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Embryonic Development

1. Introduction

Embryonic development begins with the first mitotic division of the zygote nucleus and terminates at hatching. Not surprisingly, in view of their diversity of form, function, and life history, insects exhibit a variety of embryonic developmental patterns, though certain evolutionary trends are apparent. Eggs of most species contain a considerable amount of yolk. In exopterygote eggs there is such a preponderance of yolk that the egg cytoplasm is readily obvious only when it forms a small island surrounding the nucleus. In eggs of endopterygotes, the yolk:cytoplasm ratio is much lower than that of exopterygotes and the cytoplasm can be seen as a conspicuous network connecting the central island with a layer of periplasm lying beneath the vitelline membrane. This trend toward reduction in the relative amount of yolk in the egg, carried to an extreme in certain parasitic Hymenoptera and viviparous Diptera (Cecidomyiidae), whose eggs are yolkless and receive nutrients from their surroundings, has some important consequences. Broadly speaking, the eggs of endopterygotes are smaller (size measured in relation to the body size of the laying insect) and develop more rapidly than those of exopterygotes. The increased quantity of cytoplasm leads to the more rapid formation of more and larger cells at the yolk surface that facilitates the formation of a larger embryonic area from which development can take place. Compared with that of exopterygotes, development of endopterygotes is streamlined and simplified. There has been, as Anderson (1972b, p. 229) put it, "reduction or elimination of ancestral irrelevancies," which when taken to an extreme, seen in the apocritan Hymenoptera and cyclorrhaph Diptera, results in the formation of a structurally simple larva that hatches within a short time of egg laying. However, superimposed on this process of short-circuiting may be developmental specializations associated with an increasing dissimilarity of juvenile and adult habits.

2. Cleavage and Blastoderm Formation

As it moves toward the center of an egg after fusion, the zygote nucleus begins to divide mitotically. The first division occurs at a predetermined site, the cleavage center (Figure 20.1), located in the future head region, which cannot be recognized morphologically but which appears to become activated either when sperm enter an egg or when an egg is laid. Early divisions are synchronous, and as nuclei are formed and migrate

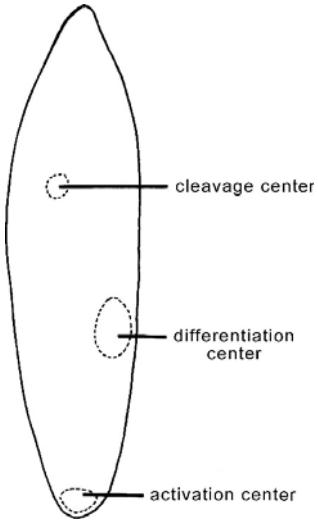

FIGURE 20.1. Positions of cleavage center, activation center, and differentiation center in eggs of *Platycnemis* (Odonata). [After D. Bodenstein, 1953, Embryonic development, in: *Insect Physiology* (K. D. Roeder, ed.). Copyright @ 1953, John Wiley and Sons, Inc. Reprinted by permission of John Wiley and Sons, Inc.]

through the yolk toward the periplasm, each becomes surrounded by an island of cytoplasm (Figure 20.2A). Each nucleus and its surrounding cytoplasm are known as a cleavage energid. In eggs of endopterygotes and possibly exopterygotes, but not those of apterygotes, the energids remain interconnected by means of fine cytoplasmic bridges.

The rate at which nuclei migrate to the yolk surface and the method of colonization are varied. In eggs of some species nuclei appear in the periplasm as early as the 64-energid state (after six divisions); in others, nuclei are not seen in the periplasm until the 1024-energid stage. In eggs of most endopterygotes and in those of paleopteran and hemipteroid exopterygotes, the periplasm is invaded uniformly by the energids. However, in eggs of orthopteroid insects the periplasm at the posterior pole of the egg receives energids first, after which there is progressive colonization of the more anterior regions.

In eggs of most insects not all cleavage energids migrate to the periphery but continue to divide within the yolk to form primary vitellophages, so-called because in most species they become phagocytic cells whose function is to digest the yolk (Figure 20.2B). In eggs of Lepidoptera, Diptera, and some orthopteroid insects, however, all of the energids migrate to the periplasm and only later do some of their progeny move back into the yolk as secondary vitellophages (Figure 20.2F). Secondary vitellophages are also produced in eggs of other insects to supplement the number of primary vitellophages. So-called tertiary vitellophages are produced in eggs of some cyclorrhaph Diptera and apocritan Hymenoptera from the anterior and posterior midgut rudiments.

After their arrival at the periplasm, the energids continue to divide, often synchronously, until the nuclei become closely packed (the syncytial blastoderm stage), after which cell membranes form by radial infolding, then tangential expansion of the original egg plasmalemma (the uniform blastoderm stage) (Figure 20.2C–F). From the resulting monolayer of cells develop all of the cells of the larval body, except in a few species where vitellophages or yolk cells contribute to the formation of the midgut (Section 7.4).

3. Formation and Growth of Germ Band

The next stage is blastoderm differentiation, giving rise to the embryonic primordium (an area of closely packed columnar cells from which the future embryo forms) and the