A Revision of the Cell Lineages Recently Reported for *Volvox carteri* Embryos

KATHLEEN J. GREEN and DAVID L. KIRK
Department of Biology, Washington University, St. Louis, Missouri 63130

Volvox offers a unique opportunity to study the segregation of reproductive potential during development of a multicellular organism. At the sixth cleavage division of an asexual embryo of *Volvox carteri*, strain HK10, one half of the 32 cells typically cleave unequally to yield 16 large gonidial (reproductive) initials and 16 smaller somatic initials, while the remaining cells divide equally to generate additional somatic initials (6, 7). Different patterns of unequal cleavage, yielding different numbers and locations of reproductive cells, are observed in sexually induced male and female individuals and in germinating zygotes (6, 7). "Pattern mutants," in which single Mendelian mutations result in modified numbers and/or locations of reproductive cells in asexual or sexual individuals (2, 5), indicate that the process of unequal cleavage is under genetic control; but so far these mutants have not yielded any insight into the mechanism by which the cells undergoing unequal cleavage are specified. Three rather different models that attempt to explain the specification process have been proposed (3, 4, 8). Detailed knowledge of the lineages of cells undergoing unequal division is of obvious significance in attempting to evaluate such models.

In a recent paper (1) we reported an extensive scanning EM study of the cleavage patterns and cell lineages in asexual *V. carteri* (strain HK10) embryos. We showed that because the fourth cleavage is much more oblique than had been reported previously, the four cells constituting each quadrant of a 16-cell embryo (cells numbered 1–4 from anterior to posterior pole) overlap much more extensively than had been recognized previously. The result is that after the fifth cleavage, in which each cell divides into an anterior (a) and posterior (p) pair, the anterior hemisphere contains the 1a, 1p, 2a, and 3a cells; not the 1a, 1p, 2a, and 2p cells as previous descriptions of cleavage would have predicted. We then reported, as had Starr earlier (7), that it was the anterior 16 cells that divided unequally to yield gonidial initials. That statement was incorrect. Careful reexamination of side views of embryos before and after the sixth division (Figs. 1*a–c*) reveals that the 3a cells of the anterior hemisphere do not divide unequally, but that the 2p cells—although lying in the posterior hemisphere—do. Thus the gonidial initials are derived from the 1a, 1p, 2a, and 2p cells of each quadrant, as Starr (7) originally described, but the gonidia derived from the 2p cells lie in the posterior hemi-

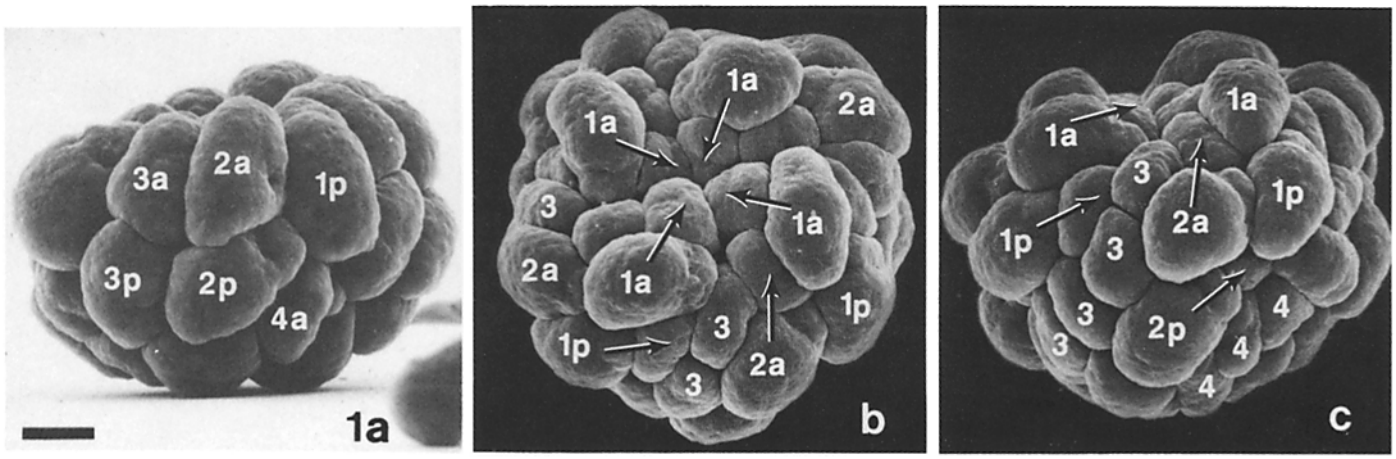

FIGURE 1 (*a*) 32-cell embryo showing the result of the fifth (equatorial) division (side view). The cell numbering system is that described in reference 1. The anterior hemisphere will be derived from the 1a, 1p, 2a, and 3a cells of each quadrant. The posterior hemisphere will be derived from the 2p, 3p, 4a, and 4p cells of each quadrant. (*b*) 64-cell embryo showing the result of the sixth (differentiative) division (anterior view). Gonidial initials are labeled with the number denoting cells of the 32-cell embryo from which each was derived. Arrows connect gonidial-somatic cell pairs resulting from the sixth division. (Note that gonidia are preparing to divide again.) (*c*) Side view of 64-cell embryo shown above in anterior view. Again, gonidial initials are designated by their cell lineage number. Note that gonidia are derived from 1a, 1p, 2a, and 2p cells, and that those derived from the 2p cells are located in the posterior hemisphere. Bar, 10 μm. × 1,000.

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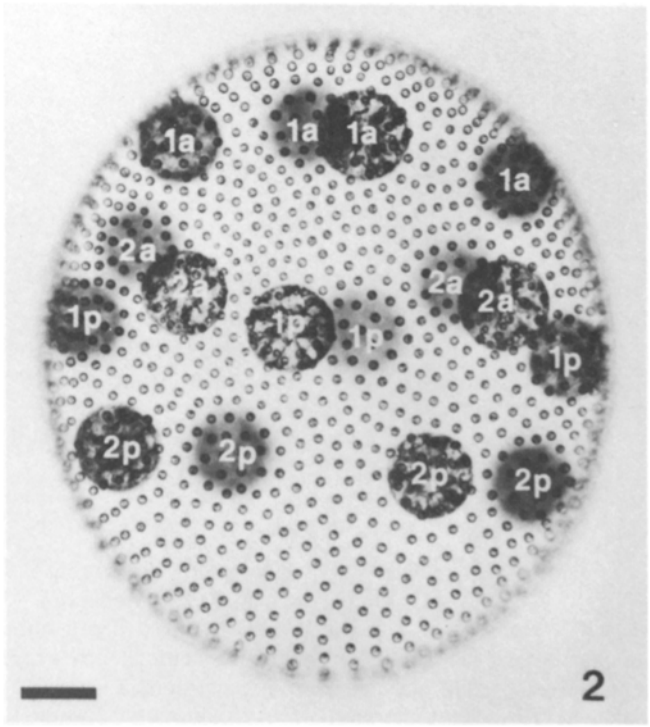

FIGURE 2 Light micrograph of an adult individual showing the distribution of gonidia (which are assigned with their probable cell lineage numbers). Note that gonidia are not restricted to a single hemisphere. Bar, 50 μm. × 200.

sphere. This lineage accounts for the fact that gonidia are not restricted to a single hemisphere in the adult spheroid (Fig. 2).

This revision of the gonidial lineages does not appear to require any revision of our evaluation (1) of models that have been proposed to date for the gonidial specification process, but it may be useful in evaluating future studies.

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