs. 8, 11, and 16 of reference 3), however, the C tubule is at a considerably larger angle than the A tubule.

Two reinforcing factors in Anderson's model cause the C tubule to be at the largest angle. The first is that the C tubule is at the largest radius and the second is that the triplet angle, as Anderson (3, 4) points out, decreases from the proximal to the distal end of the basal body. These two unequivocal factors can be made self-cancelling only if the model is altered so that the triplet tubules form approximate long-pitched helices with a right-handed sense. Right-handed helices, however, are reconcilable with Fig. 7 of reference 3 only if *a* and *b* of that figure are interchanged.

There is, of course, another possible explanation of the relative clarity of the A, B, and C tubules: the differences in clarity may arise simply from differences in structure of the tubules. However, additional support for right-handed helices is supplied by another difference between sections of the model and the basal body. Fig. 15 *c* of reference 3 shows a cross section of the basal body at the level of the alar sheets. The latter appear in cross section as straight lines. A cross section of the model (Fig. 15 *d* of reference 3), however, shows the sheets as curved lines. Again, two reinforcing factors contribute to the curvature: the decreasing triplet angle and the helical arrangement of the tubules. And again, these two factors are expected to be self-cancelling if the helices are right-handed rather than left-handed. In other words, if the helices are right-handed, then the sheets in section would appear less curved and perhaps straight.

It would seem, therefore, that a sense cannot be assigned unequivocally to the tubules. If a sense is to be assigned to the tubules, the writer could choose a right-handed sense, but no definite conclusion can be reached without further experimentation.

THE PITCH OF THE TUBULES

Anderson (3) concludes that the tubules make angles between 10° and 15° with the axis of the basal body. Elsewhere (1, 2) he states that the angle is 14°. The evidence he presents is based on two sections of a basal body, one approximately longitudinal and the other oblique (Figs. 9 *a* and 10 *a* of reference 3). His interpretation of the oblique section appears to be questionable, while independent measurements based on the longitudinal section suggest that his measurements are too large.

Lines at a small angle to the axis in the longitudinal section are interpreted as representing tubules. Anderson finds the small angle to be 10°–15°; independent measurements made on Anderson's micrograph give $4.5^\circ \pm 1.0^\circ$.

Tubules on opposite sides of the basal body in the oblique section make angles with one another of 20°–30° according to Anderson. (Using Anderson's micrograph the writer finds essentially the same, $20^\circ \pm 2^\circ$.) Anderson deduces that the tubules make an angle of half that (10°–15°) with the axis of the basal body. He does not, however, correct the measurement for the section's not being longitudinal. The angle appears larger in an oblique section. An actual angle θ will appear as θ' in a section at angle ϕ to the axis of the basal body where, from simple geometry,

$$\tan \theta = \cos \phi \tan \theta'.$$

From Anderson's Fig. 10 *a* the writer's measurements give $\theta' = 10^\circ \pm 1^\circ$. The angle ϕ cannot be measured accurately, but it is clear that the section is much closer to being a cross section than a longitudinal section; therefore, ϕ is probably greater than $\sim 60^\circ$. From the above equation it follows that θ is probably less than $\sim 5^\circ$.

Thus two independent sets of measurements favor $\sim 4^\circ$ – 5° for the angle between the tubules and the axis of the basal body, rather than the 14° of Anderson's (3) model.

THE TWIST OF THE TRIPLETS

According to Anderson (1–4), "As the triplet set traverses from base to apex, it twists toward the lumen on the longitudinal axis of the inner A tubule." If the twist of the triplet was about the A tubule, then the A tubule would be straight, not helical. Further, twists about the A, B, and C tubules are not the only possible types of twists. There is no reason to restrict the axis of twist in this

way. If the triplet angle were constant from the proximal to the distal end (and the diameter of the basal body were also constant), then the axis of twist would be the axis of the basal body. If the triplet angle decreases, then the axis of the twist is parallel to the axis of the basal body but displaced from it by an amount that depends on the decrease in the triplet angle.

THE EXTERNAL DIAMETER OF THE BASAL BODY

Anderson's (3) theoretical formulation relating the change in diameter (external or internal) of the basal body and the change in triplet angle fits the physical situation only in a limiting case. In the case of the basal body it is inaccurate and gives results larger than those observed.

Anderson (3) represents the change in external radius of the basal body, from the proximal to the distal end, by δ in Fig. 1 *a*. The triplet is represented by RS at the proximal end and RS' at the distal end, making angles α_p and α_d , respectively, with the tangent to the lumen. Simple geometry gives

$$\delta = a(\sin \alpha_p - \sin \alpha_d),$$

where a is the length of RS and RS' . A more accurate expression for the change in external radius is obtained from Fig. 1 *b*; it is the difference between r at the proximal end (r_p) and at the distal end (r_d): i.e.,

$$\Delta r = r_p - r_d$$

where r_p is given by

$$(r_p - \rho)^2 = r_o^2 + a'^2 + 2r_o a' \sin \alpha_p$$

and r_d is given by the same expression with subscript p replaced by d . Anderson's δ reduces to the more accurate expression for change in diameter only in the limit $a/r_o \rightarrow 0$ and when a is replaced by a' .

Using Anderson's figures, $a' = 40$ nm, $\rho = 10$ nm, $r_o = 85$ nm, $\alpha_p = 40^\circ$, $\alpha_d = 10^\circ$, one obtains $\Delta r = 14.9$ nm. Anderson's result (28.0 nm) is nearly double that.

According to Table 1 of reference 3, the external diameter of the basal body increases by 51.5% from the distal to the proximal end. Examination of cross sections (Fig. 1 of reference 3) and longitudinal sections (Figs. 2, 3, 4, 9 *a*, 13 *a*, 14 *a* of ref-

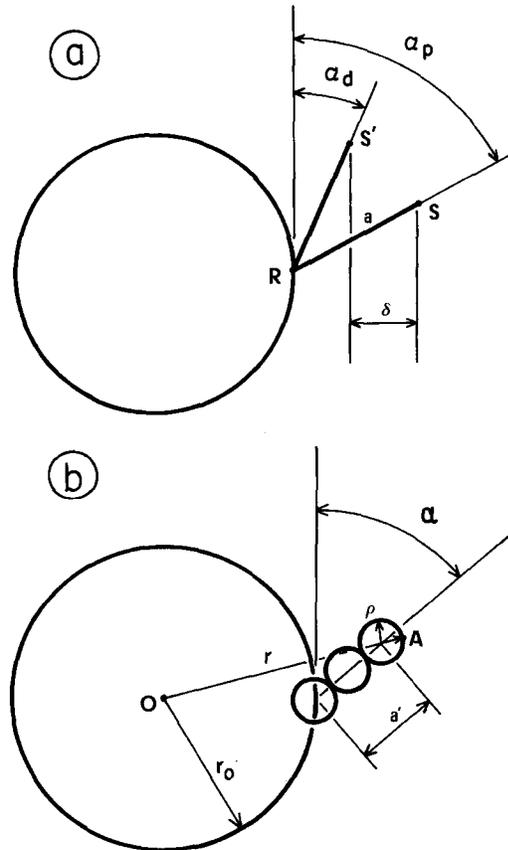


FIGURE 1 The difference in external radius of the basal body between the proximal and distal ends. Anderson's interpretation is shown in (a) by δ . RS and RS' represent a triplet at the proximal and distal ends making angles α_p and α_d , respectively, with a tangent to the lumen. A more accurate expression for the difference in radius is obtained from (b). The radius r is shown by OA . The triplet angle is α . The magnitude of r is calculated at the proximal and distal ends of the basal body.

erence 3) does not support such a large increase. The change is considerably less and varies somewhat from figure to figure. Nevertheless, it is not inconsistent with the change in radius (14.9 nm) obtained above.

Anderson (3) extends his theoretical formulation to cases where the luminal diameter of the basal body changes. Here, too, the formulation is not accurate and doubt is cast on the conclusions drawn. In particular, Anderson is probably not entirely justified in criticizing measurements of the luminal diameter and triplet angle made by Stubblefield and Brinkley (11).

DISCUSSION

For the various reasons given above, Anderson's (3) reconstruction of the basal body, while probably correct in outline, is doubtful in some of its details. A reinterpretation of the experimental results suggests some modifications. But more confirmatory experimental work is needed. A reinterpretation suggests the following: the tubules of the triplets make a smaller angle (probably $\sim 4^\circ$ – 5°) with the axis of the basal body than 14° ; they do not all necessarily make precisely the same angle with the axis; they define approximate long-pitched helices with a sense that may well be right-handed, rather than left-handed; the triplets are not twisted about the A tubules, but rather they are twisted about an axis parallel (or nearly so) to and displaced from the axis of the basal body; the external diameter of the basal body changes from one end to the other by an amount smaller than the figure Anderson finds.

There is, of course, no reason to believe that the pitch of the tubules constituting the triplets is constant. It is quite possible that both it and the triplet angle (6) change with time. These changes could be effected, at least partly, by contractile fibers making up the alar sheets. A changing pitch results in a relative displacement between tubules, one component of which represents slip or sliding. Could this have anything to do with slip that Satir (10) describes between filaments in an active cilium? Perhaps it is in the basal body where slip begins and where movement is coordinated, much as the baseplate of a T-even bacteriophage appears to control or trigger the contraction of the tail sheath (9).

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