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Conserved Mechanism of Dorsoventral Axis Determination in Equal-Cleaving Spiralians

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Abstract

Many members of the spiralian phyla (i.e., annelids, echiurans, vestimentiferans, molluscs, sipunculids, nemerteans, polyclad turbellarians, gnathostomulids, mesozoans) exhibit early, equal cleavage divisions. In the case of the equal-cleaving molluscs, animal–vegetal inductive interactions between the derivatives of the first quartet micromeres and the vegetal macromeres specify which macromere becomes the 3D cell during the interval between fifth and sixth cleavage. The 3D macromere serves as a dorsal organizer and gives rise to the 4d mesentoblast. Even though it has been argued that this situation represents the ancestral condition among the Spiralia, these inductive events have only been documented in equal-cleaving molluscs. Embryos of the nemertean *Cerebratulus lacteus* also undergo equal, spiral cleavage, and the fate map of these embryos is similar to that of other spiralians. The role of animal first quartet micromeres in the establishment of the dorsal (D) cell quadrant was examined in *C. lacteus* by removing specific combinations of micromeres at the eight-cell stage. To follow the development of various cell quadrants, one quadrant was labeled with DiI at the four-cell stage, and specific first quartet micromeres were removed from discrete positions relative to the location of the labeled quadrant. The results indicate that the first quartet is required for normal development, as removal of all four micromeres prevented dorsoventral axis formation. In most cases, when either one or two adjacent first quartet micromeres were removed from one side of the embryo, the cell quadrant on the opposite side, with its macromere centered under the greatest number of the remaining animal micromeres, ultimately became the D quadrant. Twins containing duplicated dorsoventral axes were generated by removal of two opposing first quartet micromeres. Thus, any cell quadrant can become the D quadrant, and the dorsoventral axis is established after the eight-cell stage. While it is not yet clear exactly when key inductive interactions take place that establish the D quadrant in *C. lacteus*, contacts between the progeny of animal micromeres and vegetal macromeres are established during the interval between the fifth and sixth round of cleavage divisions (i.e., 32- to 64-cell stages). These findings argue that this mechanism of cell and axis determination has been conserved among equal-cleaving spiralians.

Keywords

induction; cell interactions; unequal cleavage; Nemertea

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