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Biological Morphogenesis as Multiscale Transformations of Soft Matter

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Living tissues are condensed materials, with inherent physical properties in common with their nonliving counterparts. Tissues are both viscoelastic materials and excitable media. Early-stage embryos have liquid-like properties due to the random mobility of their constituent cells. The shaping of embryonic tissues can be understood, in significant part, on the basis of these properties, as can the "equilibrium" configurations of mixtures of cells with different cell-cell adhesive strengths. Interaction of cell aggregates with their microenvironments give rise, in certain instances, to sheet-like arrangements of cells known as epithelia. Their elastic properties cause them to fold, bulge, and undergo other morphogenetic changes. The molecular composition of cells is regulated by networks of interacting genes whose collective "expression" exhibit multistable and oscillatory dynamics. Cell aggregates, moreover, produce their own microenvironments by secreting diffusible signal molecules and structurally complex extracellular matrices. Together, these properties cause tissue masses to exhibit a wide range of nonlinear and self-organizing behaviors which are integrated and fine-tuned by evolution to produce developmental systems: species-specific temporal sequences of organized patterns and arrangements of different cell types.