

UNCORRECTED PAGE PROOFS

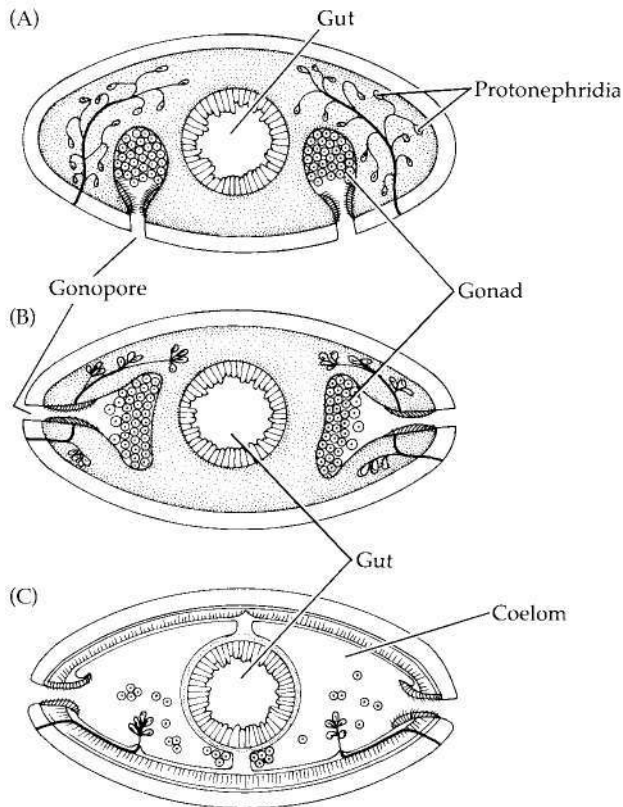


Figure 4.20 A version of the gonocoele theory (schematic cross sections). (A) The condition in flatworms, which have mesodermally derived gonads leading to ventral gonopores. (B) The condition in nemerteans, which have serially arranged gonadal masses leading to laterally placed gonopores. (C) The condition in polychaetes, in which the linings of the gonads have expanded to produce coelomic spaces with coelomoducts to the outside.

the ancestral protostome may have arisen simultaneously, and the acoelomate condition may be secondarily derived from coelomate precursors (see Rieger 1985, 1986).

To derive deuterostome and protostome clades from a common immediate coelomate ancestor creates a complicated scenario. The most parsimonious hypothesis might be to view the deuterostome ancestor as a diploblastic animal, perhaps a planuloid form, in which enterocoely occurred. Deriving the deuterostome lineage *separately* from the evolution of spiral cleavage and the other features of protostomes avoids many of the complications inherent in a monophyletic view of coelom origin. Imagine a hollow, invaginated, gastrula-like metazoan swimming with its blastopore trailing, as do the planula larvae of some cnidarians. Enterocoely may have accompanied a tendency toward benthic life, giving the animal a peristaltic burrowing ability. The archenteron may have then opened anteriorly as a mouth, and the new coelomate creature adopted a deposit-feeding lifestyle. If such a story began at the level

of diploblastic Metazoa (e.g., cnidarians), then the radial cleavage seen today in deuterostomes was also present in the ancestor to this group. A diphyletic origin of the coelomic condition from larval-like ancestors has been presented by Nielsen and Nørrevang (1985). In their hypothesis, a pelagic gastraea gave rise to the cnidarians and to a second lineage—another larval-like creature they call a **trochaea**. This ancestor was the precursor to the protostomes and the deuterostomes, but the coelom arose separately in each group.

Prominent among contemporary workers who have speculated on origins of major metazoan groups—and introduced yet more hypothetical ancestors (and names)—is Claus Nielsen. Nielsen envisions the two major metazoan clades radiating from an ancient common ancestor that conforms to Haeckel's radially symmetrical gastraea. From this planktonic ancestor there evolved two separate lines. One line led to the protostomes via a series of at least two hypothetical ancestors, called by Nielsen the **gastroneuron** and the **trochaea**. The other line, to the deuterostomes, was by way of a hypothetical **notoneuron** ancestor. (The names *gastroneuron* and *notoneuron* refer to the ventral versus dorsal positions of the major nerve cords in most protostomes and deuterostomes, respectively.) Nielsen claims that the notoneuron ancestor (and its descendant deuterostomes) retained the monociliated cell condition of the gastraea ancestor, whereas the gastroneuron ancestor (and its descendant protostomes) evolved a more advanced condition of multiciliated cells. In addition, the gastroneuron line came to rely on "downstream ciliary feeding," in which the larvae capture food particles from the water on the downstream side of the ciliary feeding bands, whereas the notoneuron line developed "upstream feeding," in which the larvae capture food particles from the water on the upstream side of the ciliary feeding bands.

As you can see, evolutionary analysis at the level of phyla, when it attempts to describe hypothetical ancestors, can be convoluted and problematical, and many different viewpoints exist. We trust, however, that you have gained some insights not only into the particular hypotheses discussed here, but also into evolutionary speculation. A fundamental caveat should be kept in mind: any number of evolutionary pathways can be proposed and made to appear convincing on paper by imagining appropriate hypothetical ancestors or intermediates, but one must always ask whether these hypothetical creatures would have worked. Do they possess realistic bauplans? Clark (1964) spends a good deal of time on this point and emphasizes it in his conclusion with the following passage (p. 258):

The most important and least considered of these [principles] is that hypothetical constructs which represent ancestral, generalized forms of modern groups, or stem forms from which several modern phyla diverge, must be possible animals. In other words, they