The Role of the Polar Lobe in Cell Specification

E. B. Wilson and his student H. E. Crampton observed that certain spirally cleaving embryos (mostly in mollusks and annelids) extrude a bulb of cytoplasm—the polar lobe—immediately before first cleavage. In some species of snails, the region uniting the polar lobe to the rest of the egg becomes a fine tube. The first cleavage splits the zygote asymmetrically, so that the polar lobe is connected only to the CD blastomere (Figure 1A). In several species, nearly one-third of the total cytoplasmic volume is contained in this anucleate lobe, giving it the appearance of another cell (Figure 1B). The resulting three-lobed structure is often referred to as the trefoil-stage embryo (Figure 1C).

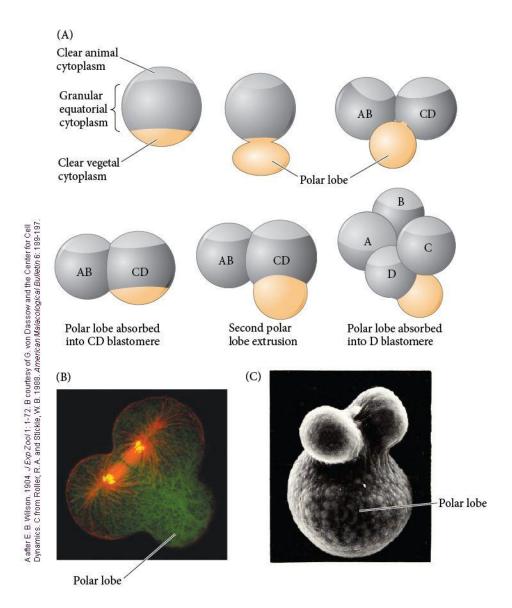


Figure 1 Polar lobe formation. (A) During cleavage, extrusion and reincorporation of the polar lobe occur twice. The CD blastomere absorbs the polar lobe material but extrudes it again prior to second cleavage. After this division, the polar lobe is attached only to the D blastomere, which absorbs its material. From this point on, no polar lobe is formed. (B) Late in the first division of a scallop embryo, the anucleate polar lobe (lower right) contains nearly one-third of the cytoplasmic volume. Microtubules are stained red, RNA is green, and the chromosomal DNA appears yellow. (C) Section through a first-cleavage, or trefoil-stage, embryo of *Dentalium*, a marine mollusk.

Crampton (1896) showed that if one removes the polar lobe at the trefoil stage, the remaining cells divide normally. However, the resulting larva is incomplete (Figure 2), wholly lacking its intestinal endoderm and mesodermal kidney and heart, as well as some ectodermal organs (such as eyes). Moreover, Crampton demonstrated that the same type of abnormal larva can be produced by removing the D blastomere from the 4-cell embryo. Crampton thus concluded that the polar lobe cytoplasm contains the heart and intestinal-forming determinants and that these determinants (as well as their inducing ability) are transferred to the D blastomere. Crampton also showed that the localization of these endomesodermal determinants is established shortly after fertilization.

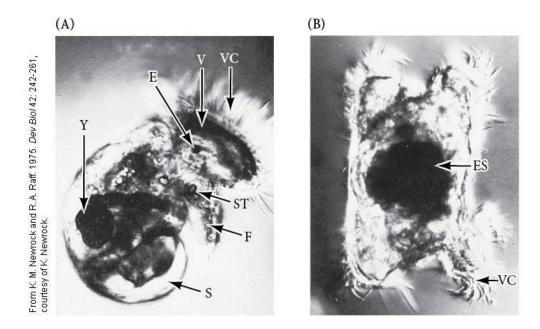


Figure 2 Importance of the polar lobe in the development of *Ilyanassa*. (A) Normal trochophore larva. (B) Abnormal larva, typical of those produced when the polar lobe of the D blastomere is removed. E, eye; F, foot; S, shell; ST, statocyst; V, velum; VC, velar cilia; Y, residual yolk; ES, everted stomodeum.

Centrifugation studies have demonstrated that the cell fate specifying determinants sequestered in the polar lobe are probably located in the lobe's cytoskeleton or cortex, not in its diffusible cytoplasm (Clement 1968). van den Biggelaar (1977) obtained similar results when he removed the cytoplasm from the polar lobe with a micropipette. Cytoplasm from other regions of the cell flowed into the polar lobe, replacing the portion he removed, and subsequent development of these embryos was normal. In addition, when he added the diffusible polar lobe cytoplasm to the B blastomere, no duplicated structures were seen (Verdonk and Cather 1983). Therefore, the diffusible part of the polar lobe cytoplasm does not contain the cell fate specifying determinants; these as-yet-unidentified factors probably reside in the nonfluid cortical cytoplasm or on the cytoskeleton. Further intriguing evidence found that aggregated vesicles in the polar lobe (called the vegetal body) of the snail *Bithynia tentaculata* were required for normal development (vann Dam et al. 1982).

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¹ Although this looks like a great case for autonomous specification, it is possible that signaling from the micromeres is needed to activate the cytoplasmic determinants brought to the D blastomere by the polar lobe (Gharbiah et al. 2014; Henry 2014). In addition to having these roles in cell differentiation, the material in the polar lobe is responsible for specifying the dorsal-ventral polarity of the embryo. When polar lobe material is forced to pass into the AB blastomere as well as into the CD blastomere, twin larvae form that are joined at their ventral surfaces (Guerrier et al. 1978; Henry and Martindale 1987).