Endless larval forms most beautiful: what a larva is

BRUNO COSSERMELLI VELLUTINI

The Latin word *lärva* means *evil spirit, ghost or mask*. In the 18th century, the naturalist Carolus Linnaeus was the first to employ the word larva to describe a stage in the life of an animal in which its adult form is still hidden or masked (Linnaeus, 1767, p. 534). An exemplar case of this new biological meaning is the maggot—the larval stage of a fly—whose wormy form and life style truly differs from its flying adult stage.

Not all larvae, however, are masked forms. The larval body of some marine snails, for example, is very similar to its adult body, except for the dazzling presence of a ciliated velum, used by the larva to swim and gather food (Collier, 1997). In more general terms, larval stages are considered to be a modification of embryonic development usually characterized by a morphology and habitat that are disparate from the adult stage (Hall and Wake, 1999). Because embryonic development can change in a multitude of ways, as evidenced by the great diversity of larval forms in nature (see below), there is no precise definition of *larva* (Hickman, 1999; Strathmann, 1993). Thus in practice, what a larva is, is defined case by case according to the organism and to one’s research background.

The majority of animals on this planet have a complex life cycle with one or more larval stages. Collectively, marine invertebrates represent a great part of the observed larval diversity. Molluscs have the *veliger*, a shelled larva with the ciliated velum mentioned above; echinoderms have the *pluteus*, a spaceship-like larva with eight food-capturing arms, and the *brachiolaria*, a free-swimming larva driven by body-length dancing arms; bryozoans have the *cyphonautes*, a paper-thin triangular larva that sails over kelp blades; crustaceans have the *zoea*, an armored larva that swims as if using a jet pack; nemerteans have the *pilidium*, a larva with lobes and lappets in the form of a deerstalker cap… and this list goes on. The diversity of larval forms is astonishing.
Most of these charismatic larval figures were discovered in the 19th century by the naturalist founders of comparative embryology (Hall and Wake, 1999). At the time, the ideas of Karl Ernst von Baer and Ernst Haeckel had great influence on the understanding of embryonic development (Guralnick, 2002; Hall, 2000). Ontogeny was seen as the unfolding of an immutable process that represents the evolutionary history of an organism—an idea known as recapitulation or Haeckel’s biogenetic law: “ontogeny is a rapid and shortened recapitulation of phylogeny.” (Gould, 1977; Haeckel, 1866).

These influential ideas were directly challenged by the mere existence of larvae. Or more generally, challenged by the existence of differentiated developmental stages that are, at the same time, functionally adapted to their environment and morphologically diverse. Such impressive variety of larval forms instigated questions about the relationship between the embryonic development of an individual (ontogeny) and the evolutionary history of a lineage (phylogeny).

Do larvae represent ancestral adult forms? How many times have larvae evolved? Are larval structures homologous or independently evolved? Soon, there was an urge to rationalize the diversity of larval forms into an evolutionary context.

[This text is a section of my PhD thesis]

REFERENCES


2. Michael Sars, one of the Norwegian biologists giving the name to the Sars Centre, was among the first to describe the development of molluscs from a swimming larva (Sars, 1837; Young, 1990).