PATTERNS OF BASAL BODY ADDITION IN CILIARY ROWS IN *TETRAHYMENA*

D. L. NANNEY

From the Provisional Department of Genetics and Development, University of Illinois, Urbana, Illinois 61801

ABSTRACT

Most naked basal bodies visualized in protargol stains on the surface of *Tetrahymena* are new basal bodies which have not yet developed cilia. The rarity of short cilia is explained by the rapid development of the ciliary shaft once it begins to grow. The high frequency of naked basal bodies (about 50%) in log cultures indicates that the interval between assembly of the basal body and the initiation of the cilium is long, approximately a full cell cycle. Naked basal bodies are more frequent in the mid and posterior parts of the cell and two or more naked basal bodies may be associated with one ciliated basal body in these regions. Daughter cells produced at division are apparently asymmetric with respect to their endowment of new and old organelles.

The usual equality of cell division requires that the parts necessary for the composition of two cells be fabricated under the discipline of one, but that they be capable of reintegration into essentially identical separate cells. The replication and distribution of nuclear elements have long been studied, but our understanding of the organized deployment of cytoplasmic elements is more primitive. In the case of plastids and mitochondria (see reference 15), the decentralized and differentiated genetic depots allow the investigator to tag organelles and to study their distributions. For other organelles this procedure is not feasible, but some success has come from labeling newly synthesized components and then examining their location and distribution (3, 7, 8, 30). In the present instance we use a stage in the development of a complex organelle as a convenient marker of a new unit, and examine the distribution of new structures in the cell surface at different times in the cell cycle.

The structures we employ are the "ciliary units," each of which is composed of an external ciliary shaft, its extension into the subcortical basal body or kinetosome, and a complex array of other fibers and membranes with characteristic associations. The cilium itself is widely assumed to be homologous in all eucaryotic cells, and the basal body is believed to be homologous to the centrioles involved in nuclear division. Even at the electron microscope level a ciliary unit is complex, and chemical analysis reinforces this impression. Witman et al. (32) report that the presumably homologous *Chlamydomonas* flagellum contains some two dozen separable proteins. Electron microscope studies show that new basal bodies commonly arise in close association with pre-existing basal bodies and in a similar way in a diversity of organisms (see references 1, 5, 29, 33). In ciliates the new basal body is preceded by a "generative disk" which ordinarily develops just anterior and at right angles to a pre-existing basal body (but see references 16 and 17). The circlet elongates, tilts toward the surface, moves away from its origin, and gradually acquires its full complement of accessory structures, including the externally projected ciliary shaft.

We are not here concerned, however, with either

the ultrastructural or the biochemical aspects of basal body proliferation, but with the location of new units on the cell surface. The developing basal body, after it reaches approximate maturity, can be easily visualized through the use of silver stains, and changes occurring in the basal bodies can be followed through the cell cycle. Nanney (21), for example, showed that in *Tetrahymena* the numbers of basal bodies increase in all ciliary rows throughout the cell cycle, but that the rates of increase are somewhat stage- and region-specific.

Although a count of basal bodies in staged cells gives some information on patterns of organellar increase, it does not permit the identification of individual new elements. Perlman (24) has recently supplied the basis for such identification. Williams and Scherbaum (31) thought that naked basal bodies, i.e. basal bodies without external ciliary shafts, might be new kinetosomes. Although all cilia must surely pass through such a stage, those observed in cytological preparations might not consist exclusively or even predominantly of such developmental stages. Perlman, focusing attention on the postoral ciliary meridians at the time of their most rapid increase (just before cell division), showed that the distribution of naked basal bodies was that expected for developmental and not for artifactual structures. The naked basal bodies tended strongly to be distributed alternately with ciliated basal bodies. He showed, furthermore, that naked basal bodies could be found at any position along the ciliary row, but he did not examine that distribution in detail.

The present study extends the Perlman analysis to include ciliary rows other than the postoral meridians and times other than the late predivision stages. The results do not bear particularly on the mechanisms whereby cells with small numbers of basal bodies or centrioles manage to equip each of their progeny with the appropriate equipment; rather, they are concerned with the more general issue of how cells monitor the assembly and distribution of organelles present in large number in the cell, so that the appropriate numbers in the appropriate places are maintained. One simplistic hypothesis concerning the management of the numbers of organelles is disposed of in the present instance; new organelles are not "enumerated" by a one-to-one counting against pre-existing organelles.

MATERIALS AND METHODS

These studies were confined to inbred strain C3-3685 of syngen 1 *T. pyriformis*, grown in 1% proteose peptone, stained by the protargol procedure (6, 18) while in log growth. The cells were staged by examination of the oral apparatus as described by Frankel (10). The new oral apparatus arises as a cluster of basal bodies just to the left of the (cell's) right postoral meridian and midway back in the cell. The originally "anarchic" field increases in size and in organization and progressively acquires the three complex membranelles and the undulating membrane which give the organism its name. The stage at which the oral primordium first appears is designated as stage 1; cell division occurs after the familiar "peanut" configuration in stage 6. The entire stomatogenic sequence occupies approximately half the cell cycle, and the six stages are estimated (10) to require the following percentages of the total cycle: 16%, 5%, 4%, 7%, 8%, and 12%.

Only well-stained cells with clearly defined cilia were examined, and only a few ciliary rows per cell, generally rows at the margins of the cell where the basal bodies can be seen in profile (Fig. 1). Each row counted was classified by the usual conventions, which refer to the cell's right postoral meridian as row no. 1, with enumeration proceeding to the cell's right.

RESULTS

The Proportion of Naked Basal Bodies in Somatic Ciliary Rows

Perlman (24) reported that 43% of the basal bodies in the postoral meridians were without cilia just before cell division (stage 6). This large number, nearly half of the total, was thought to be unusually high and to reflect the recent addition of new basal bodies in these rows during late stomatogenic stages. To get comparable data on other ciliary rows, 50 somatic ciliary rows from stage 6 cells were counted in 19-rowed cells, taking care that at least 1 of each of the 17 possible somatic rows was included. A total of 1,064 basal bodies were scored and of these, 524 were nonciliated. This fraction, 49%, is even greater than that in the rows most active in basal body addition at this time, and requires further consideration.

The fraction of naked basal bodies observed depends upon the time between the development of the basal body to the point the basal body is observable and the development of the cilium so that the cilium can be stained. If this time interval is very short, few basal bodies will lack cilia. If cilia are added only after a long lag, many of the basal bodies will lack cilia. Since, on the average, half of the basal bodies must be added in each cell cycle, the probability that a basal body will be nonciliated can be established as a function of the

fraction of the cell cycle required for cilium development. Although we must return to this point, we will assume for present purposes that the interval between the appearance of a basal body and the appearance of its cilium is about the same at different times and places. The period of cilium growth itself must be very short, because cilia of intermediate length are rare. Since, for the cell as a whole, basal bodies are added at a fairly uniform rate (21), the fraction of nonciliated basal bodies is a simple projection of the time required before the addition of the cilium. Thus, if cilium addition is delayed half a cell cycle, half the basal bodies developed in the last cycle (half the total) will still lack cilia and one-fourth of the total basal bodies will be nonciliated. If the time required before ciliation is a full cycle, then none of the basal bodies developed during the previous cycle will be ciliated and half the total basal bodies will be without cilia. This result is in fact very near to that observed: 49% of the basal bodies in the general somatic ciliary rows were nonciliated. The simplest interpretation of these results is, then, that the period before ciliation is relatively long, requiring nearly a full cell cycle.

Naked Basal Bodies in Postoral Ciliary Rows

Perlman (24) examined the postoral rows at the end of their period of maximal proliferation (stage 6), and reported a frequency of nonciliated basal bodies which was no higher than, indeed slightly below that which we here report in the general somatic ciliature at the same time. To probe this issue, counts were made on additional samples of postoral ciliary rows in anterior fission products (proters) at stomatogenic stages 1–6. Similar studies on the posterior fission products would be desirable but are much more difficult because the demarcation between the ciliary rows and the posterior margin of the oral anlagen is much less distinct. At least 22 counts were made at each stage with the following results (see Table I): stage 1, 17%, stage 2, 10%; stage 3, 19%; stage 4, 29%; stage 5, 38%, stage 6, 46%. Thus, during early stages of stomatogenesis, only 10–20% of the basal bodies lacked cilia, but this proportion rose during stages 5 and 6 to nearly half. The number of *ciliated* basal bodies in these postoral rows remained essentially constant throughout the interval, the means being 6.0, 6.4, 6.0, 5.6, 6.4, and 6.4. Thus, none of the basal bodies arising in these rows during stomatogenesis developed cilia in the same period. These observations also bear on the timing of ciliary assembly, but discussion of their implications is reserved until later.

The Location of Naked Basal Bodies within Postoral Ciliary Rows

Perlman (24) reported that unciliated basal bodies could be seen at any position in the postoral rows, but he did not further study their distribution to see if they occurred preferentially in any particular region. The staged postoral meridians surveyed for numbers of naked basal bodies were also scored so as to identify the row positions of the new elements, and the data from these "maps" are summarized in Table I. The analysis presumes that naked basal bodies are in fact new basal bodies and that they have arisen in association with the nearest ciliated basal body to the posterior. If these assumptions are correct, we can conclude that new basal bodies do not arise at uniform rates along these rows. At early stomatogenic stages very few of the ciliated anterior basal bodies (positions 1 and 2) have new basal bodies associated with them, and even by the late stages less than one-fourth of them have associated nonciliated bodies. In contrast, nearly all the posterior ciliated basal bodies have one or more new basal bodies by the end of stage 6. Because of the failure of the anterior basal bodies to develop new basal bodies, only 62% of the ciliated basal bodies had associated new units. Yet the total number of new basal bodies nearly equals the number of old basal bodies, because several naked basal bodies sometimes come between ciliated units. No tandem naked basal bodies were found in stage 1 cells; only one case each was seen in stages 2 and 3. Three cases were scored in stage 4 cells and six in stage 5 cells. 24 examples were observed in stage 6 cells, and 10 of these included three naked basal bodies in a row.

The observations thus demonstrate that basal body addition is not by a one-to-one mechanism, whereby organellar number is regulated by associating each new organelle with an old one. Rather, old organelles in some locations are not associated at all with new elements, and those in other regions are associated with several.

The Location of Naked Basal Bodies within Stage 6 Somatic Ciliary Rows

Additional somatic rows were mapped in a fashion similar to that used with the postorals. The

TABLE I

Probabilities of a Ciliated Basal Body in a Proter Postoral Ciliary Row having One or More Naked Basal Bodies between It and the Next Anterior Ciliated Basal Body

	Stage of stomatogenesis					
Position	1	2	3	4	5	6
1	0/25 0.00	0/26 0.00	0/22 0.00	2/23 0.09	5/23 0.22	3/25 0.12
2	0/25 0.00	1/26 0.04	0/22 0.00	1/23 0.04	7/23 0.30	5/25 0.20
3	3/25 0.12	0/26 0.00	4/22 0.18	5/23 0.22	9/23 0.39	16/25 0.64
4	6/25 0.24	4/26 0.15	8/22 0.36	13/23 0.57	17/23 0.74	19/25 0.76
5	8/25 0.32	6/26 0.23	10/21 0.48	12/22 0.55	16/22 0.73	21/24 0.88
6	9/17 0.53	4/23 0.17	7/17 0.41	11/17 0.65	15/19 0.79	19/21 0.90
7	2/5 0.40	2/11 0.18	2/6 0.33	4/7 0.57	6/9 0.67	16/17 0.94
8	0/2 0.00	0/2 0.00	0/1 0.00		2/2 1.00	5/5 1.00
9			0/1 0.00		0/1 0.00	
Mean ciliated	6.0	6.4	6.0	5.6	6.4	6.4
Mean naked	1.2	0.7	1.4	2.3	3.8	5.6
% non-ciliated	17.1	9.8	19.3	28.6	37.6	46.3

somatic rows in the cells in these samples range from 18 to 24 in number, and include about twice as many basal bodies as do the postorals. The counts were made almost exclusively on the incipient posterior fission products (the opisthes) because these rows are straighter and less crowded than those in the proter. The results generally confirm the analysis on the postorals of the proters. Of the 500 basal bodies comprising the anterior 10 units of 50 rows, only 195 (39%) were without cilia. In contrast, 291 (58%) of the posterior 10 units were without cilia. Thus again, some areas of the surface contribute more than their share to the organellar input to the next generation. To test if the midregions of the cell were more active in this respect than either end, the 10 basal bodies composing the central "belts" of the cells were separately scored, and yielded 263/500 or 53% nonciliated basal bodies, close to halfway between the other measures but more similar to the pattern in the posterior end. On this basis, organellar morphogenesis would appear to be distributed as a shallow gradient increasing in activity from the anterior to the posterior end.

The situation is more complex than this, however, because the naked basal bodies show some circumcellular specificity also. The first basal bodies on rows just to the right and left of the oral apparatus tend to be ciliated, while first basal bodies farther away will eventually compose part of the nonciliated apical "coronet" (20), a characteristic double ring of basal bodies at the anterior end. The first basal bodies (position no. 1) of all samples (6) of rows 2, 3, and 4 were ciliated. In contrast, of 37 samples representing rows 5–16, only two first basal bodies were ciliated. Three of seven samples of rows 17–18 had the first basal body ciliated.

The absence of a cilium on the first basal body (position 1) of the rows contributing to the apical coronet obviously requires an explanation different from that applying to other cases. They are naked basal bodies but they are not necessarily new basal bodies. Whether the cilia regularly develop and are later discarded, or whether the cilia do not ordinarily develop, has not been established. But when these "naked-but-not-new" basal bodies are removed from consideration, the anterior-posterior gradient of organellar morphogenesis is shown to be steeper. 39 of the 195 naked basal bodies attributed to the anterior 10 basal bodies have to be discounted, and the frequency of probable new basal bodies in this sample is reduced from 39% to 31%; within the anterior region a sharp gradient is seen. Only 5 of 50 (10%) second basal bodies examined were devoid of cilia. The number rose to 9 for the third basal body, 6 for the fourth, 20 for the fifth. By the ninth basal body 32 of 50 were

without cilia, and this generally high level of nonciliated units continues to the end of the row. The apparently uniform gradient of organellogenesis is thus changed, on more careful inspection, to a sharp gradient limited to the anterior half of the cell.

Tandem naked basal bodies are also found in these somatic rows and provide further evidence of development of two or more basal bodies in a region within a short time, i.e. within the interval ordinarily required for a visible basal body to develop a cilium.

The Location of Naked Basal Bodies in Somatic Rows during Early Stomatogenesis

In early stomatogenesis the new oral apparatus appears first as a cluster of new basal bodies to the left of ciliary row no. 1. This stage was chosen for a final check on the distribution of naked basal bodies in somatic ciliary rows. At this stage, counting entire rows is often difficult because of the cellular curvature particularly at the anterior end, but the long straight portions of rows of the midregion are relatively easily scored. For this reason, only portions of the midregions of 100 somatic rows were mapped. For the first sample, 50 segments of 10 basal bodies ranging from approximately a quarter cell behind the apex and overlapping into the stomatogenic region were counted. For the second sample, another 50 segments of 10 basal bodies were selected to range from the anterior limit of the stomatogenic region backward. One may start mapping a segment at a ciliated or at a nonciliated basal body. For uniformity, in this case ciliated basal bodies were chosen for initiating all segments.

The results (Table II) generally confirm, for this time and place, the conclusions previously developed. The sample segments from the more anterior regions of the cell have fewer naked basal bodies than does the sample from a more posterior region (44% vs. 55%). Within the anterior sample, basal bodies nos. 2–5 are less likely to be without cilia than are the more posterior basal bodies (37.5% vs. 53.6%). The posterior segments, in contrast, do not show this internal discordance.

This manner of scoring, incidentally, also supports Perlman's (24) observations on the general alternate distribution of ciliated and nonciliated basal bodies. The basal body no. 2, just posterior to the first chosen ciliated basal body (no. 1), is likely to be nonciliated. The basal body just behind no. 2 is in turn likely to be biased in the other direction. This alternating pattern gradually damps out, though the odd-numbered basal bodies continue to show low frequencies of cilia throughout the arrays. Because the nine-body samples include five even and four odd basal bodies, the estimate of the frequency of naked basal bodies is biased upward, and these frequencies should not be compared directly to those based on complete mapping.

TABLE II

Distribution of Naked Basal Bodies in Somatic Ciliary Rows in Stomatogenic Stages 1–2

Basal body	No. naked basal bodies in a sample of 50 rows	
	Anterior segments	Posterior segments
1	0 (by design)	0
2	22	44
3	11	20
4	18	27
5	24	23
6	27	33
7	23	21
8	29	31
9	23	23
10	32	26
% distribution of basal bodies:		
2–10	44.0	55.1
2–5	37.5	57.0
6–10	53.6	53.4

DISCUSSION

The wide distribution of the 9 + 2 cilium and its centriole-like basal body has long attracted attention to these structures (33). Because of the extensive use of these elements in their cytoarchitecture, the ciliates have been especially favorable objects for their study, and long ago Lwoff (19) raised many of the questions still being asked in the context of ciliate studies.

Because in light microscope studies new basal bodies were commonly observed to arise in association with old basal bodies, basal bodies were early considered to be in some sense "autocatalytic" elements (19, 26). This interpretation led in recent years to attempts to identify unique nucleic acid components of basal

bodies. Although the issue is not settled to everyone's satisfaction, the more recent studies (see 9, 14, 25, 28, 34) do not support the expectation of special basal body DNA. Moreover, the necessity for a pre-existing basal body as a "model" for a new basal body has been seriously challenged. New basal bodies sometimes arise in various relationships to old basal bodies, in regions widely separated from old basal bodies (16), and sometimes even in cells devoid of demonstrable basal bodies (17). The "spontaneous" origin of centrioles in other organisms has similarly been well documented (see reference 14).

The commonly observed association between new and old basal bodies is thus probably not to be explained on the basis of a transfer of molecular information between the two structures. The old structure, however, probably does serve as a source of architectural information, useful in the integration of new structures into cellular fabrics. This use of pre-existing structures is associated with the concept of "cytotaxis" set forth by Sonneborn (27, 12) and supported particularly by experimental studies on *Paramecium* (2).

We are not primarily concerned here, however, with the mechanisms of origin of new basal bodies, but rather with problems of cellular integration (see 12, 28). A previous analysis (21) had shown that in *Tetrahymena* new basal bodies are developed continuously through the cell cycle, and at a nearly constant rate for the cell as a whole. Differences were shown, however, in the times of greatest assembly in different ciliary rows. The present study shows that basal body addition is not random within a ciliary row. It is rare in the anterior end of the cell and becomes more common in the middle and posterior half. Two or more basal bodies may develop between old basal bodies in the posterior region to compensate for the lack of new basal bodies at the anterior end.

This pattern of organellar addition is different from that in other ciliates. In *Paramecium*, for example (see references 7 and 28), new basal bodies appear just before cell division and are added first and more commonly near the future cleavage line at the cell's equator. Basal body addition in *Condylostoma* occurs only at the time of cell division (4). In *Euplotes* also (11, 13), new basal bodies develop in a restricted area near the midline and at a time just before cell division. In all these cases the new and old organelles are asymmetrically distributed to the daughter cells; for each daughter either the anterior or the posterior half is equipped preferentially with new units, but the two daughters from a single fission differ in this respect. In *Tetrahymena* the distribution of new organelles is less asymmetric in individual daughter cells, but the proter receives a disproportionate number of old basal bodies. The anterior end of the proter is also preferentially equipped with old elements.

This pattern of organellar assembly has not been rationalized. The continuous assembly of organelles might be more efficient than assembly at a delimited time, but it might also create problems of adjustment to the increase which a time-restricted synthesis just before division would avoid. *Tetrahymena* appears to be structurally less complex than either *Paramecium* or *Euplotes*, and the continuous addition of organelles to straight ciliary rows may not bring about significant shifts in shape and proportion. For such reasons, *Tetrahymena* may be able to tolerate continuous processes that are intolerable to more complex forms, which then must resort to a crisis transformation in preparation for division.

The data here presented provide some insight into the time spent in certain stages of ciliary development. Light microscopy cannot, of course, explore the early stages of basal body assembly. But the time between the establishment of a stainable basal body and the full development of a ciliary shaft can be estimated. Two observations lead to acceptable conclusions, while the third is problematical. The observation that most basal bodies (see Fig. 1) are either naked or equipped with a fully developed cilium establishes the assembly of a cilium as a rapid process. The fact that log cells have half of their basal bodies unciliated also leads to an unambiguous conclusion: the interval between basal body formation and ciliary assembly is approximately one cell cycle. Some basal bodies (such as those in the newly developing oral membranelles) obviously have a shorter period before ciliary shaft development, but the average for the somatic ciliature must be close to one cell cycle. We do not yet have means of estimating the variations in the timing of ciliation for different basal bodies.

The problematical observations are those associated with the distribution of unciliated basal bodies in the postoral ciliary rows. The proportion of naked basal bodies at stage 6 agrees well with the proportion reported by Perlman (24). The increase in basal bodies in these rows during midstomatogenesis was not entirely expected.

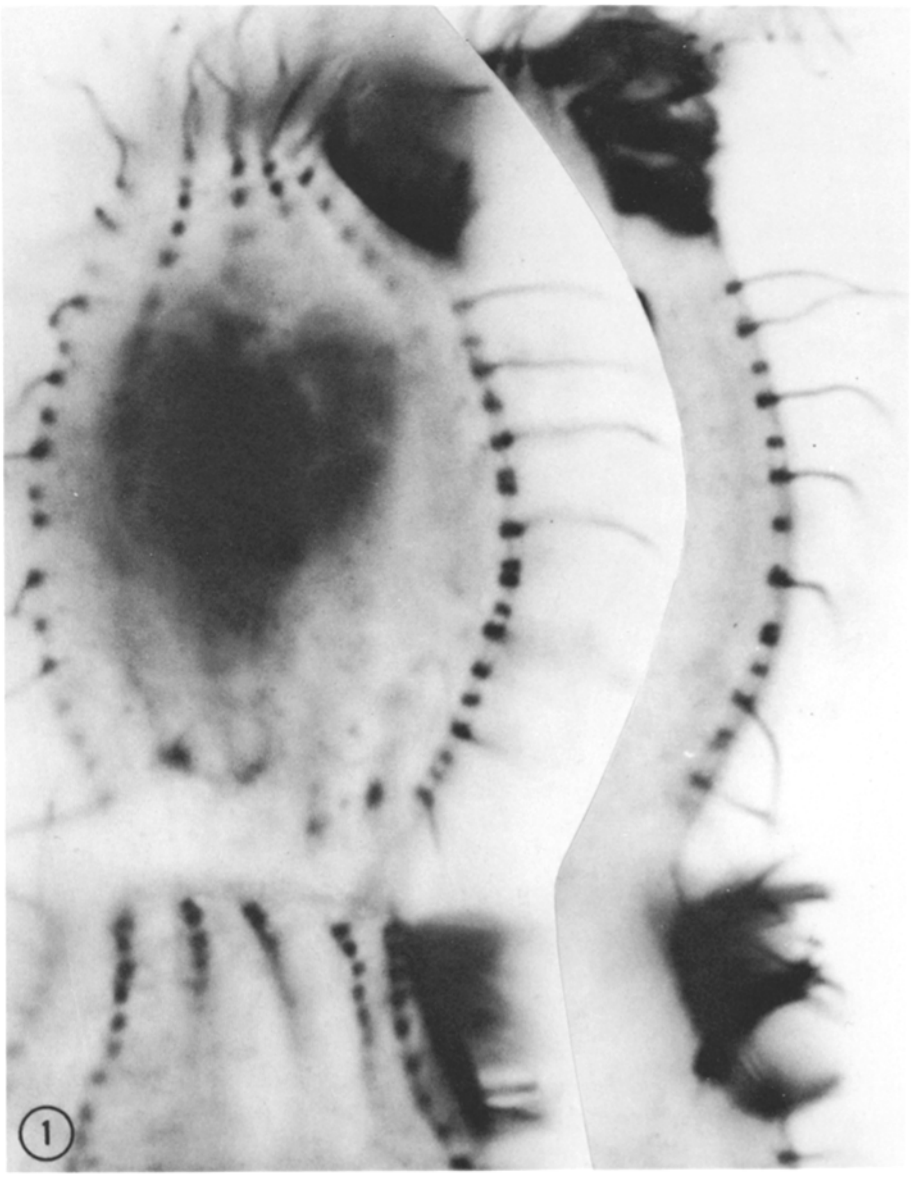

FIGURE 1 Adjacent optical sections of a stage 6 syngen 1 *Tetrahymena pyriformis* cell: stained with Protargol and focused on basal bodies in profile in row 1 (left) and *n* (right) of anterior daughter (proter). All cilia are not visible in an optical section, but the photographs illustrate well the materials being evaluated and show the general alternation of ciliated and nonciliated basal bodies. Note the nonuniform spacing of the basal bodies and the occasional appearance of two and three adjacent naked basal bodies. The patterns of organellar insertion in adjacent ciliary rows are not identical.

Nanney (21) had earlier found very little increase before stage 6 and assumed that the multiplication required to bring the basal body count up to that observed in stage 0 must occur in late stage 6 or early stage 0. Although different strains were also used, the most probable basis for the discrepancy is a difference in growth conditions. In the earlier study the cells were "approaching plateau," and intracellular competition with stomatogenesis might have reduced basal body production in adjacent cortical areas during these stages. The observations here reported may better represent the pattern of assembly in log cells.

Even if this is so, the estimation of the time lag

for ciliary development is complicated. If the population of basal bodies in postoral rows of stage 1 proters fairly represents the behavior of the basal bodies in postoral rows of stage 6 proters of the previous generation, we can calculate the time for these basal bodies to develop cilia. 46% are unciliated at stage 6, and by the following stage 1 (a half cell cycle later) only 17% are without cilia. If no new basal bodies arise in stage 0 (between stage 6 and stage 1), then the fraction of unciliated basal bodies in stage 6 acquiring cilia during stage 0 is 46 minus 17, or 29%. This is 63% (29%/46%) of the unciliated stage 6 basal bodies which have developed cilia within half the cell cycle. But earlier studies (21) showed that basal bodies are added during stage 0, so that some and perhaps all the unciliated stage 1 basal bodies are probably basal bodies that arose during stage 0 and not carry-overs from the previous cell cycle. This analysis then suggests that the new basal bodies arising in these rows during stomatogenesis commonly develop cilia at some time during the following stage 0, and do not require a full cell cycle for completion of their development.

The postoral rows (particularly row no. 1) differ from ordinary ciliary rows in that they not only replace themselves in each cell cycle, but contribute a substantial number of their basal bodies to the new oral apparatus. Hence, these ciliary rows must more than double their number in each cycle. If they completed their ciliary development at the same rate as the somatic basal bodies, a larger fraction should be without cilia, instead of a smaller fraction. This observation supports the idea of different developmental times for different basal bodies.

One other confounding consideration needs to be mentioned. Basal bodies appear not to be added equally along a ciliary row; at least unciliated basal bodies are more common in the posterior than in the anterior regions. While this difference could be explained by a more rapid developmental rate for anterior basal bodies, the presence of double and triple unciliated basal bodies in the mid and posterior regions strongly suggests a compensation for failures to add new organelles in the anterior portions, rather than a difference in developmental rate. Joseph Frankel[1] has called to our attention the effect of this asymmetry on our considerations of developmental rate. All our data on postoral ciliary rows are derived from anterior cells. Hence, the stage 1 cells (with 17% naked basal bodies) are not derived from a stage 6 population with 46% naked basal bodies but from the anterior portion of that population which has markedly fewer. Under these circumstances, one need not postulate so large a fraction of the naked basal bodies developing cilia during stage 0. At this point, estimates of development time are fairly rough in any case. Mapping the postoral ciliary rows in posterior daughter cells would be instructive, but the uncertain boundaries between the developing oral apparatus and the ciliary row during stomatogenesis make such studies difficult.

Even though the ciliary units in ciliates are probably homologous to the centrioles and basal bodies distributed throughout the eucaryotes, the phenomena here considered probably do not illuminate the transmission of these specific organelles in other kinds of organisms. The centriole or the basal body is ordinarily a unique or at least an uncommon organelle for the cell bearing it, and the cell must devise a means of making another organelle like the original and assuring that one goes to each daughter. Under these circumstances a cell might very well restrict organellogenesis to a special microenvironment strategically associated with the pre-existing organelle, and perhaps temporally constrained to one period in the cell cycle. This device would assure the fabrication of precisely the number of organelles required, and explain the association of old and new organelles. The cell then solved the distribution problem by associating organellar assortment with the mitotic apparatus.

With ciliates, however, the ciliary unit is compounded into a major structural component and a single cell may have hundreds of approximately equivalent organelles. It must, in each cell cycle, produce an average of one new organelle for each old organelle present. It must place the new organelles in functioning fabrics capable of continuing their functions as the cell grows and divides. While the first task, of producing the proper number of organelles, might be accomplished by matching each new organelle to an old organelle, this device might prejudice the functioning of the organellar system. Although the number of basal bodies in *Tetrahymena* is maintained with great reliability (22, 23), this result is not achieved by a one-to-one control of organellogenesis. New basal bodies appear always to arise in association with a pre-existing basal body, but not all old basal bodies are employed in

[1] Personal communication.

any single cell cycle. Instead, some basal bodies in more advantageous positions are used repeatedly. How the cell maintains its inventory remains to be discovered. It is this latter problem that the ciliate basal body may share with many kinds of cellular components in many kinds of cells.

This paper is belatedly but respectfully dedicated to Vance Tartar, the pioneer student of the ciliate cortex, on the occasion of his retirement.

The author is pleased to acknowledge the able technical assistance of Mrs. Margaret Chow whose skillful cytological preparations made this analysis possible. He also thanks several colleagues for critical reviews of the manuscript: J. Frankel, E. Orias, and T. M. Sonneborn.

This work was supported by research grants GM-07779 from the United States Public Health Service and GM 23910 from the National Science Foundation.

Received for publication 25 October 1974, and in revised form 10 February 1975.

REFERENCES

1. ALLEN, R. D. 1969. The morphogenesis of basal bodies and accessory structures of the cortex of the ciliated protozoan *Tetrahymena pyriformis*. *J. Cell Biol.* **40**:716–733.
2. BEISSON, J., and T. M. SONNEBORN. 1965. Cytoplasmic inheritance of the organization of the cell cortex in *Paramecium aurelia*. *Proc. Natl. Acad. Sci. U. S. A.* **53**:275–282.
3. COLE, R. M. 1965. Bacterial cell wall replication followed by immunofluorescence. *Bacteriol. Rev.* **29**:326–344.
4. DE TERRA, N. 1972. Kinetosome production in *Condylostoma* occurs during cell division. *J. Protozool.* **19**:602–603.
5. DIPPELL, R. V. 1968. The development of basal bodies in Paramecium. *Proc. Natl. Acad. Sci. U. S. A.* **61**:461–468.
6. DRAGESCO, J. 1962. L'Orientation actuelle de la systématique des ciliés et la technique d'imprégnation au Proteinate d'argen.. *Bull. Microsc. Appl.* **12**:49–58.
7. EHRET, C. F., and G. DEHALLER. 1963. Origin, development and maturation of organelles and organelle systems of the cell surface of Paramecium. *J. Ultrastruct. Res.* (Suppl.). **6**:1–42.
8. EHRET, C. F., N. SAVAGE, and J. ALBLINGER. 1964. Patterns of segregation of structural elements during cell division. *Z. Zellforsch. Mikrosk. Anat.* **64**:129–139.
9. FLAVELL, R. A., and I. G. JONES. 1971. DNA from isolated pellicles of Tetrahymena. *J. Cell Sci.* **9**:719–726.
10. FRANKEL, J. 1964. The effects of high temperatures on the pattern of oral development in *Tetrahymena pyriformis* GL. *J. Exp. Zool.* **155**:403–436.
11. FRANKEL, J. 1973. Dimensions of control of cortical patterns in Euplotes: the roles of preexisting structure, the clonal life cycle and the genotype. *J. Exp. Zool.* **183**:71–94.
12. FRANKEL, J. 1974. Positional information in unicellular organisms. *J. Theor. Biol.* **47**:439–481.
13. FRANKEL, J. 1975. An analysis of the spatial distribution of ciliary units in a ciliate. *J. Embryol. Exp. Morphol.* In press.
14. FULTON, C. 1971. Centrioles. *In* Results and Problems in Cell Differentiation. 2. Origin and Continuity of Cell Organelles. J. Reinert and H. Ursprung, editors. 170–221.
15. GILLHAM, N. W. 1974. Genetic analysis of the chloroplast and mitochondrial genomes. *Annu. Rev. Genet.* **8**:347–391.
16. GRIMES, G. W. 1973. Origin and development of kinetosomes in *Oxytricha fallax*. *J. Cell Sci.* **13**:43–53.
17. GRIMES, G. W. 1973. Morphological discontinuity of kinetosomes during the life cycle of *Oxytricha fallax*. *J. Cell Biol.* **57**:229–232.
18. JERKA-DZIADOSZ, M., and J. FRANKEL. 1969. An analysis of the formation of ciliary primordia in the hypotrich ciliate *Urostyla weissei*. *J. Protozool.* **16**:612–637.
19. LWOFF, A. 1950. Problems of Morphogenesis in Ciliates. John Wiley & Sons, Inc., New York. Vol. IX. 1–103.
20. MCCOY, J. W. 1974. New features of the tetrahymenid cortex revealed by protargol staining. *Acta Protozool.* **13**:155–166.
21. NANNEY, D. L. 1971. The pattern of replication of cortical units in Tetrahymena. *Dev. Biol.* **26**:296–305.
22. NANNEY, D. L. 1971. The constancy of cortical units in Tetrahymena with varying numbers of ciliary rows. *J. Exp. Zool.* **178**:177–182.
23. NANNEY, D. L., and M. CHOW. 1974. Basal body homeostasis in *Tetrahymena*. *Am. Nat.* **108**:125–139.
24. PERLMAN, B. S. 1973. Basal body addition in ciliary rows of *Tetrahymena pyriformis*. *J. Exp. Zool.* **184**:365–368.
25. RATTNER, J. B., and S. G. PHILLIPS. 1973. Independence of centriole formation and DNA synthesis. *J. Cell Biol.* **57**:359–372.
26. SONNEBORN, T. M. 1950. The kinetosome in cytoplasmic heredity. *J. Hered.* **41**:222–224.
27. SONNEBORN, T. M. 1963. Does preformed structure play an essential role in cell heredity? *In* The Nature of Biological Diversity. J. M. Allen, editor. McGraw-Hill Book Company, New York. 165.
28. SONNEBORN, T. M. 1974. Ciliate morphogenesis and its bearing on general cellular morphogenesis. Progress in Protozoology. Proceedings of the 4th

International Congress on Protozoology. Actualités Protozoologiques. **1**:327–355.

29. STUBBLEFIELD, E., and B. R. BRINKLEY. 1967. Architecture and function of the mammalian centriole. *Symp. Int. Soc. Cell Biol.* **6**:175–218.
30. WILLIAMS, N. E., O. MICHELSEN, and E. ZEUTHEN. 1969. Synthesis of cortical proteins in *Tetrahymena*. *J. Cell Sci.* **5**:143–162.
31. WILLIAMS, N. E., and O. H. SCHERBAUM. 1959. Morphogenetic events in normal and synchronously dividing *Tetrahymena pyriformis*. GL. *J. Embryol. Exp. Morphol.* **7**:241–256.
32. WITMAN, G., K. KARLSON, J. BERLINER, and J. ROSENBAUM. 1972. Chlamydomonas flagella. I. Isolation and electrophoretic analysis of microtubules, matrix, membranes, and mastigonemes. *J. Cell Biol.* **54**:507–539.
33. WOLFE, J. 1972. Basal body fine structure and chemistry. *Adv. Cell Mol. Biol.* **2**:151–192.
34. YOUNGER, K. B., S. BANERJEE, J. K. KELLEHER, M. WINSTON, and L. MARGULIS. 1972. Evidence that synchronized production of new basal bodies is not associated with DNA synthesis in *Stentor coeruleus*. *J. Cell Sci.* **11**:621–637.