

## **YOLK SAC MORPHOLOGIES IN CEPHALOPOD EMBRYOS**

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The basic pattern of embryogenesis is rather uniform throughout the class Cephalopoda. Depending on the specific ovum size, which may vary from less than 1 mm to about 30 mm, the organ-forming part (called the "embryo cap", or the "embryo proper") of the epibolic gastrula covers a larger (in small eggs) or smaller part (in large eggs) of the animal hemisphere of the uncleaved yolk mass. The rest of the gastrula forms an envelope for the yolk that remains outside the embryo cap and becomes the so-called outer yolk sac.

The overall shape of the yolk mass at early embryonic stages varies among systematic groups of cephalopods, from nearly globular to elongate/oval, to a certain degree also as a function of egg size. At advanced stages of organogenesis, the outer yolk sac becomes increasingly distinct due to a constriction of the brachial and cephalic zone of the embryo proper; an exception are some teuthoid squids (especially the Ommastrephidae), in which the outer yolk sac remains rudimentary. Starting out from a roughly globular form, the outer yolk sac may subsequently take on a different shape in the embryos of certain taxa.

The portion of the yolk mass lying inside the embryo proper is called the inner yolk sac and yolk neck (the latter connects the inner with the outer yolk sac). Whereas the yolk neck is a simple strand, which is more or less strongly compressed by the organs of the head, the inner yolk sac takes on a shape that is only partly due to simple "moulding" by the surrounding organs. There seems to be a shift of partial pressure between the outer and the inner yolk sac at late embryonic stages, and the final shape of the inner yolk sac is also influenced by the morphogenetic processes shaping the whole visceral complex of the embryo. More or less distinctive morphologies of the inner yolk sac can be recognized; for example, a peculiar "four finger" pattern appears in sepiolid embryos.

In a strictly functional perspective, the various yolk sac morphologies can be viewed as different modes of yolk storage during the developmental phase that leads to hatching. In most cephalopods, the newly hatched young can survive some time without food (from a few days to several weeks, depending on the juvenile physiology and ecology). Under normal conditions, the embryonic nutrient remaining in the inner yolk sac of the hatchling is resorbed independently from the onset of digestive processes that are induced by capture and ingestion of prey. This coexistence of lecithotrophy and active feeding is due to the morphological and physiological separation of the embryonic and post-embryonic alimentary organs; the actual duration of this concomitancy is partly conditioned by the volume of the yolk reserve, which in turn depends largely on the yolk storage capacity of the visceral mass.

This paper views evolutionary variation in developmental morphology of cephalopod "yolk organs" against the background of some pervasive functional constraints in yolk absorption.

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Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Berichte der Geologischen Bundesanstalt](#)

Jahr/Year: 1999

Band/Volume: [46](#)

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Artikel/Article: [Yolk sac morphologies in cephalopod embryos 23](#)