

the costaclavine produced here is the only ergot alkaloid which has been assigned<sup>1,4</sup> to have the hydrogens at C-5 and C-10 in *cis*-configuration.

**Zusammenfassung.** Es wurden in *Penicillium* Mutterkornalkaloide nachgewiesen, die bisher nur unter den Pilzen aus *Aspergillus* und *Claviceps* bekannt waren.

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<sup>3</sup> W. A. TABER and L. C. VINING, *Canad. J. Microbiol.* **4**, 611 (1958)

<sup>4</sup> S. YAMATODANI and M. ABE, *Bull. Agr. Chem. Soc. (Japan)*, **20**, 95 (1956).

<sup>5</sup> For the identification of the species used in this investigation, I am indebted to Dr. J. R. KINSLEY, Purdue University. The technical assistance of Miss S. Roos and the financial support from the Swedish Natural Science Research Council was appreciated. The sample of authentic costaclavine was generously provided by Dr. M. ABE.

## Avian Oogenesis and Yolk Deposition

The yolk of the hen's egg is often given as an example of a huge cell containing a food supply for the developing chick embryo. Current views hold that oocytes grow by removing nutrients from the blood and the follicle cells which surround them. Thus yolk deposition is thought of as primarily an intracellular phenomenon<sup>1</sup>. We believe that this viewpoint is inadequate, and wish to propose the following alternative hypothesis.

After they have enclosed an oocyte, the follicle cells of the young chick's ovary begin to participate in the deposition of material into the follicle. The oocyte, in contrast, assumes a relatively passive role in yolk formation. Indeed, the cytoplasm of the oocyte is eventually lost, in a functional sense, in the large mass of accumulating yolk. The remnants of the cytoplasm form a network around the germinal vesicle. The follicle cells secrete materials into the follicular space during the slow period of yolk deposition; during the period of major yolk deposition the follicle cells permit blood plasma to flow between them towards the center of the follicle. At the same time, they transport sodium, water, and many solutes from the plasma back to the blood. Some major plasma proteins, potassium, lipids, and other substances are left behind in the enlarging follicle, and form the egg yolk.

The above proposal is based on the view that the major functional unit of yolk deposition is the ovarian follicle, not the oocyte. Certain facts favor consideration of such a proposal. The transport of intact blood proteins<sup>2</sup> and subcellular constituents<sup>3</sup> into the avian egg has been well documented. Although not yet observed in the avian ovary, it has recently been shown that in the moth, protein materials pass between and not through the follicle cells<sup>4</sup>. BELLAIRS et al.<sup>5</sup> have shown that the vitelline membrane of mature avian eggs is a non-cellular, open network of fibers which would offer little resistance to the flow of large molecules.

Current theories of yolk formation require that the germ cells actively transport large amounts of material across their cell membranes. Active transport processes demand readily available sources of energy. In the mature ovum the region of the egg closest to the follicle cell is seemingly devoid of mitochondria<sup>6</sup> but there are many of these particles in the follicle cells. Moreover, there is no definitive evidence to indicate that the living margin of avian oocytes is apposed to the follicle cells during later stages of oogenesis.

Our observations of living oocytes, conducted with phase-contrast microscopy, reveal little gross structure inside the developing follicle. However, what is seen differs from that found in fixed and stained sections, and

indicates that a clear region, interpretable as a follicular cavity, is present in oocytes of 0.1 to 1.0 mm diameter. This cavity lies between the follicle cells and numerous highly refractile globules (the primordial yolk<sup>7</sup>) which surround the transparent, eccentrically located germinal vesicle.

SOTELO and PORTER<sup>8</sup> have reported that mammalian follicle cells are separated from the surface of the developing germ cells by the zona pellucida, a non-cellular, jelly-like region. They noted that long microvilli extended from the follicle cells through the zona pellucida to the egg cell surface and that short, slender projections extended from the egg cell into the same region. If the zona pellucida of mammalian follicles were much enlarged and yolk were deposited within it, the situation would be similar to that which we envisage for birds.

We propose first that follicle cells extract sodium, water and other substances from the plasma as a major part of their role in yolk formation. Second, we hold that bird yolk is primarily extracellular and that transport of yolk material by avian oocytes is not required for yolk formation.

**Zusammenfassung.** Es wird die Auffassung vertreten, dass bei Vögeln die grosse Masse des Eidotters extrazellulär ist. Dieser wird durch selektive Absorption von Blutplasma abgelagert, welches zwischen den Follikelzellen in die Follikelhöhle eindringt. Wasser, Natrium und andere gelöste Stoffe werden wieder ins Blut abgegeben, und der kaliumreiche Eidotter bleibt zurück. Das Cytoplasma der Eizelle geht funktionell im Eidotter auf und spielt bei der Ablagerung des Dotters nur eine passive Rolle.

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