

## Macroevolutionary interplay between planktic larvae and benthic predators: Comment

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Peterson (2005) has hypothesized that planktotrophic larvae originated between the Late Cambrian and Middle Ordovician as a consequence of benthic predation operating on lecithotrophic ancestors. The evidence used to support this viewpoint is based on an extrapolation of larval trophic mode (planktotrophy versus lecithotrophy) for four types of extant larvae back to the time of taxon origin using molecular clock data. There are three problems with this approach: 1) In some cases, the developmental mode of an extant larva has not been properly assessed. For example, the planula larva of Cnidaria is referred to as lecithotrophic; however, the planulae of a number of anthozoans, which are the basal class in this phylum (Bridge, et al., 1995), are planktotrophic (Tardent, 1985). 2) Changes from planktotrophy to lecithotrophy, and vice versa, have been documented in the context of phylogenetic work on extant species within mollusks, annelids, and echinoderms (McHugh and Rouse, 1998). Given the frequency of these transitions, it is risky to assume that the ancestors of a specific clade had larvae with the same kind of trophic mode as their descendants. 3) In a number of phyla from the Lower Paleozoic, it is possible to infer developmental mode from their fossils. This direct approach shows that Lower Cambrian trilobites, mollusks, hyoliths, and brachiopods had planktotrophic larvae and that lecithotrophy evolved during the Ordovician in some of these phyla. These data, showing that planktotrophy is basal and lecithotrophy is derived, directly contradict Peterson's hypothesis.

Trilobites have a life cycle involving molts of the exoskeleton; the cycle begins with a small protaspis followed by a meraspis period. During molts within the protaspis period, or at the molt that generates the meraspis stage, the shape of the cephalon and its appendages can change radically or uniformly. A radical change in morphology (metamorphosis) is indicative of a change from a planktotrophic larval to a benthic existence, while a life history without metamorphosis is one that occurs exclusively in the benthos and involves direct development (Chatterton and Speyer, 1997). Trilobites from the Lower Cambrian have a planktotrophic life cycle. During the Ordovician, groups with pelagic larvae went extinct and were replaced by groups with benthic development.

In extant mollusks, there is a correspondence between feeding and non-feeding larvae and the size and number of protoconchs (Jablonski and Lutz, 1980). Protoconch I is about the size of the egg and forms during embryogenesis. Protoconch II is much larger because it is generated during growth of the feeding larva. This methodology has been used to make inferences about the life histories of bivalves, rostroconchs, and monoplacophorans. In bivalves from the Lower Cambrian, the size and number of the protodissoconchs indicate that development was planktotrophic (Runnegar and Bentley, 1983; Runnegar and Jell, 1976). Rostroconchs and monoplacophorans from the Lower Cambrian have a single protoconch comparable in size to protodissoconch II of extant bivalves, indicating that they were planktotrophs (Pojeta and Runnegar, 1976).

At the apex of small hyolith fossils, there is a roundish conch that Dzik (1978) has homologized with protoconch I of embryonic molluscs; this is followed by a tubular conch that he homologized with larval protoconch II. Some time after these larvae moved from the plankton into a benthic environment, the embryonic and larval region of the shell broke off in most cases, giving an adult that lacked this region; however, the adult

has an operculum with a central region that corresponds to the diameter of the opening of the skeletal tube at the end of the larval period. Hyoliths are present in the Lower Cambrian; these fossils have structures identical to protoconchs I and II of the Ordovician species (Mambetov, 1972).

Brachiopod shells have a protogulum that forms during metamorphosis on mantle laid down during the embryonic and/or larval periods. By examining the number of protogular regions and their size, inferences can be made about planktotrophy or lecithotrophy. Both the Linguliformea and the Rhynchonelliformea have families that originated during the Lower Cambrian. In the Linguliformea, ten families originated during the Lower Cambrian. All members of these families have large protogula indicating planktotrophy (Freeman and Lundelius, 1999). The extant members of this group have planktotrophic larvae, and there are no cases from the fossil record documenting a transition from planktotrophy to lecithotrophy. In the Rhynchonelliformea, all three families in the Obolellata originated during the Lower Cambrian. Data are only available on protogular size for one family, which indicate that the larvae were planktotrophs. Two families in the Rhynchonellata originated during the Lower Cambrian, but no information is available on protogular size. However, a Middle Cambrian representative of one of these families had a large protogulum (Freeman and Lundelius, 2005). A member of the Pentamerida served as a progenitor for a part of the radiation that gave rise to derived taxa with lecithotrophic larvae during the Middle Ordovician and to the lecithotrophic larvae of extant Rhynchonellata. This example also shows that planktotrophs originating during the Lower Cambrian gave rise to lecithotrophs during the Ordovician.

In assigning a trophic mode to larvae of fossil groups, inferences made from extant species and phylum-level molecular phylogenies must be tested against the realities of the available fossil record.

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